Ecological Effects of Water-Level Fluctuations in Lakes

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Ecological Effects of Water-Level Fluctuations in Lakes

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Cover illustration: The littoral zone of Lake Constance near the city of Konstanz (background) during winter 2005/2006. The water level is low due to snow storage in the catchment area. Lake Constance is one of the last naturally pulsing lakes in Central Europe, having water-level fluctuations averaging 1.5 m. Photograph by Karl M. Wantzen.

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WATER-LEVEL FLUCTUATIONS

Ecological effects of water-level fluctuations in lakes: an urgent issue

**Karl M. Wantzen · Karl-Otto Rothhaupt ·
Martin Mörtl · Marco Cantonati ·
László G.-Tóth · Philipp Fischer**

Water-level fluctuations (WLF) affect the ecological processes and patterns of lakes in several ways. Aquatic habitats and feeding or breeding grounds are gained or lost, as light, climate and wave impacts change to mention only a few phenomena. While the phenomenon of WLF has been studied in many rivers (better known as flood pulse, Junk & Wantzen, 2004) and environmental flows (Bunn et al., 2006), so far it has not received due attention in lakes (Coops et al., 2003). A potential reason for why WLF in lakes have been overlooked for such a long time may be that central Europe and North America—the cradles of limnological research—are situated in landscapes which have been shaped by man for long time. Most central European lakes have been regulated since the middle ages; therefore, naturally fluctuating lakes such as Lake Constance (Fig. 1) are rare today.

This lack of knowledge is most remarkable, as all climate change models consistently state that severe increases in climatic stochasticity can be anticipated and water availability will be reduced due to climate change (IPCC, 2001; Sophocleous, 2004). This means a decrease in snowfall and hence spring floods at mid- and high-elevations in temperate regions, which is countered by an increase of exceptionally strong rainfall events and severe droughts for all areas. Thus, there is an urgent need for comprehensive scientific approaches that address the impacts of WLF through socially and economically feasible mitigation schemes.

However, it needs to be stressed that WLF are natural patterns which are necessary for the survival of many species, i.e. natural WLF in lakes guarantee both productivity and biodiversity (Gafny et al., 1992; Gafny & Gasith, 1999; Wantzen et al., 2002). Only extreme or untimely floods and droughts have deleterious effects for both biota and man (Sparks et al., 1998, Bond et al., 2008).

The dramatic effects of climate change that can be witnessed today (extreme droughts and floods) remind us of the necessity to implement studies to

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For the sake of brevity, the articles published in this special issue do not appear in the bibliography of this text.

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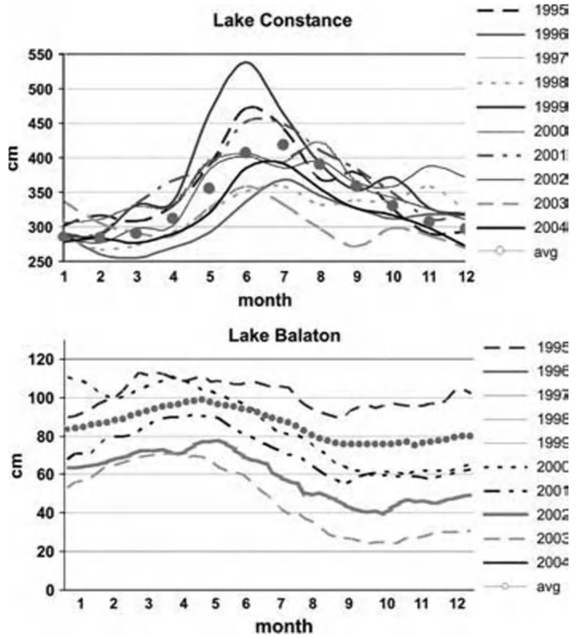

Fig. 1 Ten-year series of hydrographs of Lake Constance (data: Konstanz harbour authorities) and of Balaton, the largest shallow lake in Central Europe (data by Varga, 2005). Mind different scales

Fig. 2 The dry-fallen littoral near Konstanz, December 2005. Photograph by Karl M. Wantzen

develop environmentally and socially sound management schemes for future generations. Care must be taken not to replace one evil with another through over-regulation (thereby crippling) of naturally dynamic systems (an error repeatedly committed with rivers), but rather to increase the resilience and adaptability of lakes and their physical and social environments for future climate changes.

The following articles are an attempt to compile current knowledge on ecological effects of WLF in lakes. They span a wide range of geographic regions, morphological lake types and applied scientific disciplines. The publications presented here are the results of a workshop hosted by the collaborative research centre on lake littoral ecology at the University of Konstanz (SFB 454—Bodenseelitoral) in December 2005. Participants at this conference witnessed Lake Constance during an extreme drought of the lake which occurred that winter, exposing large parts of the littoral zone (Fig. 2) and causing dramatic reduction of the *Dreissena* mussel population in frost-exposed zones, which are an important food source for water fowl (Werner et al., 2005). The recently reported invasive clam *Corbicula fluminea* also suffered a dramatic decline (Werner & Rothhaupt, this issue) during this time.

The introduction is followed by an annotated bibliography (Leira & Cantonati, this issue) which provides an overview of WLF's extensive literature since 1991 in an attempt to give this volume a more general perspective through its contributors. The term Water-Level Fluctuations (WLF) is not yet definitively defined. Hoffmann & Lorke (this issue) suggest to extend the time-scale for WLF from seconds to hundreds of years as a temporal dimension and to discuss the equivalent spatial scale as data based on sets of lakes in different climatic zones.

WLF, especially pronounced floods, have been identified as major potential causes of reed decline (Dienst et al., 2004); however, the ultimate causes were not yet clear. Nechwatal et al. (this issue) showed that WLF and temperature have a significant influence on the performance of a reed-pathogen fungus, *Pythium phragmitis*, and suggest that predicted climate change events will help foster the development of this species.

In a study of WLF effects on littoral invertebrates in East-German lowland lakes, Brauns et al. (this issue) compared eulittoral and infralittoral habitats to simulate climate change-driven summer droughts. While species richness did not differ significantly, there was a significant change in the species communities consisting of coarse woody debris in the eulittoral habitats (with high abundances of beetles, mayflies and the functional feeding groups of piercers, predators and shredders) and the sandy habitats of the infralittoral. However, reed habitats might serve as refuges for these benthic invertebrates. This is indicated by the lack of significant differences between invertebrate communities developing on reed habitats in the eulittoral and infralittoral zones.

Baumgärtner et al. (this issue) studied the same question on stony substrates in a naturally fluctuating lake, Lake Constance, applying intensive temporal and spatial sampling efforts. They showed that the community patterns of the drift line were influenced by the previous water level. WLF accounted for most of the variation in these benthic communities. This finding was corroborated by White et al. (this issue) who studied the effects of natural water-level fluctuations in 16 small Laurentinian lakes. They found significant correlations between water quality parameters and WLF; however, among the biotic variables, only macroinvertebrates demonstrated significant relationships with WLF.

WLF potentially interfere with the influences that benthic macroinvertebrates exert on ecosystem functions. In Swedish lakes that experienced small WLF, invertebrate shredders were shown to be very influential on leaf-litter decomposition (Bjelke et al., 2004). However, Pabst et al. (this issue) did not observe strong impacts by this functional feeding group from the wave-impact zone in Lake Constance. Rather the wave action was important for physical degradation of leaves, as was indicated by experiments in wave mesocosms.

Boreal lakes often suffer from winter drawdown due to hydroelectric power plant operation in their tributary or outlet rivers. These WLF often cause freezing of the exposed littoral. In Finland, over 300 lakes (i.e. one-third of all inland water area) are regulated in such a fashion. Sutela & Vehanen (this issue) studied WLF effects on fish communities in regulated and reference lakes in Finland by electrofishing. In spite of finding large differences in density (10.3 vs. 32.7 ind m^{-2}, respectively), they were not really significant, because variables such as nutrient level and lake size affected the fish communities. Another study in Finnish lakes focused on macroinvertebrate assemblages in naturally fluctuating (maximum winter drawdown: 55 cm) and regulated lakes (up to 675 cm winter drawdown). In this article, Aroviita & Hämäläinen (this issue) revealed a strong decline in species richness with increasing amplitude in WLF. They identified indicator species sensitive to these effects. Keto et al. (this issue) presented the WLF-analysis tool “REGCEL” that was developed for the metric analysis of such impacts and to help implement successful sustainable management schemes in northern European countries.

In mediterranean regions, irrigation often consists of drawing water from lakes resulting in their shrinkage and increased eutrophication. The combination of summer drought and intense water use reinforces the severity of this problem. Skoulikidis et al. (this issue) showed that lowering of the water table exposes polluted sediments and mobilises toxics such as arsenic and chrome in a deep lake in Greece as well.

One article focused on WLF effects of invasive invertebrates in Lake Balaton where large sections of shore in the littoral have been covered by rip-rap. Balogh et al. (this issue) focused on a temporal decline of zebra mussels resulting from a drought in 2003, which exposed most of the rip-rap substrates. The plankton community including the planktonic larvae of *Dreissena polymorpha* was influenced by this drought as well.

The impacts of climate change on WLF and their effects on lake shores make an adaptive management plan necessary. Abrahams’ (this issue) proposal uses Grime’s CSR theory as a framework to assess such impacts and to develop practical management techniques for hydrological controls, substrate conditions, shoreline topography and vegetation establishment. Lastly, an overarching concept (Wantzen et al., this issue) was introduced based upon the flood pulse concept (Junk et al., 1989; Junk & Wantzen, 2004), for use in developing categories of WLF and their interactions with lake ecosystem functioning.

These articles show the large variety of issues that involve WLF in lakes. When attempting to summarise the manuscripts for the current article, we found how many lacunae still exist and how necessary it is to intensify research in this interesting and important field of ecology.

Konstanz, 15.11.2007
The editors

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

**Mario Brauns · Xavier-François Garcia ·
Martin T. Pusch**

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

Keywords Climate change · Habitat–species relationships · Reed · Roots

Introduction

According to current knowledge, the average air temperature in central Europe will increase by 3–5°C within the next century, depending on the future emissions of greenhouse gases (Intergovernmental Panel on Climate Change, 2001). Air temperature has

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

Methods

Invertebrate sampling

The six studied lakes are located in East Germany and cover different lake types, i.e. hypertrophic riverine lakes and groundwater supplied mesotrophic lakes (Table 1). Invertebrates samples were taken from the five major habitat types in East-German lowland lakes, i.e. roots within the eulittoral zone (0–0.2 m water depth) and coarse woody debris (CWD), reed, sand and stones within the infralittoral zone (0.2–1.2 m water depth). Sampling was conducted in October 2003 and in April 2004 on a total of 40 sampling stations (eight per habitat type). Each habitat type was sampled separately using the sampling technique best adapted to the degree of structural complexity of the habitat. This should ensure a maximum of sampling efficiency and allows for a comparison of samples from different habitat types. We took five subsamples from submerged roots of riparian alder trees (*Alnus glutinosa*) with a hand net (250-μm mesh, 24 cm width) and estimated the sampled area by multiplying hand net width with the respective sampling depth. Invertebrates from CWD habitats were brushed from three pieces of CWD with comparable states of decay, and subsamples were sieved through a mesh (250 μm). Subsequently, length and diameter of each piece of

Table 1 Geographical location, area, trophic status and hydraulic residence time (RT) of the studied lakes

	Geographical location		Area (km^2)	Trophic state	RT (year)
	Latitude	Longitude			
Grienericksee	53°06′22″	12°53′12″	2.69	Eutrophic	0.40
Langer See	52°24′32″	13°36′50″	2.51	Hypertrophic	0.10
Müggelsee	52°26′16″	13°38′55″	7.70	Eutrophic	0.16
Plauer See	52°23′33″	12°26′33″	6.70	Hypertrophic	0.01
Unteruckersee	53°16′41″	13°51′51″	10.40	Mesotrophic	2.00
Werbellinsee	52°55′16″	13°42′43″	1.80	Mesotrophic	54.79

CWD were measured, and surface area was calculated assuming a cylindrical shape. We took five 1 m sweeps from reed habitats using a hand net (250-μm mesh, 24 cm width). We estimated the sampled area of reed habitats by multiplying hand net width with length of the sampled area. Sand habitats were sampled with 10 subsamples using a modified Surber sampler for lentic conditions (area 0.05 m^2, 250 μm mesh). For stone habitats, we randomly chose 10 stones from each sampling station and brushed off attached invertebrates. From each stone, surface area was calculated based on its length, height and width assuming an ellipsoid shape. Subsequently, subsamples from each habitat type were pooled to create a composite sample per habitat type. Samples were preserved in the field, and invertebrates were identified in the laboratory to species level. Chironomidae and Oligochaeta could only be determined to family or order level, respectively, and were omitted from further analyses because information on their ecological traits, e.g. functional feeding groups, is imprecise on these taxonomic levels (Lenat & Resh, 2001). Similarly, non-indigenous species *Dreissena polymorpha* (Pallas, 1771) Bivalvia, *Atyaephyra desmaresti* (Millet, 1831), *Chelicorophium curvispinum* (Sars, 1895), *Dikerogammarus haemobaphes* (Eichwald, 1841), *Dikerogammarus villosus* (Sowinsky, 1894), *Echinogammarus ischnus* (Stebbing, 1906), *Gammarus tigrinus* (Sexton, 1939), *Pontogammarus robustoides* (Sars, 1894) (Crustacea) and *Potamopyrgus antipodarum* (Gray, 1843) (Gastropoda) were excluded from further analyses, as their occurrence is mainly independent from habitat type (e.g. Van den Brink et al., 1993; Devin et al., 2003) and their dominance could supersede compositional differences among habitats that are related to native species. Information on invertebrate functional feeding groups was taken from Schmedtje & Colling (1996).

Statistical analysis

Since sampling techniques for the different habitat types were not fully comparable, we converted species densities into relative abundances. Prior to analyses, we tested whether there are differences in the invertebrate community measures from autumn and spring using non-parametric Mann–Whitney test (SPSS, Version 9.0, SPPS Inc., Chicago). Since from 19 community measures only percentages of Gastropoda, Heteroptera, Scrapers, and Parasites were significantly different between seasons, we pooled the data from autumn and spring. We used non-metric multidimensional scaling (NMS) and analysis of similarity (ANOSIM, PRIMER, Version 5, Primer-E Ltd., Plymouth) to test for differences in community composition between eulittoral root and the four infralittoral habitat types using Bray–Curtis similarity as the distance measure. ANOSIM is based on the assumption that if the community composition of two habitat types significantly differ, the similarities between habitats should be lower than the similarities within a habitat. This is expressed by the R-statistic, which ranges from 0 to 1, where $R = 1$ if all replicates of a habitat type are more similar to each other than to any replicate from the other habitat type. Indicator species for each habitat type were defined using the indicator species analysis (Dufrene & Legendre, 1997) (PcOrd, Version 4.25, MjM Software, Gleneden Beach) where indicator values close to zero mean no indication and indicator values close to 100 mean perfect indication of a habitat type by a species (Dufrene & Legendre, 1997). Differences in species richness, relative abundance of major taxonomic and functional feeding groups between roots and the four infralittoral habitat types were tested with non-parametric Mann–Whitney tests (SPSS, Version 9.0, SPPS Inc., Chicago) using Bonferroni correction to adjust the level of significance of the pairwise comparisons.

Results

Non-metric multidimensional scaling ordination of the invertebrate community of root and the four infralittoral habitats revealed strong compositional differences (Fig. 1). NMS ordination of root and CWD samples showed that both habitat types were colonised by distinct communities (Fig. 1A) that significantly differ from each other (ANOSIM: *R*-statistic = 0.37, $P = 0.001$). Similarly, invertebrate communities significantly differed between root and sand (ANOSIM: *R*-statistic = 0.65, $P = 0.001$, Fig. 1C) and between root and stones (ANOSIM: *R*-statistic = 0.49, $P = 0.001$, Fig. 1D). NMS ordination of the invertebrate communities of root and reed revealed that samples from both habitat types strongly overlap (Fig. 1B). Consequently, ANOSIM did not detect significant differences between communities of both habitat types (*R*-statistic = 0.05, $P = 0.241$). Median invertebrate richness (range) ranged from 22 (9–37) on sand habitats to 15 (13–28) on stone habitats but did not significantly differ between roots (21, 14–52) and any of the infralittoral habitat types (Mann–Whitney test, $P > 0.05$). Conversely, differences between eulittoral root and the four infralittoral habitats were apparent in the abundances of the major taxonomic groups. Here, the strongest differences were found for Coleoptera as well as for Odonata, Ephemeroptera and Trichoptera (Table 2). For example, the abundance of Coleoptera was highest in the root habitat and significantly lower in reed, sand and stone habitats. Abundances of Odonata were highest in root habitats, but they were absent within the infralittoral zone from all but the reed habitats (Table 2). The abundance of Ephemeroptera was significantly lower on CWD than on roots, and abundance of Trichoptera was significantly lower on sand than on root habitats. Distinct indicator species were found in roots, CWD, sand and stones (Table 3). For example, the dragonfly *Ischnura elegans* (Vander Linden, 1820) and the water beetle *Haliplus flavicollis* (Sturm, 1834) were highly indicative for root habitats, while sand habitats were particularly characterised by species of the genus *Pisidium* (Bivalvia) (Table 3). No indicator species were found for reed habitats.

Major differences in the functional feeding group composition between eulittoral roots and the four infralittoral habitat types were found for sand habitats (Table 4). Here, relative abundances of piercer,

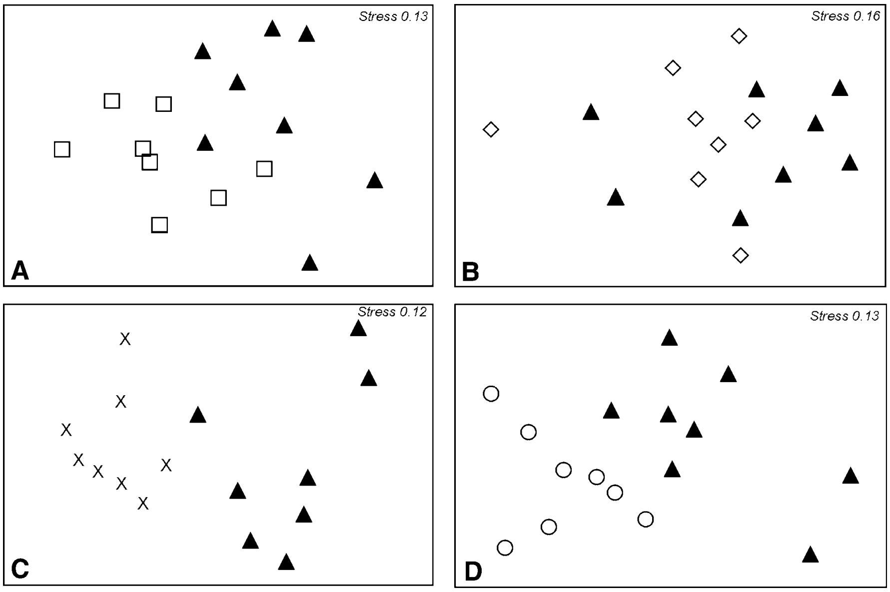

Fig. 1 Non-metric multidimensional scaling (NMS) ordination of the invertebrate community of roots (triangles) together with the invertebrate community of (**A**) coarse woody debris (squares), (**B**) reed (diamonds), (**C**) sand (crosses) and (**D**) stone habitats (circles)

Table 2 Median (range) relative abundances of the major invertebrate taxonomic groups at the five studied habitat types present in the eulittoral and infralittoral zone

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

Significantly lower abundances (Mann–Whitney test, Bonferroni adjusted P) between root and infralittoral habitats are indicated by asterisks (** $P < 0.01$, * $P < 0.05$)

predator, shredder and xylophagous species were significantly lower than on the roots habitats. Furthermore, abundances of shredder were significantly lower on all but the reed habitats (Table 4).

Discussion

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

The strongest differences in the examined community parameters were found between root and sand habitats. Despite a similar level of species richness, both communities differed significantly and were characterised by indicator species that primarily reflect the physical properties of the habitat types. For example, roots constitute a three-dimensional structured habitat that provides niches for large-bodied species of Coleoptera and Odonata, while structurally uniform sand habitats were dominated by small Bivalvia such as *Pisidium*. Furthermore, root habitats provided various food resources such as periphyton or CPOM as indicated by the dominance of scrapers and collector/gatherers, while functional feeding group composition on sand was dominated by filter feeders that rely on seston. In the littoral zone of several US lakes, periphyton production accounted for 98% of the whole lake primary production (Vadeboncoeur et al., 2003), and carbon derived from this food resource was used by species of subsequent trophic levels. Hence, an extreme drawdown of the water level that would be paralleled by

Table 3 Indicator species analysis of the five studied habitat types present in the eulittoral and infralittoral zone

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

For each indicator species, its indicator value and level of significance (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$) are given

the loss of all, but the sand habitats would disrupt a major pathway of carbon in the littoral zone of lakes. This conjecture is supported by studies on an US reservoir, where strong water-level fluctuations caused a shift of food resources of invertebrates from benthic-derived carbon to pelagic-derived carbon (Black et al., 2003). Hence, sand habitats may not substitute root habitats if an alteration of the hydrological regimes would cause a receding water level within the studied lakes. In contrast to sand habitats, community composition of reed did not significantly differ from that of root habitats. Despite differences in the abundance of Coleoptera, none of the major taxonomic groups found in the root habitats were completely absent in the reed habitat, most likely as the result of a comparable degree of habitat complexity compared. Hence, dense reed habitats may substitute the loss of the root habitats. However, reed stands are subjected to various kinds of human impairments such as wave disturbance or eutrophication that reduces their stem density (Ostendorp et al., 1995). Consequently, the ability of reed habitats to substitute the loss of root habitats could be limited in lakes with significant human impacts on the lake shore.

In summary, we demonstrated that submerged roots of riparian trees constitute an important habitat in the littoral zone colonised by a distinct invertebrate community. However, eulittoral root habitat may fall dry for extended time periods if water-level fluctuations increase as predicted for East and Central Europe. The loss of root habitats could partially be

Table 4 Median (range) relative abundances of the invertebrate functional feeding groups at the five studied habitat types present in the eulittoral and infralittoral zones

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

Significantly lower abundances (Mann–Whitney test, Bonferroni adjusted *P*) between root and the infralittoral habitat types are indicated by asterisks (*** $P < 0.001$, ** $P < 0.01$)

substituted by a dense infralittoral reed stand, which seems to offer similar habitat conditions. However, total habitat area available for the species found in root and reed habitats will be clearly reduced at lowered water levels. Conversely, CWD, stone and especially sand habitats may not provide an appropriate substitute habitat due to their limited habitat complexity. Our results on the potential effects of water-level fluctuations on littoral invertebrates have to be verified by further studies, especially as the amplitude of future water-level fluctuations is currently not assessable and might more be severe than assumed.

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WATER-LEVEL FLUCTUATIONS

Effects of water-level regulation on the nearshore fish community in boreal lakes

Tapio Sutela · Teppo Vehanen

Abstract The fish community in the littoral areas of eight regulated lakes and five reference lakes in Finland was sampled by electrofishing. No significant effect of winter drawdown on species richness was recorded across lakes. Total fish density for stony bottoms of the regulated and reference lakes averaged 19.3 and 32.7 individuals per 100 m^2, respectively, but this difference was not statistically significant. The combined proportion of littoral fish species, including minnow (*Phoxinus phoxinus*), bullhead (*Cottus gobio*), alpine bullhead (*Cottus poecilopus*), nine-spined stickleback (*Pungitius pungitius*), and stone loach (*Barbatula barbatula*), supplemented with zoobenthos feeders ruffe (*Gymnocephalus cernuus*) and young burbot (*Lota lota*), was much lower in the regulated lakes than in the reference lakes. Besides winter drawdown, other variables, such as nutrient level and lake size, affected the fish community.

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Ecological Effects of Water-Level Fluctuations in Lakes

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Introduction

The water level of about 220 lakes (area > 1 km^2) in Finland is regulated, mainly for hydroelectric purposes (Alasaarela et al., 1989). The water level is lowered 0.5–7 m by increasing discharge in winter, when the consumption of electricity is highest. Finnish lakes are typically shallow with a considerable proportion of the bottom area falling dry and partly freezing during the winter. Ice of about 0.5–1 m in thickness descends on the littoral zone and presses the bottom, thus extending the impact of winter drawdown still deeper. In the spring, snow melts refilling the lakes with the aid of the reduced discharge. Spring flooding does not exist, and the water level is usually kept quite constant over the summer until late autumn.

Water-level regulation via a winter drawdown has been documented to affect littoral geomorphology (Hellsten, 1997), vegetation (Hellsten & Riihimäki, 1996), zoobenthos (Palomäki & Koskenniemi, 1993), and fish fauna (Gaboury & Patalas, 1984; Paller, 1997). The impact of abnormal water fluctuation is generally most evident in the littoral zone exposed to temporal falling dry. This pattern suggests that littoral fish species are especially vulnerable to winter drawdown. Littoral fish are forced to leave their habitat temporarily to avoid falling dry in winter. Fish species may have different strategies in responding to limited habitat availability in the low-water-level period (Fischer & Öhl, 2005). Breeding of fish species that spawn in shallow littoral waters may be disturbed by water-level fluctuation (Gafny et al., 1992). Available food resources for fish may diminish following the reduction in zoobenthos biomass in the littoral areas of the regulated boreal lakes (Grimås, 1961, Palomäki & Koskenniemi, 1993, Koskenniemi, 1994). Thus, littoral and zoobenthivore fish species may be especially vulnerable to winter drawdown. In this study, we sampled littoral fish assemblages in regulated and non-regulated lakes in order to examine differences between them and to evaluate possible impact mechanisms of winter drawdown.

Materials and methods

Lakes studied

Five natural reference lakes with normal water-level fluctuation and eight regulated lakes in Northern Finland were studied (Table 1). The magnitude of water-level fluctuation is expressed as winter drawdown, which denotes the difference in water level between freeze-up in late autumn and the annual minimum of late winter. The range of the average winter drawdown in the regulated lakes was 1.54–6.75 m, whereas in the reference lakes the natural winter drawdown was less than 0.4 m. Lake size ranged from 12 to 887 km^2, while mean depth varied between 4.2 and 9.7 m. The lakes can be classified as oligotrophic or mesotrophic on the basis of their total phosphorus content (Forsberg & Ryding, 1980). Brown colour reflects the effect of organic compounds originating from boggy catchment. Nutrient loading from agriculture and forestry has caused deterioration in water quality on a small scale in all the lakes.

Electrofishing

In August of 2003–2005, a total of 256 electrofishings were conducted in the five reference lakes and eight regulated lakes (Table 2). Only the deepest, non-wadable rocky shores were excluded from the randomised site selection. The mean number of electrofishings per lake was 20, with large lakes usually having higher numbers. Average depth in the sampled 100-m^2 areas was 30 cm. Fish were captured with Hans Grassl GmbH ELT 6011 GI Honda GXV50 electrofishing gear using pulsed (50-Hz) DC current with a voltage of 800–1000 V. Each area was fished once by two waders, one using the anode and an assistant collecting the stunned fish with a dip-net. Escape nets were used only with some exceptional sand bottoms having no stones or vegetation, which could offer a hiding place for the fish.

Table 1 Characteristics of the lakes studied

Lake	Water-level fluctuation	Winter drawdown (m)	Surface area (km^2)	Mean depth (m)	Total phosphorus (μg/l)	Brown colour (mg Pt/l)	pH
Simojärvi	Natural	0.22	90	5.0	9	33	6.8
Pesiöjärvi	Natural	0.27	13	4.2	12	50	6.5
Änättijärvi	Natural	0.32	24	9.7	9	60	6.6
Lentua	Natural	0.40	78	7.4	9	50	6.6
Kellojärvi	Natural	0.43	22	5.0	16	80	6.7
Oulujärvi	Regulated	1.54	887	8.4	14	57	6.7
Koitere	Regulated	1.76	164	8.2	11	70	6.5
Kiantajärvi	Regulated	3.12	169	7.6	11	60	6.5
Iso-Pyhäntä	Regulated	3.50	12	6.9	16	85	5.7
Ontojärvi	Regulated	3.51	105	5.7	15	60	6.6
Kostonjärvi	Regulated	4.02	44	5.1	11	40	7.0
Vuokkijärvi	Regulated	4.71	51	5.0	18	70	6.4
Kemijärvi	Regulated	6.75	206	5.5	16	80	6.8

Table 2 Sampling dates and characteristics of the sampled areas (reference lakes in italics)

	Sampling year	Sampling date	Electro-fishings (N)	Water temp. (°C)	Mean depth (cm)	Stony bottom (N)
Simojärvi	2005	10–11 Aug.	21	18.6	29	19
Pesiöjärvi	2004	19 Aug.	12	16.7	24	8
Änättijärvi	2003	18–21 Aug.	20	17.2	31	17
Lentua	2003	11–22 Aug.	23	17.9	35	15
Kellojärvi	2005	1–2 Aug.	16	19.1	27	9
Oulujärvi	2004	4–8 Aug.	22	21.5	31	15
Koitere	2005	3–4 Aug.	20	20.1	27	15
Kiantajärvi	2004	16–18 Aug.	18	16.5	30	13
Iso-Pyhäntä	2004	2–5 Aug.	18	19.7	40	3
Ontojärvi	2003	25–28 Aug.	20	15.9	29	12
Kostonjärvi	2005	8–9 Aug.	20	18.2	27	17
Vuokkijärvi	2004	9–12 Aug.	20	19.4	27	14
Kemijärvi	2004	23–27 Aug.	26	14.1	29	20
Mean			20	18.1	30	13.6

Environmental conditions, including water temperature, mean and maximum depth over the area, bottom quality, and percentage coverage of vegetation, were recorded. Bottom quality was assessed as percentages of the area in the classes organic bottom, sand bottom (particle size of 0–2 cm in diameter), and stony bottom (particle size > 2 cm). Stony bottoms dominated in our material (Table 2).

Statistical methods

Canonical correspondence analysis (CCA) (ter Braak, 1986, ter Braak & Verdonschot, 1995) was used to analyse species/environment relationships with the program PC-ORD (McCune & Mefford, 1999). The significance of the patterns detected was tested with Monte Carlo permutations (100 permutations). ANOVA and ANCOVA were used to compare average species richness in the regulated and reference lakes, and Mann–Whitney for fish densities. In addition, Pearson and Spearman correlation analyses were applied on different occasions.

Results

Species richness

In total, 11 fish species were recorded in the littoral electrofishings (Table 3). The number of fish species recorded for a single lake varied between 3 and 9, averaging 5.6 in the reference lakes and 6.8 in the regulated lakes. As a biasing factor, the size of the lake correlated with the number of species recorded (Pearson correlation, $R^2 = 0.63$, $P < 0.01$, area of the lake ln-transformed). The mean area of the regulated lakes was greater than that of the reference lakes. Secondly, the number of electrofishings tended to increase with lake area. When we harmonised the data by counting the number of species recorded after 16 electrofishings and excluded Pesiöjärvi lake (number of electrofishings: 12), we still had higher average species richness for regulated lakes (6.4) than in reference lakes (5.5). This difference was not statistically significant, whether or not we took lake area (ln-transformed) as a covariate (ANCOVA and ANOVA, $P > 0.05$ in both cases).

Stone loach (*Barbatula barbatula*), nine-spined stickleback (*Pungitius pungitius*), and dace (*Leuciscus leuciscus*) were recorded only in regulated lakes. None of the fish species emerged as an evident indicator species for lake regulation in terms of its existence or non-existence in the reference and regulated lakes.

Fish densities

Total fish density and species composition varied considerably among the lakes (Fig. 1). Total fish density averaged 18.3 individuals per 100 m^2 (SD

Table 3 Fish species identified in the electrofishing catch of the five reference lakes with natural water-level fluctuation (in italics) and the eight regulated lakes

	Minnow	Nine-spined stickleback	Bullhead	Alpine bullhead	Stone loach	Perch	Ruffe	Pike	Burbot	Roach	Dace	Number of species
Simojärvi			x			x	x	x	x			5
Pesiöjärvi	x							x	x			3
Änättijärvi	x		x	x		x	x	x	x	x		8
Lentua	x		x			x	x	x	x	x		7
Kellojärvi			x			x	x	x	x			5
Oulujärvi		x	x		x	x	x	x	x	x	x	9
Koitere	x			x		x	x	x	x	x	x	8
Kiantajärvi	x	x		x		x	x	x	x			7
Iso-Pyhäntä						x	x	x	x			4
Ontojärvi	x		x			x	x	x	x	x		7
Kostonjärvi	x		x			x	x		x			5
Vuokkijärvi						x	x	x	x	x	x	6
Kemijärvi		x	x			x	x	x	x	x	x	8

13.3) in the regulated lakes and 23.7 per 100 m^2 (SD 9.9) in the reference lakes, but this difference was not statistically significant (Mann–Whitney, $P > 0.05$). For stony bottoms of regulated and reference lakes, total fish density averaged 19.3 and 32.6 ind./100 m^2, respectively, but even this difference was not statistically significant (Mann–Whitney, $P > 0.05$).

The most abundant fish species were minnow (*Phoxinus phoxinus*), perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernuus*), and bullhead (*Cottus gobio*). Perch density was high in regulated lakes, with the exception of the two lakes with the greatest winter drawdown (Fig. 1). The high density of 0+ cyprinid fish in the lake Oulujärvi was based on one electrofishing catch of about 400 small individuals that could not be identified as to species.

Five of the fish species caught—minnow, bullhead, alpine bullhead (*Cottus poecilopus*), stone loach, and nine-spined stickleback—were classified as littoral species because they spend their entire life in littoral areas and were thus caught also as adults. The individual size in these species is small, usually below 10 cm in total length (TL). With other fish species—namely, perch, ruffe, pike (*Esox lucius*),

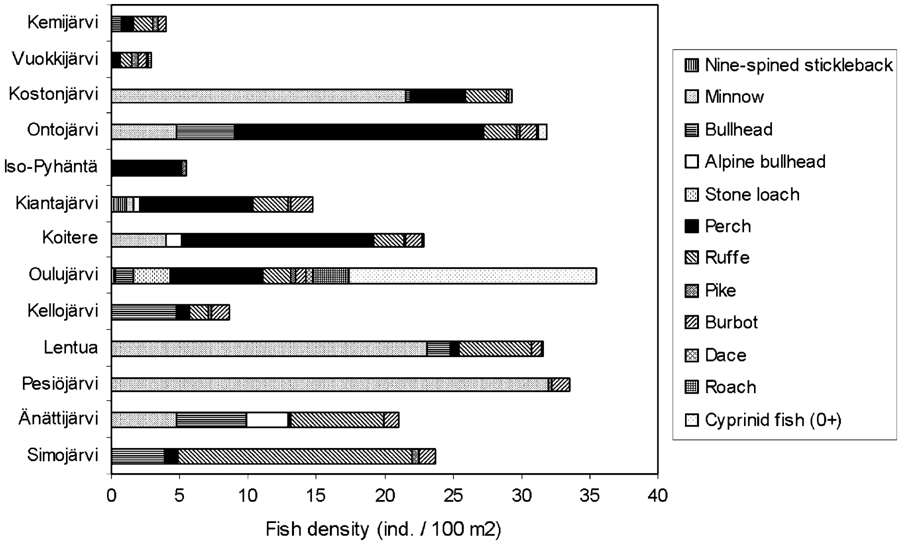

Fig. 1 Average fish densities in the five reference lakes (Simojärvi–Kellojärvi) and in the eight regulated lakes (Oulujärvi–Kemijärvi), based on a single electrofishing run

burbot (*Lota lota*), roach (*Rutilus rutilus*), and dace—young individuals in 0+ and 1+ age classes dominated in our catch. The majority of these individuals were below 15 cm in TL.

According to our preconception, littoral and zoobenthivore fish species were considered especially vulnerable to winter drawdown because of the possible impact in over-winter predation mortality, reproductive success, and food availability. Winter drawdown explained 62% of the variance ($P < 0.01$) in the combined proportion of littoral species and zoobenthos feeder (juvenile burbot and ruffe) biomass for stony shores of the lakes (Fig. 2). Lake Iso-Pyhäntä was omitted from this figure because of its small amount of stony shores (Table 2). Judged from the figure, there may be a threshold value for winter drawdown at about one metre, after which the increase in winter drawdown elevates the response no further. The average percentages of littoral species plus zoobenthos feeders in the regulated and reference lakes were 55.6 and 91.9 %, respectively. This difference was statistically significant (Mann-Whitney, $P < 0.001$).

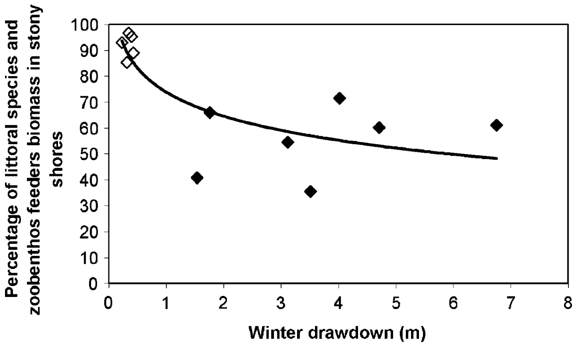

Fig. 2 Combined percentage of littoral species (minnow, bullhead, alpine bullhead, stone loach, and nine-spined stickleback) and zoobenthos feeder (young burbot and ruffe) biomass for stony shores (%) in relation to winter drawdown (m) in the regulated lakes (*filled diamonds*) and reference lakes (*open diamonds*). The curve follows the equation $y = -13.51 \ln(x) + 73.94$, $R^2 = 0.62$

Effects of environmental variables on fish assemblage

The three significant axes of CCA explained 24% of the variance in the density data of the fish species (Table 4). The first CCA axis was most strongly correlated with lake area and the second axis with coverage of macrophytes. The third axis was strongly correlated with water colour and winter drawdown. In the biplot of axes 1 and 3, the overlap of the electrofished areas in reference lakes and regulated lakes is limited to a small area (Fig. 3). The separate clump in the right section of the figure is formed from the electrofishing areas of lake Oulujärvi. The biplot

Table 4 Summary of the results from canonical correspondence analysis (CCA) relating the densities of all fish species in electrofished areas and lake-specific environmental factors

Total variance in the fish species abundance data = 5.26	Axis 1	Axis 2	Axis 3
Eigenvalues	0.658	0.328	0.268
Cumulative proportion (%) of variance explained	12.5	18.7	24.2
Monte Carlo test (*P*-value, 100 permutations)	0.01	0.01	0.01
Environment/fish species correlations*			
Winter drawdown	0.076	0.036	−0.608
Latitude	−0.226	−0.098	0.489
Elevation above sea level	−0.731	0.290	0.233
Lake area	0.957	−0.109	0.176
Total phosphorus	0.645	−0.148	−0.317
Colour of the water	0.186	−0.125	−0.809
Proportion of stony bottom in the electrofished area (%)	0.011	−0.280	0.558
Coverage of macrophytes (%)	0.415	0.737	−0.127
Maximum depth in the electrofished area	−0.074	−0.204	−0.086

* Intra-set correlations (ter Braak, 1986)

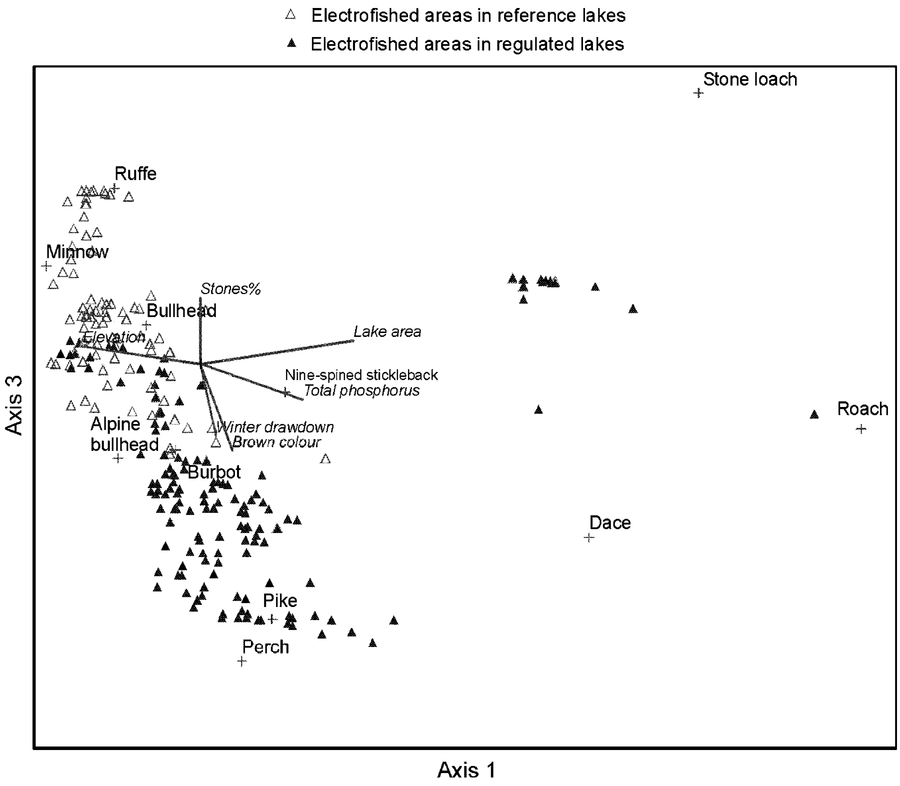

Fig. 3 Biplot of axes 1 and 3 of the canonical correspondence analysis (CCA) relating environmental variables and fish abundances. Open and filled triangles represent the electrofished areas in the reference and regulated lakes, respectively. Environmental variables are represented by lines that roughly point towards the factor direction of maximum variation. The length of the line corresponds to the importance of that variable in assemblage ordination

suggests that increasing water colour and winter drawdown favoured perch and pike but depressed minnow and ruffe.

Minnow were not caught in the five lakes where total phosphorus exceeded 14 µg/l. One of these five lakes was a reference lake (Fig. 4). In all other lakes with lower phosphorus content, minnow were recognised, with the exception of lake Simojärvi. Minnow density correlated negatively with phosphorus content (Spearman r -0.61, $P < 0.05$). Of the other fish species, ruffe also density correlated negatively with total phosphorus content (Spearman r -0.72, $P < 0.01$).

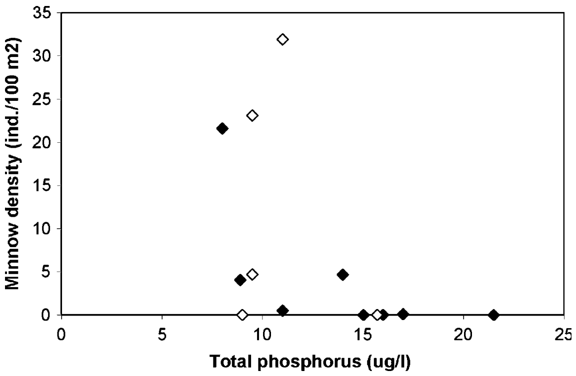

Fig. 4 Average minnow density in relation to total phosphorus (µg/l) in regulated lakes (*filled diamonds*) and reference lakes (*open diamonds*)

Discussion

Our results suggest that water-level fluctuation from man-made winter drawdown did not have clear response in terms of species richness or total fish density in the nearshore areas. Still, some changes probably affected by winter drawdown were seen in the relative abundance of certain fish groups. Also, other factors, such as lake area, had an impact on the littoral fish assemblages.

Our hypothesis that all littoral fish species are highly vulnerable to winter drawdown may be wrong. Nine-spined stickleback was recorded only in three large regulated lakes, including the most heavily regulated lake, Kemijärvi. Unlike all other littoral species, nine-spined stickleback did not seem to hide under stones; moreover, this species was often caught in the surface water. Benthic fish species, like stone loach and bullhead, favour stony habitat where they can hide within stone interstitials for shelter (Smyly, 1955; Sauvonsaari, 1971, Hyslop, 1982; Fischer & Eckmann, 1997). Besides predation effects, lack of sheltering stony habitat may substantially affect metabolism and somatic growth rates in benthic fish (Fischer, 2000). Winter drawdown may force fish to migrate to a much deeper zone with limited areas of stony bottom. Running dry of the stony littoral habitat may not harm nine-spined stickleback as much as benthic fish species.

Littoral fish species may move to deeper areas during winter even in non-regulated lakes. In Ovre Heimdalsvatn, southern Norway, minnows moved from very shallow water to deeper water of about 1 m, where they possibly remained throughout the period of ice cover (Lien, 1981). We lack knowledge concerning the habitat choice and preferred depth of littoral fish in winter. Littoral species favouring stony bottoms in the open-water period probably follow the same habitat choice in winter, if possible.

In the two highly regulated lakes Vuokkijärvi and Iso-Pyhäntä, no littoral species existed. These lakes showed some individual characteristics possibly coupled with the littoral fish assemblage. In the nearshore areas of Vuokkijärvi, we noted a specially clear pattern of stones being embedded in the sand in such a way that no hiding place remained under them for fish. The shores of lake Iso-Pyhäntä often had a narrow (1–2 m wide), stony, deeply sloping belt after which there started a gently sloping sandy bottom without stones. These special characteristics in the littoral morphology may arise from the degree by which the water level was raised at the start of their regulation (see Hellsten, 2000).

Besides this study, the positive impact of lake area on species richness has been documented in several other studies (e.g. Browne, 1981, Matuszek & Beggs, 1988). Stone loach was found only in Oulujärvi, which is a large, relatively southerly, and mildly regulated lake. The northernmost lake in our study, Kemijärvi, is outside the distribution range of stone loach (Koli, 1990).

Several studies have found minnow to be especially sensitive to eutrophication or other deterioration of water quality (Bagge & Hakkari, 1985, Rajasilta et al., 1999, Karels & Niemi, 2002). The results of this study support these findings. In our heterogeneous lake group, simultaneous responses to several coexistent environmental variables probably hindered clear identification of the effects of winter drawdown in fish species level. Still, after grouping of the fish species our results suggested an impact of water-level regulation on fish community level.

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WATER-LEVEL FLUCTUATIONS

Natural lake level fluctuation and associated concordance with water quality and aquatic communities within small lakes of the Laurentian Great Lakes region

M. S. White · M. A. Xenopoulos · K. Hogsden · R. A. Metcalfe · P. J. Dillon

Abstract Long-term ($\sim$20 year) data on water level, water quality and aquatic biota from four remote research areas in the Laurentian Great Lakes region were compiled to reveal patterns of natural water-level fluctuation (WLF) and associated effects on water quality and aquatic communities. Of the 16 natural lakes (no dam impoundment and lowest possible anthropogenic disturbance) yearly amplitude in water level did not exceed 1.27 m ($\bar{x} = 0.26 \pm 0.15$ m) and yearly average water levels did not deviate greater than 0.75 m ($\bar{x} = 0.10 \pm 0.11$ m) from the long-term mean. Linear and waveform regression analyses revealed a significant ($P \leq 0.05$) decreasing trend in water levels and a 10-year oscillation in WLFs. Similarly, linear regression analysis demonstrated a significant reduction in yearly amplitude WLF over time. Correlation analyses revealed significant correlations with water quality parameters (DOC, Ca^{2+}, Conductivity, pH, SO_4^{2-}) and WLFs in Boreal Shield research areas. Of the long-term biotic information available (periphyton, macrophytes, macroinvertebrates and fish) only macroinvertebrates demonstrated a significant relationship with natural WLFs. Species richness followed a unimodal response ($P = 0.002$, $r^2 = 0.66$) with richness decreasing in years when water levels were either higher or lower than the long-term mean. The novel results of this study demonstrate patterns in natural WLF and associated correlations with water quality and biota across multiple lakes within the Laurentian Great Lakes region. The results are congruent with the intermediate disturbance hypothesis and have direct implications for reservoir management and climate change modeling.

Keywords Water-level fluctuations · Intermediate disturbance hypothesis · Macroinvertebrates · Climate change · Water quality · Lentic systems

Introduction

The regulation of aquatic systems for anthropogenic purposes (e.g., drinking water supply, agriculture,

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Ecological Effects of Water-Level Fluctuations in Lakes.

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shipping channels, and hydroelectric power) is becoming common place across the world (Pimentel et al., 2004). Despite a rapid increase in water level regulation, there is limited data concerning the role of water-level fluctuations (WLFs), both within (intra-annual) and between (inter-annual) years, in structuring aquatic communities and influencing water quality. Congruent with anthropogenic disturbance, climate change is also expected to alter lake hydrology (Loaiciga et al., 1996; Magnuson et al., 1997). It is imperative that the linkages between current natural (unregulated) WLFs and lacustrine ecosystems be elucidated before these systems are forever altered.

Although lacustrine systems have been studied extensively, the relationship between WLFs and ecosystem response is poorly understood (Coops et al., 2003). Natural WLFs are controlled largely by local and regional climatic conditions that span in time frame from immediate precipitation events to decadal (and longer) climate change trends. WLFs are extremely complex and are often simplified when analyzing with biological data. WLFs can be measured both inter-annually and intra-annually; however, most studies focus on intra-annual fluctuations due to time constraints. The timing of WLFs can also be extremely important in determining community structure, especially in the aquatic-terrestrial ecotone, as has been shown with macrophytes (Riis & Hawes, 2002). The majority of the literature, and our understanding of WLFs, stems from detailed comparisons of macrophytes in reservoir systems of varying intra-annual amplitudes (Furey et al., 2004; Hill et al., 1998; Wilcox & Meeker, 1991). Similarly, controlled whole lake manipulations have revealed decreases in macrophyte diversity and biomass with WLFs (Turner et al., 2005; Wagner & Falter, 2002). Although the majority of published research has focused on macrophytes, WLFs are known to affect fish (Fisher & Öhl, 2005), macroinvertebrates (Grimås, 1961), waterfowl (McIntyre, 1994) and abiotic factors such as littoral nutrients, sediments, and thermal stratification (Furey et al., 2004; Weston et al., 2004). While these studies have been instrumental in evaluating and understanding the impacts of WLFs, there exists a paucity of data concerning ‘natural’ systems and in particular, how inter-annual fluctuations may affect water quality and biota. This knowledge gap may be attributed to stable inter-annual reservoir WLFs and a lack in long-term WLF information from natural systems. There is an intrinsic understanding that the functioning of lacustrine ecosystems is controlled, in part, by the quantity and periodicity of the water resource, which is directly related to WLFs (Coops et al., 2003). It is essential that we understand, in detail, how natural WLFs affect the water quality, community structure and biodiversity of lake ecosystems.

Using long-term data (20 years) from four research areas, we describe inter-annual patterns and relationships of natural (i.e. no dam control structure) WLFs among sixteen lakes of the Laurentian Great Lakes region and relates these patterns to water quality and aquatic communities. Inter-annual WLFs were evaluated using two indices; change in yearly amplitude and the yearly difference from long-term mean water levels. Water quality parameters included; pH, SO_4^{2-}, conductivity, Ca^{2+}, dissolved organic carbon (DOC), NO_3^- and NO_2^-. Macrophyte, fish and macroinvertebrate species richness data was utilized in analyses. The underlying assumption and hypothesis of this study is that natural WLFs act as an intermediate disturbance (Hutchinson, 1953), which structures the physical, chemical, and biotic components of lacustrine ecosystems. Therefore, we predict that natural WLFs will demonstrate significant concordance with water quality parameters and species richness.

Materials and methods

Data sources

The four research areas are all located in the Laurentian Great Lakes watershed and include: (1) the Experimental Lakes Area (ELA) in northwestern Ontario, (2) the Long-term Ecological Research (LTER) area in northern Wisconsin, (3) the Turkey Lakes Watershed Study (TLWS) in northeastern Ontario and (4) the Dorset Research Centre (DRC) in central Ontario (Fig. 1). All four research areas were able to provide long-term data on water fluctuation and water quality parameters; however, only the LTER site was able to provide consistently sampled biotic information appropriate for WLF analyses. In total, sixteen lakes ($A_o = 12.1 - 1607.9$ ha, $\bar{x} = 174.8$ ha) were included in this

Fig. 1 Map of Ontario depicting approximate locations of long-term research areas; 1—Experimental Lakes Area (ELA), 2—Long-term Ecological Research area (LTER-Wisconsin), 3—Turkey Lakes Watershed Study (TLWS), 4—Dorset Research Center (DRC)

study, their names and associated research areas are as follows: L239 and L114 (ELA); Trout, Sparkling, Allequash, Crystal, and Big Muskellunge (LTER); Turkey and Little Turkey (TLWS); Blue Chalk, Chub, Crosson, Dickie, Harp, Plastic, and Red Chalk (DRC).

Although each research area is unique, the three research areas located in Ontario (ELA, TLWS, DRC) are very similar: all are situated on the Boreal Shield, and thus, have similar topography, geology and vegetation. The LTER site is situated on glacial till which increases the amount of ground water recharge its lakes receive compared to the other three research areas. A complete description of each area is given in: ELA (Department of Fisheries and Oceans, 2005), LTER (University of Wisconsin, 2004), TLWS (Government of Canada, 2005) and DRC (Molot & Dillon, 1991, 1993).

WLFs indices

In describing inter-annual WLFs two indices were chosen: amplitude and difference from the long-term mean (DLTM). Yearly amplitude was calculated as the difference between the maximum and minimum open water (May 1–Nov 31) water level. DLTM was calculated by determining the mean water level from 1980 to 2003 for each lake and then subtracting that mean value (across years) from the mean value for each particular year. These calculations result in positive and negative values indicating the mean water level for a particular year relative to the lake's overall long-term mean. It is important to note that the frequency of water level measurements differed between research areas: bi-weekly (LTER), weekly (DRC), and daily (ELA and TLWS).

Water quality parameters

The following water quality parameters were measured at the four research areas and were included in our analyses: pH, SO_4^{2-}, conductivity, and Ca^{2+}. DOC, NO_3^- and NO_2^- are also included in this analysis but were not measured across all research areas. Samples for water quality data were obtained at varying frequencies between the research areas: monthly (LTER and ELA) and weekly (DRC and TLWS).

Biological data

The only research area with available, consistently sampled, long-term biological data was the LTER site. At this area, data were available for fish, macrophytes and benthic macroinvertebrates for Trout and Sparkling Lakes. Benthic macroinvertebrates were sampled in triplicate using Hester-Dendy samplers placed 3 m apart in 1 m depth of water in nearshore areas. The Hester-Dendy samplers were deployed in mid-August and retrieved 4 weeks later. The family level of taxonomic resolution was used in analyses to maintain consistency among years. No significant results were found in this study for fish or macrophytes; therefore, their sampling methodology is not presented. For detailed sampling protocols please refer to the North Temperate lakes LTER program (University of Wisconsin, 2004).

Statistical analyses

In order to assess lake and site similarity, principal components analysis (PCA) was conducted with PC-ORD© (McCune & Mefford, 1999) using the five commonly sampled water parameters: conductivity,

Ca^{2+}, pH, SO_4^{2-} and amplitude. PCA is an acceptable ordination technique given the linear nature of the environmental variables used in this analysis. Regression techniques were employed to better understand the nature of WLFs in small lakes of the Laurentian Great Lakes region. Regression analyses, both linear and a waveform sine distribution, were preformed in SigmaPlot© (SPSS, 2000) to determine patterns in WLFs over time. WLFs (DLTM and Amplitude) concordance with water quality parameters (pH, SO_4^{2-}, conductivity, Ca^{2+}, DOC, NO_3^- and NO_2^-) was assessed with SAS© (SAS, 2001) through correlation analyses using Pearson's correlation coefficients. These analyses were conducted both on a site-by-site basis and across all sites. Data that was not normally distributed was transformed to meet the assumptions of normality necessary for both Pearson's and regression analyses. Regression analyses were used to determine whether species richness responded to WLFs. Both linear regression and Gaussian distributions (non-linear) were used in SigmaPlot© to determine the influence of WLFs on species richness. Since a Gaussian distribution follows a unimodal pattern, it was hypothesized that species richness has an optimum level, after which, either higher or lower water levels will decrease species richness.

Results

Lake characterization

The results of PCA ordination show a clear separation between the LTER lakes (located on glacial till) and the lakes of the other three research areas which are located on the boreal shield (Fig. 2). Of the five axes extracted in the PCA only axis 1 and 2 are presented as they explain the majority of the extracted variance, 90.8% in total, 74.4% and 16.4%, respectively. The LTER lakes ordinated in the upper left of the ordination biplot and are characterized as having high conductivity values and Ca^{2+} concentrations, while the boreal shield lakes ordinated to the lower right and are characterized by having higher yearly amplitude and SO_4^{2-} concentrations. Interestingly, pH was not a strong descriptor in lake partitioning when utilizing the first two axes.

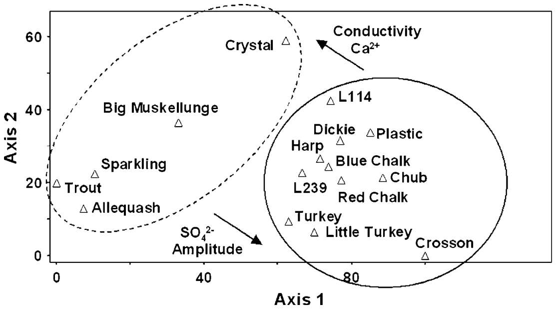

Fig. 2 PCA analyses of the 16 lakes used to characterize water-level fluctuation. The dashed ellipse encompasses lakes located on glacial till at the LTER area in Wisconsin, while the solid ellipse encompasses Ontario lakes located on the boreal shield. Lakes in the upper left corner are characterized by having higher conductivity and Ca^{2+} values while lakes in the lower right corner demonstrate higher SO_4^{2-} levels and increased within year water-level fluctuations (Amplitude)

WLF characterization

Of the 16 lakes studied, yearly amplitude did not exceed 1.27 m ($\bar{x} = 0.26$, $\sigma = 0.15$) and yearly average water levels did not deviate greater than 0.75 m ($\bar{x} = 0.10$, $\sigma = 0.11$) from the long-term mean. Linear regression analysis revealed a significant ($P = 0.0012$) negative relationship with mean water levels decreasing over time ($r^2 = 0.03$), while the waveform, Sine (3 parameter), equation $y = a*\sin(2*\pi*x/b + c)$ similarly revealed a significant result ($P < 0.0001$, $r^2 = 0.18$) (Fig. 3). Linear regression analysis also revealed a significant

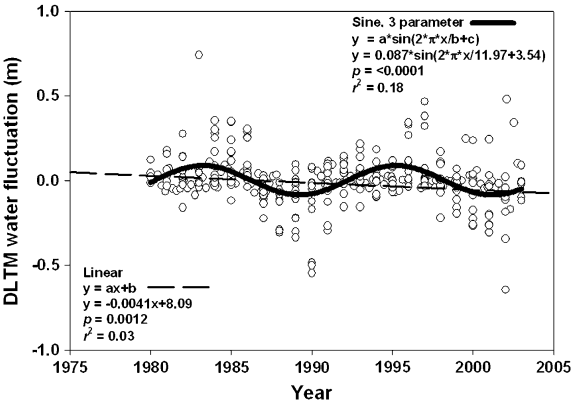

Fig. 3 Linear and waveform regression of mean water levels, expressed as difference from the long-term mean (DLTM), over time (1980–2003) for the 16 study lakes. The negative trend suggests that water levels are lowering over time; however, a 10-year periodicity (oscillation) is present

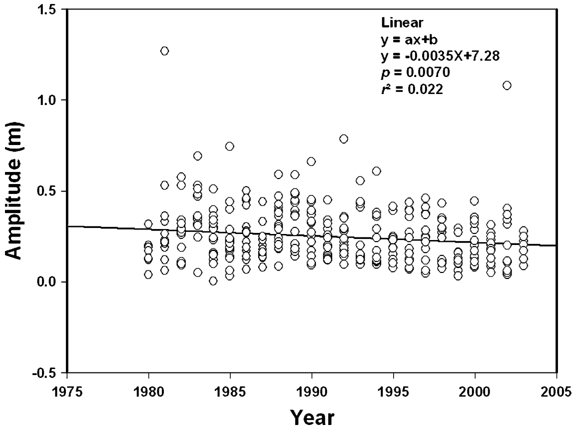

Fig. 4 Linear regression of yearly amplitude over time (1980–2003) for the 16 study lakes. The negative trend suggests that yearly amplitude has been decreasing steadily since 1980

($P = 0.007$) negative relationship with yearly amplitude decreasing over time ($r^2 = 0.022$) (Fig. 4). Although the r^2 values of the linear regressions are extremely low, due to heterogeneity between lakes and research areas, power analyses for linear regressions were high for DLTM and amplitude, 0.91 and 0.77, respectfully. Although all lakes demonstrated similar magnitudes in yearly amplitude, there was not a consistent pattern between lakes. Conversely, all lakes showed a consistent waveform pattern between lakes and across years.

WLF concordance with water quality

Pearson's correlation coefficients (r) and significance values are presented in Table 1 for DLTM and water quality parameters, and in Table 2 for yearly amplitude and water quality parameters. Significant concordance was found at the $P \leq 0.05$ level for five water quality parameters in three research areas. DOC ranged from 1.53 to 10.11 mg/l across all lakes and demonstrated a positive relationship with increasing mean water levels at the ELA site. Interestingly, DOC also showed positive concordance with DLTM and negative concordance with yearly amplitude at the DRC area; however, both were only marginally significant ($0.05 < P \leq 0.10$). DOC data were unavailable for the TLWS and no relationship was found at the LTER site. The range of pH values was 5.51–8.47 across the 16 lakes. We found a negative correlation between pH and yearly amplitude at the TLWS; however, no other significant correlations were found. Sulphate, measured as SO_4^{2-}, was found at concentrations of 1.40–8.53 mg/l across the study lakes and only one significant correlation was found. Sulphate levels were positively correlated at the DRC site with increasing yearly amplitude. Ca^{2+} ranged from 0.98 to 12.94 mg/l across all lakes and demonstrated a positive correlation with DLTM at the DRC research area. Conductivity values ranged from 12.0 to 99.5 μS/cm across the study lakes. Interestingly, conductivity demonstrated significant concordance at both the TLWS and DRC sites; however, TLWS showed negative concordance ($r = -0.36$) while DRC showed positive concordance ($r = 0.16$). These contrasting trends within similar geologic and climatic conditions demonstrate that water quality concordance with WLFs is area specific. Nitrogen was measured as NO_3^- at the ELA and TLWS and as

Table 1 Pearson's correlation coefficients (r) and P values for long-term research areas with selected water quality parameters and difference from long-term mean water levels

Research area		DOC (mg/l)	PH	SO_4^{2-} (mg/l)	Ca^{2+} (mg/l)	Cond (μS/cm)	NO_3^- (μg/l)	$NO_3^- + NO_2^-$ (μg/l)
ELA	r	0.42**	−0.16	−0.29	−0.19	−0.24	0.10	NA
(2 lakes)	P	0.01**	0.29	0.06	0.21	0.12	0.51	
TLWS	r	NA	−0.19	0.06	−0.04	−0.36**	−0.05	NA
(2 lakes)	P		0.22	0.72	0.80	0.02**	0.77	
DRC	r	0.15*	−0.01	0.07	0.17**	0.16**	NA	NA
(7 lakes)	P	0.07*	0.94	0.42	0.05**	0.05**		
LTER	r	−0.05	−0.08	−0.22	−0.11	−0.15	NA	0.07
(5 lakes)	P	0.67	0.48	0.84	0.29	0.16		0.49
All	r	NA	−0.06	0.00	0.05	−0.06	NA	NA
(16 lakes)	P		0.34	0.99	0.35	0.26		

Values with ** highlight significant concordance ($P \leq 0.05$), while values with * highlight potential concordance ($0.05 < P < 0.10$)

Table 2 Pearson's correlation coefficients (*r*) and *P* values for long-term research areas with selected water quality parameters and yearly water amplitude

Research area		DOC (mg/l)	PH	SO_4^{2-} (mg/l)	Ca^{2+} (mg/l)	Cond (μS/cm)	NO_3^- (μg/l)	$NO_3^- + NO_2^-$ (μg/l)
ELA	*r*	0.10	0.02	0.01	0.16	0.17	0.13	NA
(2 lakes)	*P*	0.52	0.90	0.95	0.30	0.27	0.41	
TLWS	*r*	NA	−0.32**	0.15	−0.06	−0.16	0.09	NA
(2 lakes)	*P*		0.04**	0.36	0.71	0.30	0.55	
DRC	*r*	−0.16*	−0.13	0.18**	−0.00	0.05	NA	NA
(7 lakes)	*P*	0.07*	0.11	0.04**	0.99	0.55		
LTER	*r*	−0.04	−0.11	0.02	−0.10	−0.03	NA	−0.07
(5 lakes)	*P*	0.72	0.32	0.88	0.35	0.82		0.50
All	*r*	NA	−0.05	0.10*	−0.02	0.02	NA	NA
(16 lakes)	*P*		0.39	0.08*	0.77	0.75		

Values with ** highlight significant concordance ($P \leq 0.05$), while values with * highlight potential concordance ($0.05 < P < 0.10$)

$NO_3^- + NO_2^-$ at the DRC and LTER and ranged from 1.4 to 367.7 μg/l and 0.3–27.0 μg/l, respectively. There was no concordance between nitrogen and WLFs at any of the research areas.

WLF relationships with biota

As stated in the methodology, Trout and Sparkling Lakes were the only lakes from the available long-term data with appropriate biological data for analyses. We did not find significant relationships with either fish or macrophyte species richness and yearly amplitude. The macroinvertebrate data did show a significant unimodal response to DLTM in Sparkling Lake (Fig. 5). The Gaussian, 4-parameter equation $y = 14.89 + 6.35*\exp(-0.5*((x - 0.04)/0.14)^2)$ yielded a significant ($P = 0.002$) relationship ($r^2 = 0.66$) between macroinvertebrate richness and DLTM. Richness was highest in years closest to the long-term mean and decreased with either increasing or decreasing water levels. Although the same response was not evident with macroinvertebrate richness in Trout Lake this could likely be due to the lower WLFs experienced in Trout Lake (−0.13 m to +0.22 m) compared to Sparkling Lake (−0.50 m to +0.38 m). Similarly, macrophyte richness appeared to be responding to DLTM with the same unimodal pattern in Trout Lake; however, a greater magnitude in WLF was likely needed to show statistical significance (data not shown).

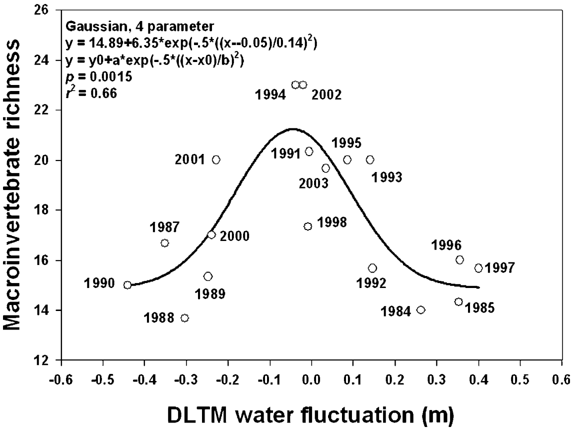

Fig. 5 Regression analysis demonstrating unimodal response of macroinvertebrate species richness (Family level taxonomic resolution) with DLTM over a 20 year period for Sparkling lake at LTER-Wisconsin

Discussion

A typical intra-annual (yearly) hydrograph for unregulated 'natural' inland lakes of the Laurentian Great Lakes region consists of a pulse of water in the spring during snowmelt (April–May) and a subsidiary pulse again in the fall (October–November). This results in a ~75 cm increase in spring water levels and a ~25 cm increase in fall water levels demonstrating a bimodal pattern and 'flashy' (Boreal Shield lakes) response due to the impermeable bedrock (Fig. 6). Limnologists have long recognized this intra-annual pattern in WLFs, but what was not evident was how inter-annual WLFs change over time, and just as importantly, the magnitude and patterns that exist across multiple lake systems. A clear oscillation, or periodicity, ($\sim$10 years) is evident across the 16 lakes, whether this pattern will persist or was present before the 20 years of available data is unknown. Interestingly, the oscillation is consistent between lakes, presumably due to the overriding effect of similar climatic conditions within the Laurentian Great Lakes watershed. This pattern in WLF could not be related to the North Atlantic Oscillation (NAO) as was found in Lake Võrtsjärv (Nõges et al., 2003) or the Southern Oscillation Index (SOI), but it is likely associated with periodicity in precipitation events driven by global climatic factors. The same concordance among lakes was not found with amplitude and analyses on a lake-by-lake basis revealed that amplitude does vary greatly between years showing no continuity within a single lake (data not shown).

The waveform response in DLTM across multiple lakes suggests that it is largely regulated by broad-scale ecoregion climatic conditions. Conversely, the minute concordance of amplitude among lakes and indiscernible scatter within and between lakes (data not shown) suggest that it is influenced by local, small-scale, ecodistrict effects. The negative slope of both linear regressions (DLTM, amplitude) across time suggests that mean water levels and amplitude intensities have been decreasing in the Laurentian Great Lakes region over the last 20 years. This pattern supports many climate change scenarios (Blenckner, 2005; Giorgi et al., 2001; Magnuson et al., 1997; Suffling & Scott, 2002), as temperate regions increase in annual temperature evaporation rates increase and rainfall becomes more consistent throughout the year.

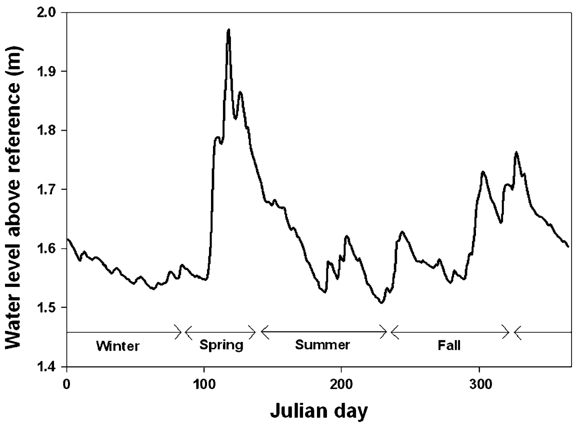

Fig. 6 Typical intra-annual hydrograph for Turkey Lake, 1994 (TLWS)

Due to the varying frequencies that water level measurements were taken between research areas, it was not feasible to assess the effect of fine scaled intra-annual differences in WLFs (timing of min and max water levels and rates of increase or decrease) with biota or water quality parameters. However, we found that inter-annual WLFs demonstrated significant concordance with water quality parameters as has been suggested by other studies. Webster et al. (1996, 2000) demonstrated that Wisconsin lakes of various landscape positions responded differently to increases in calcium and magnesium concentrations after a 2-year drought. Temperate lakes also have demonstrated concordance with DOC concentrations in relation to landscape characteristics (Rasmussen et al., 1989; Xenopoulos et al., 2003) and nitrate concentrations with winter climate conditions (George et al., 2004). Similarly, in an investigation of Boreal Plain lakes of northern Alberta, inorganic and organic nutrients were correlated with land use, soil properties and vegetation communities (Prepas et al., 2001). We show that all boreal shield research areas, but not the LTER area, exhibited concordance with WLFs (DLTM or amplitude). The lack of concordance with the LTER lakes can be explained by the porous glacial soil and resultant dominant groundwater inputs to the LTER lakes compared to the impervious bedrock found at the other three research areas. This translates to boreal lakes receiving direct surface water runoff exposed to nutrient leaching during precipitation events. The LTER-Wisconsin lakes are fed by groundwater sources that are homogenous in nutrient and elemental compositions and are less influenced by precipitation events due to percolation of surface runoff through the substratum into groundwater recharge areas. Lake separation through PCA analysis also supports the characteristically discriminant LTER-Wisconsin lakes. The demonstrated concordance of water quality with WLFs is not unexpected as water levels are directly controlled by hydrological inputs that are driven by drought and precipitation events. An increase or decrease in water level indicates a shift in a lakes hydrologic budget. The concordance of water quality with WLFs results from the multifarious interaction of landscape controls (Dillon & Molot, 2005), internal lake nutrient cycling (Hanson et al., 2003), and biotic relationships (Wagner & Falter, 2002).

Species response to WLFs has been well documented in riverine systems and relationships of macroinvertebrate community structure to riverine WLFs has been demonstrated often (Ogbeibu & Oribhabor, 2002; Wood & Armitage, 2004). Lentic systems, and in particular temperate systems, have received much less attention. This is due presumably to the subordinate magnitude of WLFs in temperate lentic systems when compared to riverine systems. Since the biota inhabiting these systems have evolved with distinctive WLFs, deviations from these regimes may dramatically alter community composition and biotic richness, particularly in littoral areas. Recently, aquatic ecologists have started to recognize the importance of WLFs in temperate lentic ecosystems through research geared toward evaluating the impacts of regulated WLFs in reservoirs. These studies have focused mainly on the effect of yearly amplitude on macrophyte diversity. All studies suggest that a fluctuation between 1.5 and 2.0 m is the optimal level at which the highest macrophyte diversity is attained (Hill et al., 1998; Wagner & Falter, 2002; Wilcox & Meeker, 1991). A New Zealand study focusing on the low growing mixed macrophyte community along lake margins of 21 lakes yielded similar results, suggesting that a 1.1-m fluctuation yielded highest species richness in this zone (Riis & Hawes, 2002). The same study also conjectured that inter-annual WLFs were just as important as intra-annual WLFs in establishing high levels of species richness.

While these studies concerning macrophytes in regulated systems provide enormous insight into the confounding influences of WLFs, the results are limited as they are short-term (2 years max), evaluate yearly amplitude only, focus on macrophytes and often do not incorporate pristine reference conditions. They do not assimilate the dynamic patterns of WLFs across multiple years, or account for the fact that amplitudes are not consistent between years in any natural lake system.

Macrophyte diversity did not show a significant response with changes in WLFs in this study; however, the data obtained from Trout lake suggest that macrophytes near the lower limit of the photic zone (~4 m) begin to demonstrate decreased diversity in years experiencing maximum amplitudes (~25 cm) events (data not shown). This is not surprising as aquatic plants inhabiting these depths are likely Photosynthetically Active Radiation (PAR) limited in the spring during the start of the growing season when amplitudes would be at their highest. Similarly, macrophyte richness attained its highest numbers in years closest to the long-term mean (data not shown). This suggests that macrophyte diversity may be responding to WLFs but a significant pattern is not discernable at current natural WLFs. Changes to the current pattern of natural WLFs (i.e., climate change) may elicit a response in macrophyte richness.

In this study, macroinvertebrates demonstrated a classical unimodal response to DLTM and WLFs. Maximum species richness was attained in years closest to the mean water level and decreased as mean water levels deviated (+ or −) from the long-term mean. It can be postulated that this is a result of mean DLTM community structures containing species which favor both high and low water levels. The sensitivity of macroinvertebrates to WLFs compared to macrophytes and fish in this study is not surprising. Macroinvertebrate communities have long been considered paramount in biomonitoring projects due to their inherent characteristics; diverse functional feeding groups, importance in food webs, sensitivity to water quality, confined to specific area, and they are easy to sample (Mackie, 2001). These same properties result in their highly responsive nature to WLFs and appropriateness in assessing associated impacts to aquatic systems. Previous research concerning macroinvertebrates and WLFs in lentic systems has focused on ephemeral and permanent flooding of wetlands (Hillman & Quinn, 2002; Neckles et al., 1990; Whiles & Goldowitz, 2005). The effect on boreal lakes (where species are not adapted to extreme WLFs) is largely unknown. The few studies that have been conducted in lentic Boreal systems involve anthropogenic changes in amplitude with increasing amplitudes resulting in decreased species diversity (Grimås, 1961) and extirpation of important taxa, including amphipods and isopods (Hunt & Jones, 1972) and *Hexagenia* sp. and *Oecetis* sp. (Cooper, 1980). Although these studies were conducted on regulated systems they do demonstrate the highly responsive nature of macroinvertebrates to WLFs.

The stimulation of species diversity associated with the intermediate disturbance hypothesis has been demonstrated in many habitats (Bertrand et al., 2004; Johst & Huth, 2005; Valdivia et al., 2005; Wilcox & Meeker, 1991). This study demonstrates that the amount of disturbance created by natural WLFs in the Laurentian Great Lakes watershed stimulates diversity in biotic communities. Nevertheless, the plasticity of these systems to uncharacteristic increases or alterations to natural WLFs due to anthropogenic effects (climate change and water regulation) is uncertain. Much of our current understanding of WLFs in temperate lentic systems stems from detailed studies of regulated systems. The majority of this research focuses on changes in yearly amplitude and suggests that $\sim$2 m yearly fluctuation results in the highest macrophyte diversity. This study demonstrates that DLTM should also be considered when making management decisions as has been suggested by Riis & Hawes (2002). Furthermore, macroinvertebrates should be utilized also due to their higher sensitivity to WLFs compared to macrophytes. More importantly, community structure and abundances need to be considered as many invertebrate species are important food sources for birds, fish and amphibians, which ultimately has unforeseen consequences for many species throughout the food web. Lastly, as is evident in Fig. 6, future studies in lentic systems should quantify other properties of hydrographs that are commonly characterized in riverine systems, such as, number of pulse events, durations of higher water level, rate of increase and decrease, and timing of pulse events to determine how these characteristics may influence lentic systems.

In conclusion, water quality responds immediately to natural WLFs in the Boreal Shield ecozone. Macro-biota appear to be less sensitive (have a delayed response) to natural WLFs; however, macroinvertebrates did show a significant unimodal response (possibly due to their higher mobility) while slight alterations to the sessile macrophyte community were noted. This study emphasizes the need for aquatic ecologists, reservoir managers and climate change modelers to assimilate the dynamic ways in which WLFs change across time, both within and between years. The role of natural WLFs are of paramount importance in structuring aquatic communities, especially in littoral habitats, and alterations to these patterns (climate change and water regulation) may result in severe consequences to water quality, biodiversity and the health of lake ecosystems. The data presented in this study, acquired from renowned lacustrine research areas, supports the hypothesis that natural WLFs act as an intermediate disturbance that structures the physical, chemical, and biotic components of lacustrine ecosystems. The incorporation of long-term data in aquatic ecosystem assessments cannot be understated (Kratz et al., 2003). It is only with long-term monitoring programs that we can truly comprehend the complex way in which communities interact with their stochastic environments.

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WATER-LEVEL FLUCTUATIONS

Climate change and lakeshore conservation: a model and review of management techniques

Carlos Abrahams

Abstract Climate change is expected to cause significant changes to the hydrology of lakes, reservoirs and other wetlands. In particular, there will be an increase in the level of disturbance produced by water-level fluctuations. This may have adverse consequences for biodiversity, water quality and human uses. Strategies to cope with these climate change impacts are currently poorly developed. This article proposes the use of Grime's CSR theory as a framework to understand the potential impacts of climate change on shoreline vegetation. It is also used to recommend a series of practical management techniques that will contribute to the adaptation capacity of shoreline ecosystems. Four key areas are highlighted: hydrological controls, substrate conditions, shoreline topography and vegetation establishment.

Keywords Shoreline conservation · CSR model · Climate change · Adaptation strategies · Aquatic macrophytes · Water-level fluctuations

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Ecological Effects of Water-Level Fluctations in Lakes

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Introduction

The influence of hydrology on the shoreline vegetation of lakes and reservoirs has long been recognized (e.g. Preston, 1895; Pearsall, 1920). Despite this, many authors have identified an urgent requirement for continued research into the relationship between water-level fluctuations and littoral vegetation dynamics (Levine & Willard, 1990; Zedler & Weller, 1990; Merritt, 1994; Middleton, 1995). Equally important, however, is the need for such research to be synthesized and developed into specific applied guidance for the practitioners whose role it is to conserve lakes, reservoirs and other wetlands (Nilsson & Keddy, 1988; Kusler & Kentula, 1990; Keddy, 1999; Halse & Massenbauer, 2005). A key tool for this knowledge transfer is the development of simple and clear conceptual models for nature conservation managers (Steel & Duncan, 1999; Ogden et al., 2005). Based upon ecological theory and empirical evidence, they can help to define management issues, identify trends and processes and allow the development of strategies for practical implementation (Keddy & Fraser, 2000). Examples of such models in the field of wetland ecology are centrifugal organization (Wisheu & Keddy, 1992), the flood pulse concept (Middleton, 2002), the wetland continuum (Euliss et al., 2004) and the succession model proposed by van der Valk (1981).

This article proposes an application of Grime's (1979) CSR theory to model the potential impacts of climate change on shoreline vegetation. This conceptual framework is then used to provide a context for a series of practical strategies that can be implemented to mitigate the adverse impacts of climate change, i.e. adaptation *sensu* IPCC (2001)—“adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities”.

Climate change and water-level fluctuations

Although there is still considerable uncertainty about the potential impacts of climate change on freshwater ecosystems, understanding has developed significantly in recent years. Impacts will include increased water temperatures, sedimentation and pollution of wetland systems and heightened nutrient levels (Hossell et al., 2000). There will also be major impacts on hydrology. Annual average streamflows are expected to increase in northern Europe and decrease in southern and central Europe, but in areas where snowfall has normally been a large component of precipitation, increasing temperatures will result in more winter runoff from rain and less snow-melt during spring. In Britain, northwest regions will have an increased positive water balance, with wetlands having to adapt to higher water levels and increased flooding, while in the southeast a net decrease will cause more frequent and severe summer droughts (Dawson et al., 2001). Due to the general increase in seasonal variability in precipitation, river flows and evapotranspiration, the influence of climate change is likely to have significant impacts on the magnitude, timing and variability of the hydroperiod of waterbodies and the frequency and nature of extreme flood or drought events (Lins et al., 1991; Arnell, 1999; Cannell et al., 1999; Schindler, 2001; Kundzewicz et al., 2002; Fowler et al., 2003; Eisenreich, 2005). Although this may create new habitat in the form of temporary pools or riverine wetlands in areas with increased winter precipitation, the effect for the majority of existing wetland systems will be an increase in the incidence and scale of summer drawdown (Dawson et al., 2001). Currently stable waterbodies will develop into two-phase environments with increasingly separate submersed and terrestrial conditions. This will increase the area of bare substrate that is seasonally exposed around waterbodies and made available as potential habitat for marginal species (Salisbury, 1970). However, the ability of plants to colonize and become established in this newly available habitat will depend upon the frequency, timing and duration of drawdown events. Conversely, the existing habitat of submerged and obligate aquatic species, with stable water levels, will become increasingly unsuitable to support these types of vegetation. Given these potential interactions, changes to water level regimes are likely to have a more critical impact upon the structure, function and biodiversity interest of wetland communities than temperature increases *per se* (van Dam et al., 2002; Hulme, 2005). However, despite this potential for considerable change and the major importance of wetlands as habitat for a diverse suite of rare plant species, little attention has been given, thus far, to the impacts of climate change on wetland vegetation by scientists and policy makers (Dawson et al., 2001). The studies that have been carried out also focus primarily on rivers or groundwater wetlands, to the exclusion of open water bodies such as lakes and reservoirs. One exception to this has been the study of prairie potholes in the USA (e.g. Johnson et al., 2004), which indicates that water levels would be much lower under climate change scenarios, with some wetlands being without standing water for considerable periods of time. Major changes to vegetation would be likely to result, with consequent impacts for other wildlife such as waterfowl.

The CSR model

The classification of species according to their functional characteristics provides a useful context to investigate relationships between vegetation and environmental parameters. Functional criteria, such as leaf and shoot morphology, seed production and growth rates, can be used either as individual attributes or in groups, to define assemblages of plants and enable predictions to be made of changes in vegetation type and species composition (Willby et al., 2000). This approach can, therefore, allow the impacts of events or trends like global climate change to be predicted and assessed.

The key mechanism linking increased water-level fluctuations from climate change with impacts on shoreline vegetation communities is likely to be the disturbance regime (*sensu* Grime, 1979) produced by repeated drawdown and re-flooding on lakeshores. When combined with a fertility gradient (e.g. Day et al., 1988), this can be understood in terms of Grime's CSR theory, which proposes a three-way classification of plant life histories, dividing species into competitive, stress-tolerant or ruderal groups depending on their observed traits. These different classes are arranged on the two opposing environmental axes, one describing the level of habitat disturbance, the other its fertility. These two axes produce four possible types of environment, three of which are inhabitable by plants. The characteristic vegetation of each environmental type has a corresponding life-history: (i) low disturbance, fertile habitats favour competitive species, (ii) low disturbance, low fertility habitats favour stress-tolerant species and (iii) high disturbance, fertile habitats support ruderal species (Fig. 1). The fourth type of environment, with high disturbance and low fertility, is uninhabitable (Grime, 1979).

Shorelines are particularly appropriate subjects for the application of CSR theory, as the two key axes are often clearly expressed in the ecology of their vegetation: variation in environmental parameters causing stress or disturbance is often coarse-grained in scale, and subsequent differences among plant communities are usually well-defined (Spence, 1982; Keddy, 1983). In addition, changes in environment over a relatively short period of time can cause significant differences among communities, for example, as seen in a shift from a competitive marginal community to a ruderal annual vegetation with drawdown. However, these broad changes may be complicated by issues of phenotypic plasticity and the wide ecological amplitude of some wetland species, which may make clear predictions difficult (Willby et al., 2000).

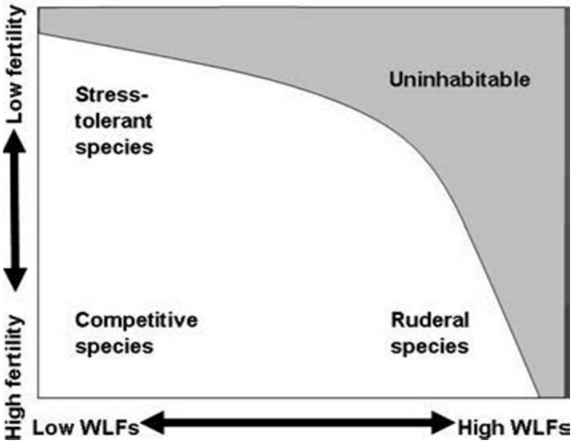

Fig. 1 Grime's CSR triangle applied to shoreline situations, with fertility and disturbance axes shown (WLFs—water-level fluctuations)

There are a number of potential sources of disturbance on lake shorelines, including wave action (Grelsson & Nilsson, 1991), ice scour (Begin & Payette, 1991) and herbivory (Hoffman & Stanley, 1978). However, a number of studies have identified water-level fluctuations as the key component of disturbance in terms of its influence on littoral vegetation dynamics (Gill & Bradshaw, 1971; Nilsson, 1981; Gasith & Gafny, 1990; Irwin & Noble, 1996; Fraisse et al., 1997; Hroudova & Zakravsky, 1999; Keddy, 2000). Drawdown can cause mortality of aquatic plants through heating and desiccation in summer, or freezing in winter (Blindow, 1992; Irwin & Noble 1996) and can allow colonization by a new suite of plant species (Salisbury, 1970). Flooding of terrestrial plants can also reduce cover by preventing respiration, reducing light levels required for photosynthesis, or by initiating chemical changes in the substrate with which they cannot cope (Middleton, 1995). The effects of these changes are consistent with Class I type disturbance (*sensu* Sousa, 1984), increasing resource availability, causing the removal of dominant species and setting back successional processes. As discussed above, climate change will alter hydrological patterns, with increased water-level fluctuations producing a heightened disturbance regime (Mooij et al., 2005).

On the secondary axis of habitat fertility, the level of environmental stress on shorelines is principally dictated by the underlying geology. In addition, exposure to wave action causes erosion, transport, sorting and deposition of sediments, having a major impact on the levels of organic matter, nutrients and fine particles in the substrate (Nilsson, 1981; Keddy, 1984; Wilson & Keddy, 1988; Fraisse et al., 1997). Hence, on wave-washed shores the substrate is often sandy or stony with low nutrient levels, while more sheltered areas have an organic, nutrient-rich soil with a higher proportion of silt and clay (Wilson & Keddy, 1986; Grelsson & Nilsson, 1991). The change in species complement and communities along a fertility gradient is well established (Wilson & Keddy, 1986, 1988) and has impacts upon biomass, species richness and the presence of scarce plants.

The occurrence of these two gradients is illustrated in the study by Willby et al. (2000), which analysed the habitat utilization of 120 hydrophyte species. It found that there were two key axes in habitat parameters relating to (a) flow, substratum grade, organic matter content, scour and sedimentation (a gradient from sheltered bays with fine, mixed or organic sediments to exposed lake shores with coarse-grained mineral strata), and (b) depth, water level stability and biotic disturbance (a gradient from stable, rarely disturbed sites to fluctuating sites). In addition, Hawes et al. (2003) found that the extent and diversity of shallow-growing species was related to a combination of the extent of water-level fluctuation and wave exposure. In their study of riverine marshes, Day et al. (1988) distinguished between five life-history types that broadly parallel the CSR system: clonal dominants, gap colonizers, stress tolerators, reeds and ruderals; which all occur at different positions along gradients of fertility and disturbance.

Fertile, sheltered shores, which allow the retention of organic matter, silt and clay and are not subject to frequent fluctuations (with vegetation gaps forming infrequently), promote the dominance of competitive species. This is ‘core’ habitat according to the centrifugal organization hypothesis, which is occupied by a restricted number of large leafy species capable of forming dense canopies (Wisheu & Keddy, 1992). Species characteristics that accompany this competitive dominance include high biomass, long generation times, low reproductive output and the capacity for vegetative spread. In these habitats, weaker competitors are excluded, with low species richness being a usual result (Day et al., 1988; Shipley et al., 1989; Keddy & Fraser, 2000; Willby et al., 2000). Examples of typical competitive species are lesser bulrush *Typha angustifolia* L., broadfruit bur-reed *Sparganium eurycarpum* Engelm. ex Gray and sweet flag *Acorus calamus* L. Outside of the core habitat in which these species occur, different gradients of stress and disturbance radiate, with varied groups of species and vegetation arranged peripherally along each.

On infertile, wave-eroded shorelines, with low substrate organic matter and high percentages of sand and gravel, only distinctive stress-tolerant species can be supported (Keddy & Fraser, 2000). Small, slow-growing rosette species like isoetids, with anchored tubular leaves that may be evergreen or wintergreen, are typical of this type of habitat (Wilson & Keddy, 1986; Willby et al., 2000). Typical species are often short, low in biomass, have little capacity for vegetative spread, low growth rates and large seeds with slow germination. Examples are American bulrush *Schoenoplectus americanus* (Pers.) Volk. ex Schinz & Keller, common spike-rush *Eleocharis palustris* (L.) Roem. & Schult., bald spike-rush *Eleocharis erythropoda* Steud. and bugleweed *Lycopus uniflorus* Michx (Shipley et al.,1989). Moore et al. (1989) also found that these infertile shores support a particularly high proportion of rare species, and therefore, have high nature conservation value.

On fertile shorelines subject to disturbance from frequent water-level fluctuations, with frequent and density-independent mortality, ruderal plants such as celery-leaved buttercup *Ranunculus sceleratus* L., trifid bur-marigold *Bidens tripartita* L. and marsh cudweed *Gnaphalium uliginosum* L. would be expected (Ellenberg, 1988). Fast growing annuals or short-lived perennials are often typical of this habitat, displaying characteristics such as small body size, high growth rates, early reproduction and a high output of small seeds that germinate rapidly (Shipley et al.,1989; Willby et al., 2000). The early onset of flowering and seed-ripening in taxa such as *Persicaria*, *Atriplex* and *Chenopodium* can be a key characteristic of ruderals in this habitat, allowing them to complete their life-cycle within a short drawdown period. There are also some ruderal perennials including *Ranunculus repens* L, creeping bent *Agrostis stolonifera* L. and common couch *Elytrigia repens* (L.) Desv. Ex Nevski, which are strongly rhizomatous or stoloniferous and are capable of rapid vegetative spread (Grime, 1979). In a similar vein to the study by Moore et al. (1989), work on temporary ponds in the UK has shown that these sites support a disproportionately high number of rare species (Nicolet et al., 2004). It may be possible that a trend away from stable, nutrient-rich ‘core’ habitat in any direction allows scarce plants to escape competition by dominant species and this does appear to be the case in a number of different habitat types (Keddy, 2000).

Infertile, disturbed shorelines will be devoid of vegetation. The causes of this are likely to include barriers to colonization, prevention of establishment by juveniles and removal of adult plants. It has been found that biomass on lakeshores correlates positively with altitude and hence duration of exposure, showing that the frequency of disturbance is a key factor in determining plant growth (Spence, 1982; Wilson & Keddy, 1988; Gasith & Gafny, 1990).

Climate change impacts

It has been repeatedly demonstrated that the nature of the water level regime has an important influence on wetland community structure. Key factors determining species composition on shorelines are the timing, frequency and length of drawdown events, with the growing period between disturbance events being critical for marginal or terrestrial plants growing in the eulittoral zone (Meeks, 1969; Nilsson, 1979, 1981). The current situation in many lakes is for long flooded periods with short-term drawdowns in unusually dry years. This regime allows the development of submerged aquatic vegetation, with erect marginal plants at the shoreline and a fringe of wet scrub or woodland above the waterline (Spence, 1982). However, climate change is likely to result in shorter flooded periods, with increasingly frequent drawdowns of longer duration. This will have two effects: existing aquatic vegetation will be subject to stranding and a bare ground resource will become available for colonization. These processes will reduce the cover of submerged aquatics and promote the development of species adapted to the exposed eulittoral zone (Nilsson, 1979, 1981), such as ruderal mudflat annuals (Meeks, 1969; Schneider, 1994) or grasses and sedges (Gerritsen & Greening, 1989).

As an analogy for climate change impacts, a number of studies have made comparisons between regulated and non-regulated lakes, which differ in their hydroperiod regimes. Wilcox & Meeker (1991) found that an increase in annual fluctuation in a regulated lake caused a change in macrophyte communities from structurally diverse plant communities to a more limited suite of rosette and mat-forming species, the high level of disturbance reducing structural diversity. Smith et al., (1987) recorded that lakes used for hydropower, with regular large fluctuations, were devoid of littoral macrophytes, in contrast to natural lakes and water supply reservoirs. Hill et al. (1998) found that regulated lakes were less diverse, contained more exotic species and were usually devoid of rare herbs, when compared to unregulated waterbodies. Finally, Rorslett (1989), studying hydroelectric lakes, found a decline in species richness, disappearance of shallow and mid-depth vegetation and an increased incidence of ruderal plant types.

Considering these findings and CSR theory, the model in Fig. 2 indicates that, depending on the starting point of the ecosystem, one of three pathways will be induced by the hydrological changes caused by climate change.

1. Low disturbance, fertile shorelines will be subject to heightened levels of disturbance and will become increasingly ruderal in terms of their vegetation, with highly competitive species being lost. This could, however, have a potential consequence of increasing diversity as predicted by the intermediate disturbance hypothesis (Grime, 1973), and as seen in studies of shoreline vegetation (Keddy, 1983).
2. Low disturbance, infertile habitats, when subject to increased levels of water-level fluctuations, will no longer be inhabitable, resulting in loss of plant cover and increasingly bare shores. Stress-tolerant species will be lost, with negative impacts for the distinctive rare vegetation that these habitats often support (Moore et al., 1989).
3. Shorelines currently subjected to high levels of disturbance, but that remain vegetated due to fertile conditions, will perhaps become

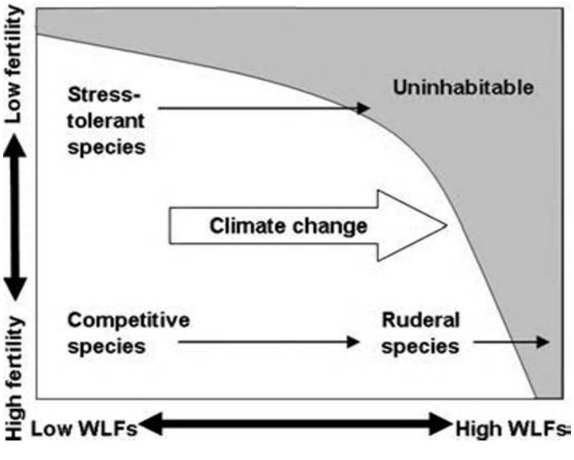

Fig. 2 Climate change impacts on shorelines

increasingly ruderal. However, there is also the potential that the frequency, duration or magnitude of hydrological changes will become too severe for even ruderal shoreline plants to cope, and plant cover will decrease, leaving bare shorelines, or those dominated by only a few species, as seen in rapid-cycling hydroelectric reservoirs (Smith et al., 1987)

In summary, the overall change in species composition in many shoreline habitats subject to increased water-level fluctuations is likely to be a loss of competitive and stress-tolerant species, with increasingly ruderal vegetation types and expanding areas of bare substrate. This will have obvious major impacts on the nature conservation value, ecosystem functioning and ecological services provided by wetland habitats. In a study of Great Lakes wetlands, Mortsch (1998) concluded that an increased frequency and duration of low water levels produced by climate change, together with changes in the timing and amplitude of seasonal water levels, would affect wildlife, waterfowl and fish habitats, water quality, wetland area and vegetation diversity. However, other evidence also suggests that, where lakes have suffered a decline in habitat or species diversity through artificial stabilization of lake levels, it is possible that climate-change induced fluctuations could reverse the adverse impacts and restore biodiversity interest (Wilcox & Meeker, 1991; Hill et al., 1998). Lakes that have become dominated by extensive stands of large competitive species could, with increased water-level fluctuations, develop a wider species complement through the creation of niches for a more diverse range of less competitive species.

Management options

Although significant levels of research have focused on climate change prediction, impact assessment and mitigation, there has been little attempt, thus far, to develop practical adaptation methods to reduce expected impacts on wetlands (Hulme, 2005). Such measures could increase the flexibility of management of important sites, enhance the possibilities for ecosystems to adapt to change and reduce the additional pressures of non-climate related impacts. A non-interventionist approach can be taken, accepting the changes to environments that will occur and allowing new habitats and communities to develop without substantial input. In many cases however, a more appropriate approach will be to implement active management strategies to mitigate the most severe effects of environmental change and allow adaptation to altered hydrologic regimes. Examples of these include the use of high priority management actions in valuable wetlands, including hydraulic controls for some wetlands to improve water management and the implementation of wetland rehabilitation and restoration projects (van Dam et al., 2002).

Building upon the potential biological effects indicated in Fig. 2, the conservation management of shorelines subject to hydrologic fluctuations and wave action should focus on four key issues (Fig. 3): hydrological management, substrate conditions, shoreline topography and the potential need for vegetation establishment (Abrahams, 2005; Abrahams, in press). These will allow the adverse impacts of increased disturbance to be mitigated and allow the protection and modification of shoreline fertility, if required, so that viable vegetation can be maintained despite the effects of climate change.

Moderate water-level fluctuations make a positive contribution to the diversity and conservation value of shoreline vegetation (Pieczynska, 1990; Schneider, 1994). However, extreme fluctuations will reduce plant cover and impoverish communities (Smith et al., 1987; Hawes et al. 2003). The threshold

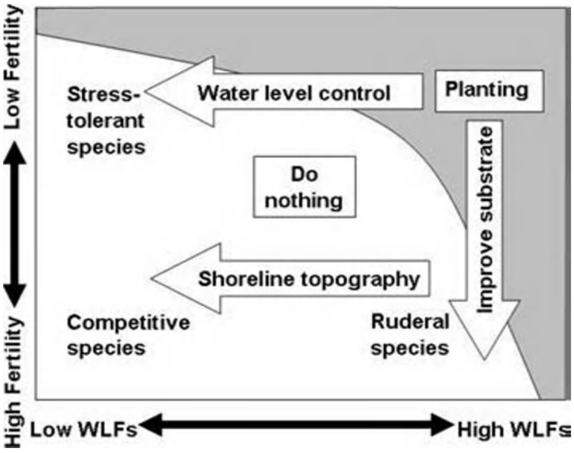

Fig. 3 Potential management options to allow adaptation to climate change

between these two levels of disturbance may be variable and is usually site-specific. There is, however, reasonable correspondence among different studies on the appropriate limits to water-level fluctuations. In temperate-zone lakes, rates of change that can sustain vegetation and produce species-rich assemblages are generally less than 0.6–2 m per month, with annual changes not exceeding 2–5 m (Petts, 1990; Wilcox & Meeker, 1991; Pyrovetsi & Papastergiadou, 1992; Smith et al., 1987). Annual fluctuations greater than 5–7 m are often too extreme and may significantly degrade littoral biota, leaving the water devoid of permanent aquatic vegetation (Nilsson, 1979; Smith et al., 1987; Rorslett, 1989; Pyrovetsi & Papastergiadou, 1992). The CSR model indicates that water level control as an adaptation strategy should seek to limit fluctuations within these thresholds, especially in lakes with nutrient-poor shorelines. For illustration, Wilcox & Meeker (1991) found that maximum species richness was produced with an annual within-year fluctuation of 1.8 m, and Hill et al. (1998) recommended an annual variation of 0.5–1 m, while Hawes et al. (2003) found the highest species richness in a range of lakes to occur in those with a monthly range of 1 m. These figures provide some indication of scale to the disturbance axis in Figs. 2 and 3.

Ecological Regulation Practices (Mark & Johnson, 1985; Hellsten et al., 1996a) and other water level management plans can offer a potential way to integrate nature conservation and operational demands in reservoirs and regulated lakes. A set of control rules can be developed to manage levels and prevent adverse ecological impacts occurring. Although there are likely to be difficulties in implementing these on sites that have high demands for water supply and flood regulation, particularly as operational demands increase, they do offer a potential method for adaptation on sites managed for nature conservation. An alternative approach to cope with increasing annual variability in the water budgets of wetland nature reserves, is to provide for additional winter water storage in connected reservoirs, so that water can be released into these systems during drier summer months (Merritt, 1994). This will enable existing hydroperiods in these systems to be maintained in their current states.

In areas of poor shoreline substrate, increased hydrological fluctuation could easily lead to the loss of capacity for plant growth as the combination of low fertility and high disturbance prevent the establishment and growth of vegetation. A potential adaptation strategy here is to reduce habitat severity by improving substrate quality (particularly organic matter content) through wave protection and substrate enhancement. The impacts of wave action, especially on a mobile sandy or silty substrate, will substantially reduce substrate organic matter content (Nilsson, 1981; Keddy, 1983). As a response to this situation, ploughing, disking and fertilizer application have all been used to improve substrate characteristics in reservoir revegetation schemes (Fowler & Hammer, 1976; Middleton, 1995). In addition, imported material can be added to the substrate to improve its suitability for plant growth, often also incorporating plant propagules to aid colonization and establishment of suitable wetland plants (Levine & Willard, 1990).

Action can also be taken to reduce the potential for wave creation, and lessen the impacts of waves on shorelines. Shelterbelts can be planted to reduce wind speed, and water depths can be reduced to decrease wave height. Artificial reefs can be built at a distance from the shoreline, generally placed in about 1 m depth of water. These installations break the waves, erosion is minimized and sheltered lagoons are created (Levine & Willard, 1990; Ferguson, 1999; Dallaire, 2001). In addition to this type of fixed barrier, the use of floating timber booms can also dampen wave energy before it reaches the shore (Andrews & Kinsman, 1990; Hall et al., 1993; Merritt, 1994). Once wave-reducing measures have been utilized, substrate support structures such as biodegradable geotextiles or other meshes provide further erosion protection for both substrate and vegetation (Cranfield University, 1999). These all help to reduce disturbance from wave impacts as well as enhancing fertility levels.

Shallow shoreline gradients will help prevent wave action, the transport of fine sediments and a consequently low fertility environment. If water levels cannot adequately be controlled in the main part of a waterbody, then stable conditions can be provided in marginal areas by the construction of bunds across bays and inlets (Reitan & Sandvik, 1996). These are used to retain a separately controlled regime or fixed depth of water in at least part of the site. Such areas may act as ‘source’ sites for emigration to the drawdown area, which may be a 'sink' for some species. On a smaller scale, the use of ridge and furrow or creation of hummocks and hollows in the drawdown zone can hold small pools of water of use to aquatic flora and fauna (Smith et al., 1987; Harper et al., 1990).

Even prior to climate change impacts, highly disturbed, low fertility severe shorelines will be devoid of vegetation. It has been hypothesized, however, that this may be due to the prevention of germination and establishment of juvenile plants (Gill & Bradshaw, 1971). If adult plants are introduced, they may be able to survive conditions that have blocked vegetation establishment, maintaining themselves despite stressed and disturbed conditions. Such artificial introductions can then help to reduce habitat severity, by introducing organic matter from leaf fall and preventing erosion of fine substrates by absorption of wave energy and the substrate binding properties of the root matrix provided (Little & Jones, 1979). Thus, revegetation schemes may be able to counteract the combined adverse effects of high disturbance and low fertility conditions.

A number of trials in different shoreline habitats have shown that a range of species are suitable for planting in areas subject to high levels of disturbance from water-level fluctuations (Little & Jones, 1979; Levine & Willard, 1990; Hellsten et al., 1996b; Fraisse et al., 1997). The use of appropriate species and management techniques, tailored to the situation and used at the correct time of year, can create plant communities that will survive and even benefit from flooding and exposure (Little, 1977; Allen & Klimas, 1986; Allen, 1988). An experimental revegetation, which showed mixed success, was undertaken by Hellsten et al. (1996b) on an eroded sandy shoreline in northern Finland. After the first summer, the average survival rates were around 45% due to the drying of seedlings, but these decreased during a high-water period until only 20% of the planted individuals were still alive. The best results were obtained with bottle sedge *Carex rostrata* Stokes, of which 30% survived and tea-leaved willows *Salix phylicifolia* L. with a survival rate of 80%. Fraisse et al. (1997) gained success in trials with eight species, but found that failures were caused by adverse hydrogical conditions or frost. Plants clearly need to have carefully controlled conditions, including water level management and quality substrate, during the early establishment phase.

Conclusion

It is anticipated that climate change will impact upon freshwater systems in a variety of ways through changes to parameters such as water temperatures, stratification processes, nutrient regime and dissolved gases (Dawson et al., 2001). However, given the fundamental importance of hydrological regimes to the functioning of aquatic systems it is likely that climate change impacts on this factor will have the most impact on sites, communities and individual species. The current paucity of research and guidance in this area is, therefore, frustrating. The biological effects of these environmental changes may include reductions in the numbers of target species, increase of invasive species, replacement of macrophyte vegetation with phytoplankton-dominated communities and an overall loss of biodiversity. These trends will prevent the effective conservation and restoration of wetlands (Mooij et al., 2005; Wei & Chow-Fraser, 2006). A greater understanding of the processes linking water-level fluctuations and littoral ecology and how these relate to climate change is a key issue that needs to be addressed in order to understand the possible compositions of future ecosystems and to develop suitable adaptive strategies to cope with climate change impacts (Gasith & Gafny, 1990; Dawson et al., 2001). Across Europe, the potential impacts of climate change on wetlands will become increasingly important with the implementation of the Water Framework Directive (Directive 2000/60/EC), which requires all waterbodies to attain 'Good Ecological Status' by 2015. The opposing forces of climate change, increasing water use and this legislation will place large demands on water resource managers, nature conservation bodies and society in general. If biodiversity, landscape and amenity elements are to be protected alongside these urgent concerns, the promotion of clear science-based management techniques will be critical (Sutherland et al., 2004). A shift in management thinking will also be required, with a move away from the paradigm that aims to ensure ecosystem stability, towards one able to predict and manage short and long-term change.

This article attempts to bring together, into one framework, some of the science relating to shoreline vegetation, the potential effects of climate change on wetlands and an introduction to practical adaptation methods. It is hoped that the use of simple models that incorporate aspects of ecology, such as the one proposed here using life history traits, will provide a valid structure for hypothesis generation and testing and will allow good habitat management decisions to be made and implemented in coming years on lakes, reservoirs and other wetlands of conservation value.

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WATER-LEVEL FLUCTUATIONS

The impact of water-level regulation on littoral macroinvertebrate assemblages in boreal lakes

Jukka Aroviita · Heikki Hämäläinen

Abstract Regulation of lake water level for power production and flood control is among the major anthropogenic disturbances in boreal aquatic ecosystems. In Finland, over 300 lakes, representing one third of the total inland water area of the country, are artificially regulated. To study the effects of regulation on lake littoral macroinvertebrate communities, samples were taken from upper stony littoral and from lower soft bottom littoral habitats of 11 lakes with different regulation amplitudes (wintertime fall in water level 1.19–6.75 m). Twelve unregulated (wintertime fall in water level 0.11–0.55 m) lakes with otherwise similar characteristics were used as a reference. Non-metric Multidimensional Scaling ordinations showed that the composition of macroinvertebrate assemblages was strongly associated with the amplitude of water level regulation. Taxon richness also decreased with increasing intensity of regulation. Freezing and flushing of sediments in late winter are probably the most important factors leading to the impoverished littoral macroinvertebrate fauna. Invertebrates with long life cycle seem to be particularly vulnerable to unnatural water level fluctuation. Our results show that regulation of water level has a major impact on functionally significant lake littoral macroinvertebrates.

Keywords Boreal lakes · Littoral · Macroinvertebrates · Species richness · Taxonomic composition · Water-level regulation

Introduction

Altered water-level fluctuation is among the major anthropogenic disturbances in lake and river ecosystems (e.g. Richter et al., 1997; Coops et al., 2003). The construction of dams and reservoirs for hydropower production and flood control, water abstraction for irrigation, along with other water uses, has changed the natural hydrologic regimes of freshwaters worldwide (Dynesius & Nilsson, 1994). Climate change is expected to accentuate these changes (Mortsch & Quinn, 1996), which can have significant negative impacts on aquatic biota. Especially susceptible to altered variation of water level is the littoral zone of lakes, where organisms may be affected directly by desiccation and indirectly by decrease in habitat availability and food resources (Gasith & Gafny, 1990).

In Finland, over 300 lakes, representing one-third of the total inland water area of the country, are artificially regulated, mainly for hydropower

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Ecological Effects of Water-level Fluctuations in Lakes

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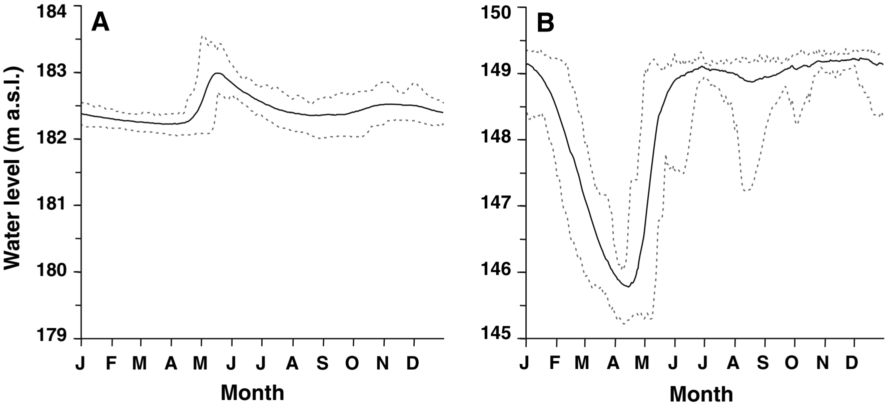

Fig. 1 Examples of annual water-level fluctuation in (**a**) an unregulated reference lake (Lake Änättijärvi, mean wintertime fall in water level 0.32 m) and (**b**) a regulated lake (Lake Iso-Pyhäntä, mean wintertime fall in water level 3.50 m). The solid line represents the mean water level in 1990–1999 and the dashed lines the minimum and maximum during the period. Data are from the Finnish Environment Institute

production. The natural annual water-level fluctuation in these boreal lakes is characterised by a spring flood caused by melting of snow (Fig. 1a). During the remainder of the annual cycle, the water level tends to stay relatively stable, decreasing only slightly during winter. In regulated lakes, however, the hydrologic regime is typically close to the inverse (Fig. 1b). During winter, the water level is drawn down because of high energy demands and because of decreased water inflow from the catchments. In spring, the lakes are refilled with water from the melting snow, so the natural flood peak is either lacking or is delayed and much decreased. From early summer until the next winter the water level is usually maintained at a relatively stable level. At the start of the regulation of Finnish lakes, the summer water level was usually elevated by 0.5–3.5 m from the natural level and has thereafter been lowered by 2–7 m in each winter (Alasaarela et al., 1989). In these boreal lakes with a thick ice cover during winter, exposure of the littoral substrate to air or ice at subzero temperatures is undoubtedly among the most important consequences of regulation affecting the biota (Palomäki & Koskenniemi, 1993).

The regulation of water level has been shown to impoverish communities of littoral macrophytes (e.g. Quennerstedt, 1958; Hellsten, 2001; Keto et al., 2006), macroinvertebrates (e.g. Grimås, 1961) and fish (Sutela & Vehanen, 2008). Existing knowledge of the effects on macroinvertebrate communities is largely based on a few case studies (e.g. Furey et al., 2006; Valdovinos et al., 2007); more general patterns in structural responses of communities to water-level regulation, based on multi-lake comparisons, have not been well documented (but see Smith et al., 1987). Also, relatively little is still known about the causes for the detected responses. Such knowledge is becoming increasingly important not least due to the obligations set by the European Union Water Framework Directive (WFD) to assess, monitor and manage the status of surface waters (European Commission, 2000).

In this study, we examined the effects of regulation of lake water level on littoral macroinvertebrate assemblages in two depth zones (habitats) of boreal lakes. We compared the taxonomic composition, numerical abundance and diversity of macroinvertebrate assemblages between regulated lakes with different regulation amplitudes, and unregulated reference lakes. We hypothesised that all these community characters would be impacted by regulation, and that the impact would increase with the amplitude of regulation and be greater in the upper than in the deeper lower littoral zone.

Materials and methods

Study lakes

The study lakes ($n = 23$) are located in the boreal coniferous zone in eastern and north-eastern Finland

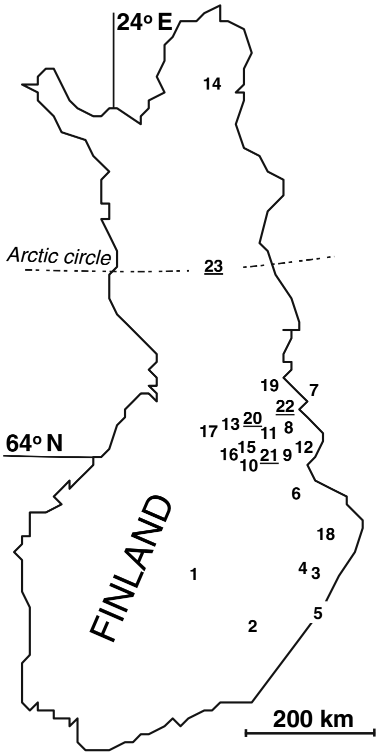

Fig. 2 Map showing location of the study lakes. For lake numbers, see Table 1. The numbers of the most heavily regulated lakes (wintertime fall in water level >3 m) are underlined

(one in Russia) between 61°44′–68°56′ N and 26°33′–30°44′ E (Fig. 2). The lakes represent medium to large sizes (lake surface area 11–1040 km^2) and clear to humic water (colour 10–90 mg Pt l^{-1}) and have mean depths between 4 and 14 m (Table 1). The lakes are oligo-mesotrophic with total phosphorus concentration between 4 and 19 μg l^{-1}. All lakes are ice- and snow-covered in winter for six to eight months each year. Apart from water level regulation, the lakes are relatively unimpacted by human activity with only some forestry and agriculture in their catchments (mean cover of developed and cultivated land 0.3 % [0–1.8%] and 4.2%, [0–12.4%], respectively).

Eleven of the study lakes have been exposed to moderate to heavy water-level regulation for power production mainly since the 1940s to 1960s. The amplitude of water-level fluctuation (REG.AMP) in the regulated lakes, measured as the mean wintertime fall (drawdown) in water level in 1980–1999, ranges between 1.19 and 6.75 m (Table 1). The twelve remaining lakes, referred to as the reference lakes, are unregulated, with maximum natural wintertime fall in water level 0.55 m (Table 1).

Macroinvertebrate data

The macroinvertebrate samples were collected in September–October in 2002–2004 from 16 of the lakes and supplemented by additional literature data from the seven remaining lakes (Table 1). Data were collected from two distinct habitats: upper stony littoral (6 reference lakes, 10 regulated lakes) and lower soft bottom littoral (11 reference lakes, 11 regulated lakes). For both habitats, three well-separated sites were sampled in each study lake. From each upper littoral site, three replicate 20-s kick-samples, each representing a 1-m stretch, were taken with a 0.5 mm mesh hand net at ca 0.4 m depth (Johnson & Goedkoop, 2002). From the lower littoral sites, three replicate lifts with an Ekman grab (surface area 270 cm^2) were taken at ca 2 m depth. Where both habitats were sampled, lower littoral samples were taken as close as possible to the upper littoral station. All samples were sieved with 0.5 mm mesh and preserved in 70% ethanol in the field. In the laboratory, all macroinvertebrates were sorted, identified to the level of species or genus (except for the Oligochaeta, mites and dipteral families) and counted. From the literature data, only observations with similar sampling effort and taxonomic resolution were accepted. Some taxonomic harmonisation was necessary, however. All nine replicates per lake and habitat were pooled for the analyses. To express numerical abundances, the species counts were converted to numbers of individuals per sample and to densities (ind m^{-2}) in the upper and lower littoral, respectively.

Numerical analyses

Taxon richness and abundance were correlated (Pearson correlation, *r*) with the regulation amplitude. Furthermore, ANOVA, followed by a Tukey-Kramer post-hoc test, was used to compare taxa richness and abundance between reference lakes, lakes with small regulation amplitude (REG.AMP < 3 m) and those with large regulation amplitude (REG.AMP > 3 m) within each habitat. ANOVA was conducted in SPSS 12.0 (SPSS Inc., 2003).

Table 1 Some physical and chemical parameters of the unregulated and regulated study lakes

No	Study lake	REG.AMP (m)	AREA (km^2)	ALT (m a.s.l.)	M.DE (m)	COND (mS m^{-1})	pH	SEC (m)	CHLA (µg l^{-1})	TP (µg l^{-1})	TN (µg l^{-1})	COL (mg Pt l^{-1})
Unregulated reference lakes												
1	Konnevesi[2, g]	0.11	189	95	10.3	4.4	7.2	5.3	2.9	7	340	25
2	Pihlajavesi[2, a]	0.17	713	76	11.4	4.8	7.0	3.5	3.2	9	420	35
3	Onkamo[2, b]	0.17	45	77	13.0	na	7.4	4.4	4.1	13	409	17
4	Pyhäselkä[2, c]	0.18	361	76	8.8	3.5	6.8	2.8	3.7	12	416	65
5	Ka Pyhäjärvi[2, d]	0.19	207	80	7.6	5.5	7.4	6.0	2.2	6	263	10
6	Kuohatti[1, e]	0.28	11	162	5.6	2	6.4	3.0	4.3	11	271	70
7	Kuittijärvi[2, f]	na*	198	ca 100	9.6	2.5	6.7	2.8	3.5	11	268	40
8	Änättijärvi	0.32	24	183	9.7	2.4	6.8	2.5	4.9	9	300	60
9	Lentua	0.40	78	168	7.4	2.4	6.8	2.5	4.0	9	320	50
10	Jormasjärvi	0.41	20	145	5.8	2.8	6.3	2.0	5.4	13	450	90
11	Kellojärvi	0.43	22	161	5.0	2.4	6.7	1.7	4.9	16	336	80
12	Lammasjärvi	0.55	47	163	4.2	2.3	6.8	1.7	3.9	13	283	60
Mean (upper, $n = 6$)		*0.40*	*34*	*164*	*6.3*	*2.4*	*6.6*	*2.2*	*4.6*	*12*	*327*	*68*
Mean (lower, $n = 11$)		*0.29*	*173*	*120*	*8.4*	*3.3*	*6.9*	*3.2*	*3.9*	*11*	*346*	*48*
Regulated lakes												
13	Iijärvi	1.19	22	133	5.2	2.7	6.7	2.0	7.7	16	320	70
14	Inari[2]	1.21	1040	119	14.3	2.9	7.2	7.5	0.9	4	160	10
15	Kiimasjärvi	1.43	41	138	3.8	2.5	6.6	1.6	5.7	19	320	54
16	Nuasjärvi	1.52	96	138	8.5	2.7	6.8	2.3	6.6	14	340	60
17	Oulujärvi	1.54	887	122	8.4	2.9	6.9	2.6	5.6	14	345	57
18	Koitere	1.76	164	143	8.2	1.9	6.6	2.9	3.1	11	300	70
19	Kiantajärvi	3.12	188	190	7.6	2.4	6.8	2.6	4.8	11	280	60
20	Iso-Pyhäntä	3.50	12	149	6.9	2.2	6.5	2.6	na	16	350	85
21	Ontojärvi	3.51	105	159	5.8	2.3	6.7	2.1	7.3	15	335	60
22	Vuokkijärvi	4.71	51	190	5.0	2.3	6.8	1.6	15.0	18	365	70
23	Kemijärvi	6.75	206	149	5.5	3.4	7.2	1.9	6.7	16	310	80
Mean (upper, $n = 10$)		*2.91*	*177*	*151*	*6.5*	*2.5*	*6.8*	*2.2*	*6.9*	*15*	*327*	*67*

Table 1 continued

No	Study lake	REG.AMP (m)	AREA (km^2)	ALT (m a.s.l.)	M.DE (m)	COND ($mS\ m^{-1}$)	pH	SEC (m)	CHLA ($\mu g\ l^{-1}$)	TP ($\mu g\ l^{-1}$)	TN ($\mu g\ l^{-1}$)	COL ($mg\ Pt\ l^{-1}$)
Mean (lower, $n = 11$)		*2.75*	*256*	*148*	*7.2*	*2.6*	*6.8*	*2.7*	*6.3*	*14*	*311*	*61*

Surface water chemistry values are median summer (June–August) values measured principally in 1990–1999. The mean in both habitat datasets is given in italic. Lake numbers refer to Fig. 2. Data are from the Finnish Environment Institute

REG.AMP = mean wintertime fall in water level in 1980–1999, AREA = lake surface area, ALT = altitude, M.DE = mean depth, COND = conductivity, SEC = Secchi depth, CHLA = chlorophyll *a*, TP = total phosphorus, TN = total nitrogen, COL = colour value

Macroinvertebrate data: [1]only from upper stony littoral, [2]only from lower soft bottom littoral, [a]Hynynen et al. (1997); [b]Liljaniemi (1998); [c]Tolonen et al. (2001), [d]Virnes (2005) [e]Tolonen et al. (2003); [f]Aroviita et al. (2006), [g]Särkkä (1983)

* Data not available, mean value of reference lakes used in analyses

Taxonomic composition of macroinvertebrate assemblages was investigated with the non-metric multidimensional scaling (NMS) ordination method, which is based on ranked distances and is well suited for non-normally distributed ecological data (McCune & Grace, 2002). NMS was run separately within both habitats using log(x + 1) -transformed macroinvertebrate abundance data. We did not include taxa with sporadic occurrence (present only in one lake and habitat) in the ordinations, since they are uninformative in grouping the lakes according to the similarity of the assemblages. We used Bray-Curtis as the distance measure and conducted 50 runs with randomised data using autopilot mode ("slow and thorough"). A three-dimensional solution was chosen for plotting, as the number of dimensions did not lower the stress value. We assessed the importance of the lake descriptors in explaining the observed patterns in macroinvertebrate community structure by Pearson correlation (*r*) between descriptors of lake character (Table 1) and lake scores of each NMS dimension.

We used indicator species analysis (ISA, Dufrêne & Legendre, 1997) to detect if any individual taxa were indicative of unregulated or regulated lakes. In ISA, within both habitats, an indicator value (INDVAL) was calculated for each taxon *i* in each lake group *j* (i.e. either reference or regulated lake groups) using the relative abundance (A_{ij}) and relative frequency of occurrence (B_{ij}), as follows:

$$INDVAL_{ij} = A_{ij} \times B_{ij} \times 100 \tag{1}$$

INDVAL describes the degree of association between the presence and abundance of a given taxon and a specific lake group, and a value of 100 represents perfect indication, i.e. all observations are confined to a single group, where relative frequency is 1. The null hypothesis that a taxon's indicator value did not differ from what could be expected by chance was tested using Monte Carlo technique with 1000 permutations ($\alpha = 0.05$). We used PC-Ord 4.37 software (McCune & Mefford, 1999) for NMS and ISA calculations.

Results

Taxon richness and abundance

A total of 108 taxa were observed, of which 86 occurred in the upper littoral and 68 in the lower littoral habitat.

The taxon richness showed a significant negative correlation with regulation amplitude in both upper ($r = -0.67$, $P = 0.005$) and lower littoral ($r = -0.55$, $P = 0.01$). However, the relationship was not linear; the number of taxa decreased rapidly first and then stabilised with increasing amplitude (Fig. 3).

Taxon richness in the upper littoral differed significantly among the three lake groups (Table 2). It was highest in the reference lakes, followed by lakes with small regulation amplitude, and lowest in lakes with large regulation amplitude (Fig. 3, Table 2). Post hoc comparisons (Tukey-Kramer) suggested that there are fewer taxa in heavily regulated lakes than in unregulated lakes (Table 2). The difference between reference lakes and lakes with small regulation amplitude was close to significant (Tukey-Kramer, $P = 0.095$).

Taxon richness in the lower littoral also differed among the three lake groups (Table 2). Taxon richness was highest in the reference lakes, followed by lakes with small regulation, and heavily regulated lakes (Fig. 3, Table 2). Lakes with large regulation amplitude had significantly fewer taxa than the reference lakes, but no difference between lakes with small regulation amplitude and reference lakes was evident (Table 2).

The abundance of macroinvertebrates was not significantly related to regulation amplitude in either upper ($r = -0.27$, $P = 0.32$) or lower ($r = -0.25$, $P = 0.26$) littoral (Fig. 3). The abundance in the upper littoral ranged from 211 ind. per sample^{-1} in reference lakes to 130 ind. sample^{-1} and 116 ind. sample^{-1} in lakes with small and large regulation amplitudes, respectively (Table 2). The average

Fig. 3 Relationships between the amplitude of water-level regulation (REG.AMP) and descriptors of macroinvertebrate taxon richness (S), abundance (upper: ind. per sample, lower: ind. m^{-2}) and taxonomic composition (NMS1) in the upper and lower littoral zone in unregulated (open symbols) and regulated (black symbols: dots: regulated < 3 m, triangles: regulated > 3 m) boreal lakes. Note that the scales of S and abundance differ

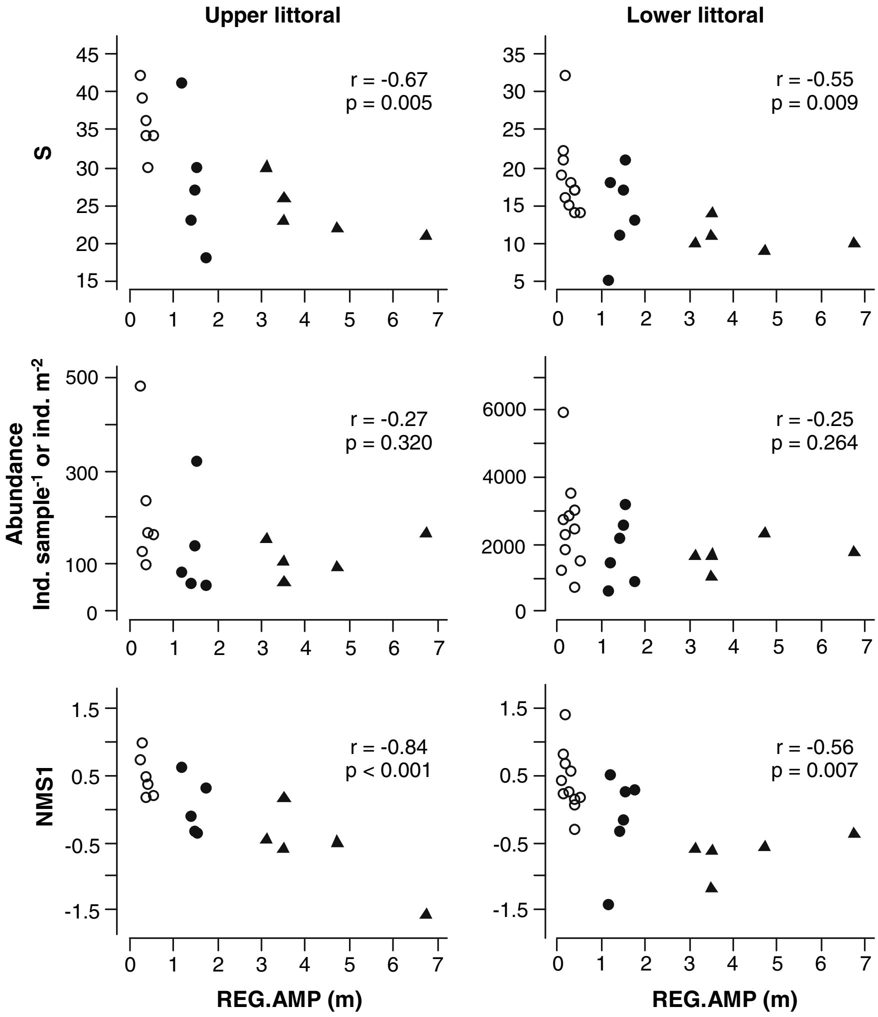

Table 2 Comparison (mean, range and ANOVA statistics) of macroinvertebrate taxon richness (S) and abundance (ABU) among the lake groups within the upper and lower littoral habitat

	Unregulated reference lakes	Regulated lakes		ANOVA	
		REG.AMP < 3 m	REG.AMP > 3 m	F	*P*
Upper littoral					
n	6	5	5		
S	36 (30–42)	28 (18–41)	24 (21–30)*	5.664	0.017
ABU (ind. sample^{-1})	211 (100–479)	130 (52–317)	116 (62–167)	1.247	0.319
Lower littoral					
n	11	6	5		
S	19 (14–32)	14 (5–21)	11 (9–14)*	4.896	0.019
ABU (ind. m^{-2})	2531 (716–5902)	1787 (580–3136)	1681 (1021–2300)	1.307	0.294

*Significantly different from reference lakes (Tukey-Kramer post hoc comparisons; $P < 0.05$)

REG.AMP = regulation amplitude

abundance in the lower littoral was 2531 ind. m^{-2} in reference lakes and 1787 ind. m^{-2} and 1681 ind. m^{-2} in lakes with small and large regulation amplitude, respectively. The numerical abundance of macroinvertebrates did not differ among the lake groups in either upper or lower littoral (Table 2).

Taxonomic composition

In the NMS ordination space based on the upper littoral macroinvertebrate assemblages most of the regulated lakes, including those with small regulation amplitude, were grouped separately from the reference lakes (Fig. 4). The most heavily regulated lakes were furthest away from the reference lakes along dimension 1 (NMS1) in this output, indicating the greatest differences in their assemblages. Accordingly, NMS1 was most strongly correlated with the regulation amplitude ($r = -0.84$, $P = 0.00004$, Fig. 3), as also indicated by the longest joint plot arrow in Fig. 4. NMS1 was also related to COND ($r = -0.56$, $P = 0.02$), and pH ($r = -0.51$, $P = 0.04$). NMS3 was also correlated with REG.AMP ($r = -0.57$, $P = 0.02$).

Altogether 11 upper littoral taxa were associated with unregulated reference lakes (Table 3), as indicated by ISA (Monte Carlo permutation test, $P < 0.05$). Species typical of reference lakes included e.g. the riffle beetles *Oulimnius tuberculatus* and *Limnius volckmari,* of which the former occurred in all reference lakes and both were absent from all regulated lakes. The mayflies *Ephemera vulgata* and *Centroptilum luteolum* and the caddisfly *Cyrnus trimaculatus* occurred in all but one of the reference lakes and in 1 or 2 of the least regulated lakes, whereas the six remaining taxa were sporadically encountered also from the heavily regulated lakes. There were no taxa indicative of regulated lakes.

Similar patterns were observed in NMS in the lower littoral as in the upper littoral (Fig. 4). Almost all regulated lakes were grouped separately from the reference lakes and along NMS1 so that the most heavily regulated lakes were furthest from the reference lakes. NMS1 was negatively correlated with (in increasing order of significance) REG.AMP, ALT, CHLA, COL and TP (range of *r*: from -0.56 to -0.68, $P \leq 0.007$) and positively to COND, M.DE, pH and SECCHI (range of *r*: from 0.55 to 0.60, $P \leq 0.01$). NMS3 was also associated with TP ($r = -0.43$, $P = 0.04$).

ISA identified altogether six significant lower littoral indicator taxa for reference lakes (Table 3), which were characterised by three of the same taxa (the mayflies *E. vulgata*, *Leptophlebia* spp. and *Caenis horaria*) as in the upper littoral zone. Here *E. vulgata* and *C. horaria* occurred in all reference lakes, in most of the moderately regulated lakes and in 1 or 2 of the heavily regulated lakes, whereas *Leptophlebia* was confined to 5 of the reference lakes. The alderfly *Sialis* spp. and the caddisfly *Molanna angustata* were absent from the heavily regulated lakes, whereas the sphaerid clams, *Pisidium* spp., occurred in all except one lake but were less abundant in regulated lakes. None of the taxa were indicative of regulated lakes.

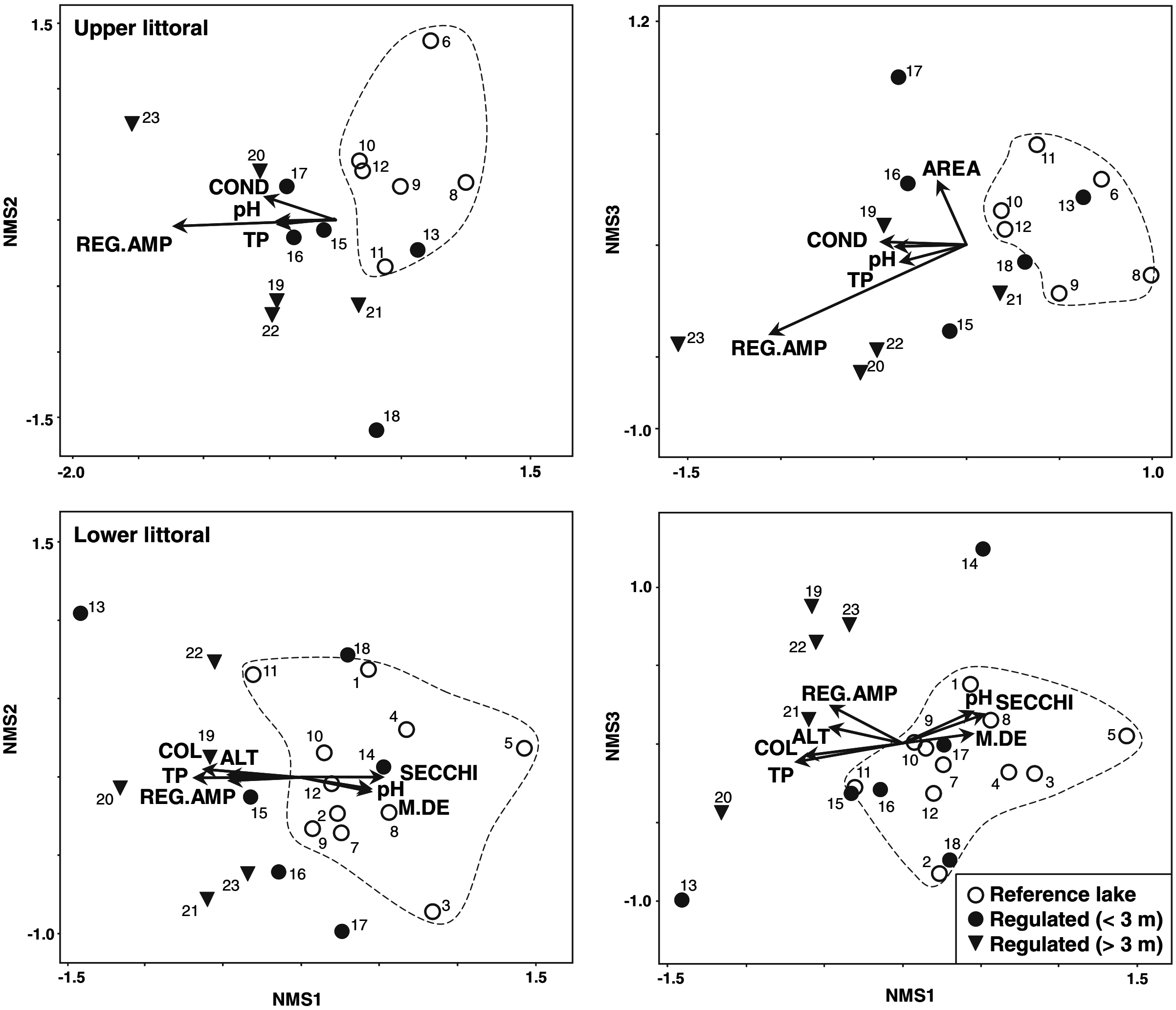

Fig. 4 Distribution of the study lakes in a three-dimensional (NMS1, NMS2 and NMS3) ordination space based on log-transformed macroinvertebrate abundance data from upper (final stress value = 7.61) and lower (final stress value = 14.47) littoral zones from unregulated reference (open symbols) and regulated (black symbols, two groups of regulation amplitude) boreal lakes. A cut-off value of $r^2 > 0.2$ was used to include variables in the joint plot. For variable abbreviations and lake numbers, see Table 1. The respective area occupied by the reference lakes is delineated by a dashed line

Discussion

Richness and abundance

The richness of littoral invertebrate fauna in the most strongly regulated lakes was significantly lower than in the unregulated lakes, and it decreased consistently with increasing intensity of regulation in both upper and lower littoral. This is consistent with previous findings from lakes in more temperate areas (e.g. Hynes, 1961; Smith et al., 1987). However, we did not detect any significant effect on numerical abundance of invertebrates. This contrasts with results previously reported from comparisons between regulated and unregulated lakes. In Lake Blåsjön (regulation amplitude 6 m) in Sweden, the density of fauna at less than 3 m depth was ten times lower than in a nearby unregulated lake (Grimås, 1961). Benson & Hudson (1975) noted a marked increase in density of invertebrates with reduced drawdown in water level in a Missouri River Reservoir. A maximum abundance of littoral invertebrates in regulated lakes has often been observed immediately below the regulated zone (i.e. the

Table 3 Results of indicator species analysis (ISA). Indicator values are shown for 14 taxa indicating significantly ($p < 0.05$) the unregulated reference lakes in either of the two or both habitats. The significance of the indicator values was tested using a Monte Carlo randomization test with 1000 permutations. Taxa are in order of decreasing significance in the upper littoral dataset

Indicator taxon	Upper littoral	Lower littoral
Oulimnius tuberculatus	100	
Ephemera vulgata	75	67
Cyrnus trimaculatus	75	
Leptophlebia spp.	64	46
Turbellaria	76	
Cyrnus flavidus	67	
Centroptilum luteolum	67	
Caenis horaria	66	70
Polycentropus flavomaculatus	68	
Limnius volckmari	50	
Hydroptila spp.	63	
Sialis spp.		56
Pisidium spp.		61
Molanna angustata		51

drawdown limit) where organic matter tends to accumulate (Grimås, 1961; Tikkanen et al., 1989; Palomäki & Koskenniemi, 1993; Furey et al., 2006). In natural lakes the benthic organic matter and abundance of invertebrates usually peaks at a shallower zone (e.g. Särkkä, 1983). This could partly explain the relatively high lower littoral (2 m) density in our study lakes with small regulation amplitude (~ 1–2 m). Nevertheless, it does not explain the observed relatively high density in the upper littoral of regulated lakes, or the relatively high lower littoral densities in lakes with larger regulation amplitude. It should also be noted that we conducted sampling in autumn, four months after the end of the drawdown. A more severe effect on abundance would likely be seen in the spring and summer, when many taxa have not yet colonised the regulated zone (Grimås, 1961). The effect might, however, be stronger on biomass of invertebrates than on numerical abundance if regulation affected large taxa more. Tikkanen et al. (1989) reported 2.5 times lower biomass, but 1.6 times lower density at 2 m depth in Lake Ontojärvi (regulation amplitude 3.5 m, see Table 1) than in unregulated Lake Lentua, whereas the corresponding difference in density according to our data from the same sites was 1.3. Also Palomäki (1994) suggested a strong negative association between the regulation amplitude and biomass of benthic invertebrates in soft littoral bottoms of Finnish lakes.

Taxonomic composition

The taxonomic composition of littoral macroinvertebrates was notably different between the regulated and unregulated lakes. As demonstrated by the NMS ordination, the taxonomic composition was strongly related to the amplitude of regulation, and perhaps surprisingly, the assemblages differed from those in the reference lakes even in lakes with smallest regulation amplitude (1.2–1.8 m), indicating a low effective threshold for the water level fluctuation in boreal lakes. This contrasts with results from Scotland where lochs with <5 m fluctuations had littoral communities similar to natural ones (Smith et al., 1987). The littoral fauna might be more susceptible to regulation in boreal lakes than in lakes of more temperate regions because the regulated zone is more exposed to subzero temperatures and subsequent freezing.

Many taxa, mainly Ephemeroptera, Trichoptera, Coleoptera or Megaloptera, were missing or occurred in low numbers in the regulated lakes. Strikingly similar effects of regulation on the littoral fauna have been reported elsewhere. For example, seven identical or closely related taxa (*Caenis luctuosa*, *Ephemera danica, Leptophlebia marginata*, *Sialis* spp., *P. flavomaculatus, O. tuberculatus* and *L. volckmari*) that were identified as indicative of reference lakes in our study (i.e. sensitive to water-level fluctuation, Table 3) had disappeared from a Welsh lake Llyn Tegid, five years after the onset of water-level regulation (amplitude 4.3 m) (Hynes, 1961), and six of them re-colonised the lake after amelioration of the regulation practice (Hynes & Yadav, 1985). Also Grimås (1961) noted that *Sialis lutaria*, among many other large-sized insect larvae, was missing from regulated Lake Blåsjön.

The species sensitive to regulation represent various higher taxa of invertebrates and it is difficult to find characters unifying them and thus help in deciphering the mechanistic explanation for their sensitivity. However, four taxa identified as susceptible to regulation (*O. tuberculatus*, *E. vulgata*, *L. volckmari* and *Sialis* spp.) are the only semivoltine (life cycle taking two or more years) invertebrates in the dataset, which suggests that a long life cycle makes invertebrates particularly vulnerable to unnatural water-level fluctuation. Perhaps species with an extended aquatic phase cannot adjust their life history events to the altered hydrologic regime of regulated lakes, or they are in danger simply because they cannot escape the disturbance events in time but have to experience them repeatedly during their life cycle. Species that are more or less permanently attached to the substrate (e.g. the net-spinning caddisflies *Cyrnus* and *Polycentropus*) might be at particular risk because they are not able to escape the retreating water levels or at least it causes significant extra costs. Changes in habitat structure (e.g. due to flushing of sediments) are also likely to have an effect on certain species, such as the burrowing *Ephemera* -mayflies (Hynes & Yadav, 1985).

The impacts of regulation on water quality (e.g. nutrient status) are considered of minor importance (Marttunen & Hellsten, 2003; Turner et al., 2005). However, this effect cannot be wholly ruled out, since limited data are available on water quality from the regulated Finnish lakes from the period preceding the regulation projects. In our dataset CHLA ($r = 0.56$, $P = 0.03$, upper littoral; $r = 0.61$, $P < 0.01$, lower littoral) and TP ($r = 0.46$, $P = 0.07$, upper littoral; $r = 0.50$, $P = 0.02$, lower littoral) correlated positively with the mean wintertime fall in water level. This might indicate a slight increase in nutrient status due to regulation, which in turn could partly explain the effects on littoral invertebrates.

More systematic investigation of species trait structures (e.g. Statzner et al., 2001) in natural and regulated lakes might help to identify those life history features that make the invertebrates vulnerable to water level regulation, to understand mechanisms of effects and thence to help in developing regulation practices that are less harmful to biota.

Conclusions

We observed clear differences in the littoral macroinvertebrate faunas between the unregulated reference and regulated lakes with lower richness and absence of many insect larvae in regulated lakes. As expected, the impact of regulation on richness and community composition was slightly greater in the upper littoral than in the lower littoral as suggested by the stronger correlation with REG.AMP (Figs. 3 and 4). The lower littoral was inundated during the winter drawdown in lakes with small regulation amplitude but not in lakes with large regulation amplitude, which could explain why the impact of regulation was not as strong in the lower littoral than in the upper littoral.

Littoral macroinvertebrates have a significant role in lake food webs, e.g. in recycling detrital material (France, 1995) and as fish food, and thus their reduced abundance or altered composition may have important consequences in the lake ecosystem. For example, Sutela & Vehanen (2008) reported a significant decrease in contribution of invertivorous fish in the littoral zone of regulated lakes, which is a likely consequence of changes in littoral invertebrate communities. Macroinvertebrates are also among those organisms that are to be used in assessment and monitoring of the ecological status of lakes according to the WFD (European Commission, 2000). The observed relatively large impact on richness and species composition suggests that at least the most heavily regulated lakes do not meet the targeted "good" ecological status (European Commission 2000). Much of the variation in littoral macroinvertebrate communities seems to be predictable from the winter drawdown, and as soon as the metrics to be used in the classification of ecological status and the class boundary values for them have been established, it will probably be possible to model the target level of water level regulation for attaining the defined environmental objectives. Relatively fast recovery of the littoral fauna could be expected, if lake management practices are changed sufficiently (Hynes & Yadav, 1985).

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Quantitative trends of zebra mussels in Lake Balaton (Hungary) in 2003–2005 at different water levels

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Abstract During the extremely dry period between 2000 and 2003, the water level of Lake Balaton decreased by 82 cm and 80% of the stony littoral, an important habitat for the zebra mussel (*Dreissena polymorpha*), became dry. A recovery period started in 2004 due to intense precipitation, which increased water levels in the lake. Seasonal and spatial variations of the relative abundance, population density, population structure and biomass of the zebra mussel and the relative abundance of the amphipod *Chelicorophium curvispinum* were monitored in the period of 2003–2005 at four different shoreline sections and in two different portions (on the bottom and near the surface portion of the rip-rap) of Lake Balaton. Along with these studies, a quantitative survey of mussel larvae found in the plankton and of the abundance of mussel feeding diving ducks were made. As a consequence of the water level fall, on the dried part of the stony littoral, numerous zebra mussel druses perished. Following the dry period in early 2004, the relative abundance of the mussel on the bottom stones was smaller than in 2003 and the bottom community was dominated by *C. curvispinum.* By the end of 2004 and during 2005, the water level returned to normal and the surfaces of the reinundated stones were conducive to the successful colonization of zebra mussels. Hence, they returned as the dominant fauna in 2005. The stones near the surface might provide a new substrate for the recruitment of zebra mussels, probably offering more suitable substrata for the settlement in 2005 than in 2003. Therefore, the new substrata available in 2005 may have encouraged better and more rapid zebra mussel colonization than before. Zebra mussels may be better competitors for new space than *C. curvispinum.* A minor change of water-level fluctuation in 2005 and the reduction in population size of the mussel feeding waterfowl could have contributed to the intensive spread of zebra mussel by 2005.

Keywords Zebra mussels (*Dreissena polymorpha*) · Littoral zone · Drought · Water-level changes · Veliger · Waterfowl

Introduction

Lake Balaton is the largest shallow lake in Central Europe (mean depth: 3.2 m; area: 596 km^2; shoreline

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Ecological Effects of Water-Level Fluctuations in Lakes

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240 km). The lake underwent an eutrophication period between 1960 and 1980s (Herodek et al., 1988), which was followed by the re-oligotrophication process. A trophic gradient still exists along the longitudinal axis of the lake (Padisák, 1994, 2001; Padisák and Reynolds, 1998; Tátrai et al., 2000; Vörös et al., 2000).

The water level of the lake is artificially regulated with the establishment (1863) of the Sió Canal. From 1997, it has been regulated between 70 and 110 cm (minimal and maximal level) (Varga, 2005). However, from the summer of 2000, the water level has significantly decreased due to evaporation from three extremely dry summers. By October of 2003, the water level was 23.7 cm, after one of the most driest periods (2000–2003) of the lake history (Varga, 2005). Similar low water levels were also recorded in 1921, 1949 and 1961, but the unequivocal reason for the drastic water level fall in 2003 was the extremely dry and hot weather between 2000 and 2003 combined with the closure of the Sió Canal from 2000 to 2005 (Varga, 2005).

As a consequence of water-level fluctuation, the entire littoral zone shifts. Total light penetration changes, and near bottom light penetration and vertical zonation of the benthos changes (Palomäki, 1994). The most visible changes, in response to the changes in light levels, were mainly observed in the littoral zone, where large numbers of benthic animals co-exist (Muskó et al., 2007). One of those is the Ponto-Caspian invasive exotic species, the zebra mussel *Dreissena polymorpha* (Pallas, 1771).

The zebra mussel is not the only exotic species in Lake Balaton. It co-occurs with the amphipod *Chelicorophium curvispinum* (Sars, 1895), originating from the Black and Caspian seas as in River Danube (Oertel and Nosek, 2003). They were accidentally introduced to the lake via the River Danube—Sió Canal—Lake Balaton system in the early 1930s (Grossinger, 1791; Sebestyén, 1934, 1938). According to van der Velde et al. (1994), the invasion of *C. curvispinum* resulted in drastic reduction of zebra mussel abundance in the Rhine River.

After the initial invasion, the zebra mussel spread rapidly and invaded the entire lake within 2–3 years (Sebestyén, 1937). Its abundance usually fluctuated (Sebestyén, 1935, 1937, 1938; Entz & Sebestyén, 1946; Sebestyén et al., 1951; Bíró & Gulyás, 1974; Entz, 1981; Ponyi, 1981) and presently, it is a dominant invertebrate on different substrata in Lake Balaton (Lakatos et al., 2001; Balogh & Muskó, 2004; Muskó & Bakó, 2005).

The soft bottom sediment of Lake Balaton (Lóczy, 1894; Miller & Wagner, 1978) is unsuitable for colonization of zebra mussels. However, the 105-km-long artificial rocky shoreline, which was constructed between the 1930s and 1965 is ideal for the colonization of the mussels. They can rapidly spread to newly-opened littoral surfaces because of the abundant pelagic veliger larvae.

Regular monitoring of the invertebrate fauna of Lake Balaton has shown that mussel populations can reach as much as 78% of all invertebrates on submerged macrophytes, and it strongly dominates the sessile invertebrate fauna of the reed belts and other subsurface objects (Muskó & Russo, 1999; Lakatos et al. 2001; Muskó et al., 2003; Muskó & Bakó, 2005).

Because of the high turnover rate of the mussels, their colonies could have an enormous effect on the aquatic ecosystem, shifting the abundance of planktonic bacteria (Cotner et al., 1995; Silverman et al., 1996), phyto- and zooplankton (Shevtsova et al., 1986; MacIsaac et al., 1991, 1995; Lavrentyev et al., 1995; Balogh & Muskó, 2006), and even suspended inorganic material (Reeders & bij de Vaate, 1990; Bunt et al., 1993; G.-Tóth et al., 1999). Mussel colonies improve water transparency by filtering out particulates (both living and dead). This results in an increase of light reach in the bottom, which is beneficial to the benthic community and the submerged macrophytes (Dermott & Munawar, 1993; Griffiths, 1993; Skubinna et al., 1995). Also, pseudofaeces production of *D. polymorpha* can affect both the structure and metabolic function of the benthic microbial community (Lohner et al., 2007), initiating new food chains in the sediment of Lake Balaton as described from other lakes (Stanczykowska et al., 1976). For another mussel, *Bathymodiolus platifrons* Hashimoto and Okutani, 1994 in the deep sea (Fujikura et al., 2003). Zebra mussels serve as a substantial food source for several fishes (*Blicca bjoerkna*, *Rutilus rutilus*, *Cyprinus carpio*) (Entz & Sebestyén, 1946; Bíró, 1974; Specziár et al., 1997) and birds (*Fuligula ferina*, *Bucephala clangula*, *Fulica atra*, *Aythya fuligula* and *Anas platyrchynchos*; Ponyi, 1994; Custer, 1996; Werner et al., 2005).

The aim of this study was to survey the distribution and the quantitative relationships of zebra mussels in the stony littoral zone of Lake Balaton. This was performed during the extremely low water level of 2003 and during the initial recovery of the water level in 2004 and 2005. The density, biomass and relative abundance of zebra mussels, along with the density of their veliger larvae, were estimated. The abundance of waterfowl, which prey on mussels, and the abundance of the associated amphipod *C. curvispinum*, which are known as strong competitors of zebra mussels, were also estimated.

Materials and methods

Quantitative sampling of invertebrates, especially zebra mussels and the amphipod *C. curvispinum* in the stony littoral zone, was performed four times yearly (May, July, September and October) in 2003–2005. The four sampling sites are located along the northern shoreline of the lake at Keszthely, Szigliget, Tihany and Balatonalmádi (Fig. 1). The most eutrophic area of Lake Balaton is the Keszthely basin and the trophic level reduces towards the east.

Three stones were collected randomly (the size of the stones during the sampling ranged between 0.02 and 0.19 m^2) by hand from the upper (near the surface), about 10–20 cm below water level and lower (near the bottom of the lake) portions from the rip-rap. The deepest station is located at Tihany, where samples were collected by a scuba diver. At Balatonalmádi, the shallowest sampling site, samples from the upper portion were taken in 2003 only in May, because the upper portion of the stony littoral zone was completely dried later. The same phenomenon was observed at Szigliget in October 2003. Each stone was put onto a plastic tray, then brushed to remove the encrustation of macroinvertebrates from the substrate and byssal threads of the zebra mussels were carefully cut to remove them. All stone surfaces were traced onto a wrapping paper to calculate the area of sampled stone surface. An algorithm for weight vs. surface area was derived. Density was represented as ind m^{-2} stone surface, using every surface of the stones and ind m^{-2} lake surface in the stony littoral zone. For the latter data, we used the largest surface area of the stones, because we assumed that the stones lay on their own largest surface. The samples were sieved (mesh size: 300 μm) and preserved in 70% ethanol.

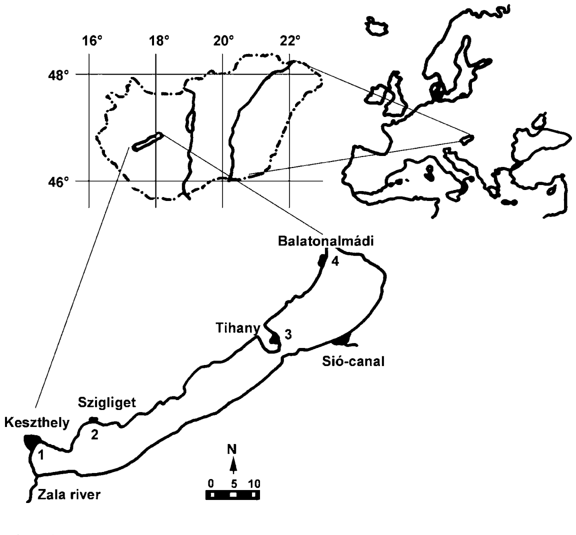


Fig. 1 Location of Lake Balaton in Hungary and the sampling sites in the littoral zone: Keszthely, Szigliget, Tihany and Balatonalmádi

Invertebrates were identified, counted and expressed as ind m^{-2} stone surface (density). Secchi transparency, water depth, conductivity, temperature, pH and turbidity were measured with a Horiba U-10 water meter. Collected water samples from each station were used to measure the chlorophyll *a* concentration with methanol extraction (Felföldy, 1987).

Five observers counted (in the late morning hours) monthly the number of waterfowl (counts per area) assembled in the sampling area during the migration period as follows: in October, November and December of 2003; all months except January and July in 2004; in January, March, April, May, June, July, August, September and October of 2005.

The relative abundance of zebra mussels and the amphipod *Chelicorophium curvispinum* were calculated as a percentage of the total number of invertebrates. We measured the length of the zebra mussel under a stereomicroscope fitted with an ocular micrometer. We estimated the biomass (g dry mass with shell m^{-2}) using the density and length–mass relationship according to previous studies on animals living in Lake Balaton (Muskó & Bakó, 2005).

Veliger larvae samples were taken biweekly from June till October of 2003–2004 and monthly in May, July, August of 2005 in the centre of the Keszthely-, Szigliget-, Szemes- and Siófok Basins using a 34-l

Schindler-Patalas-trap equipped with 58-μm pore sized funnel-trap. At each site, 5–8 samples were taken for veligers representing the whole water column. The samples were preserved with formalin (3.5%) and the veliger density was estimated using a Zeiss–Opton inverted microscope. Veliger larvae density was expressed in ind l^{-1} and ind. per entire lake area. For the calculation of the actual water level, the depth of the different basins were considered. All values were calibrated to the Adriatic sea level (Herodek et al., 1988).

Statistical analyses

We transformed datasets logarithmically (log $(x + 1)$) before analyses to achieve homogenity of variances and improve normality. The normality of the data was checked with a normal Q–Q plot of the model residuals (Sokal & Rohlf, 1995). Regional, seasonal and yearly differences in zebra mussel density and the effect of increasing depth on the density and biomass were compared using GLM ANOVA, with alpha set at 0.05 as the significance level. Post-hoc Tukey's test was used to evaluate the significance of differences among regions, seasons and years.

In order to assess the yearly variation of the density and biomass, a four-way ANOVA was used with zebra mussel density, biomass as dependent variables, and site, year, month and position as independent categorical variables. The lengths of the animals, especially among the different trophic sites, was studied with four-way ANOVA with zebra mussels length as the dependent variable and site, year, month and position as independent categorical variables. All ANOVA and Tukey's test were adapted from SPSS 11.5.

All interactions were included in the first models and nonsignificant, higher-order interactions were removed from the final models.

The dataset was analyzed using Pearson' correlation coefficient. *D. polymorpha*, the stones surface settled on, the amphipod *C. curvispinum*, and the veliger larvae of the mussel were analyzed for positive associations.

Results

Parallel with the water level decrease, a large percentage of the stony littoral zone had become dry in 2003. During the study no considerable stratification in the conductivity, temperature and pH (Fig. 2a–c) between the surface and the bottom occurred (2003–2005) in the sampling sites, but the turbidity was higher on the bottom than near the surface (Fig. 2d). The turbidity (Fig. 2d) was considerably lower at Tihany than at other sampling sites and the chlorophyll *a* (Fig. 2e) was very low in the eastern part of the lake (Tihany, Balatonalmádi).

Zebra mussels were found throughout the sampling period (2003–2005) and at every sampling station. The relative abundance of these two invasive species increased near the surface and decreased on the bottom by 2004, in contrast with the amphipod *C. curvispinum*, whose relative abundance increased considerably, especially in the bottom stones by 2004 (Fig. 3). By 2005 the relative abundance of the mussel increased considerably at both depths, while the abundance of *C. curvispinum* decreased. On the bottom, higher relative abundances of the mussel were found (37%, average relative abundance in 2003–2005) than near the surface (21%, average relative abundance in 2003–2005). In July, September and October of 2004, near the surface, a strong negative correlation was detected between relative abundances of the zebra mussel and the amphipod *C. curvispinum* (Pearson, $r = -0.954$, -0.792, and -0.808, respectively; $P < 0.001$).

The veliger larvae average density in the studied months was $2.89 * 10^{12}$ ind Lake Balaton^{-1} in 2003, which reduced by $2.25 * 10^{12}$ ind Lake Balaton^{-1} in 2004 and by $1.83 * 10^{12}$ ind Lake Balaton^{-1} in 2005 (Fig. 4). Veligers in the open-water were usually detected first in mid-May and June (Fig. 4), when weak correlation was found between the water temperature and the veliger density (Pearson, $r = 0.576$, $P < 0.01$). In 2003, the main spawning began in June, earlier than in 2004 (middle of August). The highest density was found in June 2003 ($40 * 10^{12}$ ind Lake Balaton^{-1}). Veligers were reduced to very low densities throughout the lake by early October, until the water temperatures fell below 10–12°C.

The most important period of the newly settled generation was (2003, 2005) in July (50–90% of the settled population was <2 mm). The population structure of the mussel in each year (Fig. 5) shows that the bottom contains more very small (<1.5 mm) individuals and large (>6 mm) mussels than the near surface populations, where 1.5–6 mm long mussels

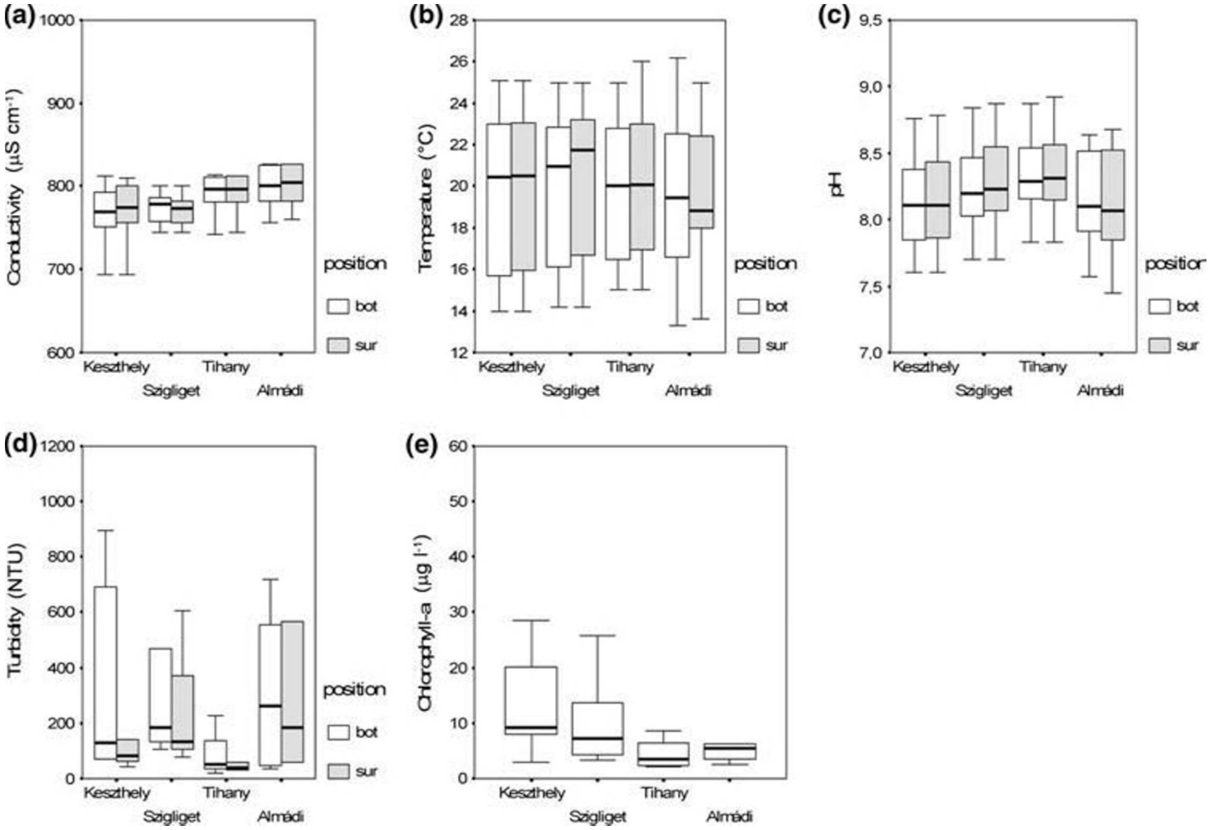
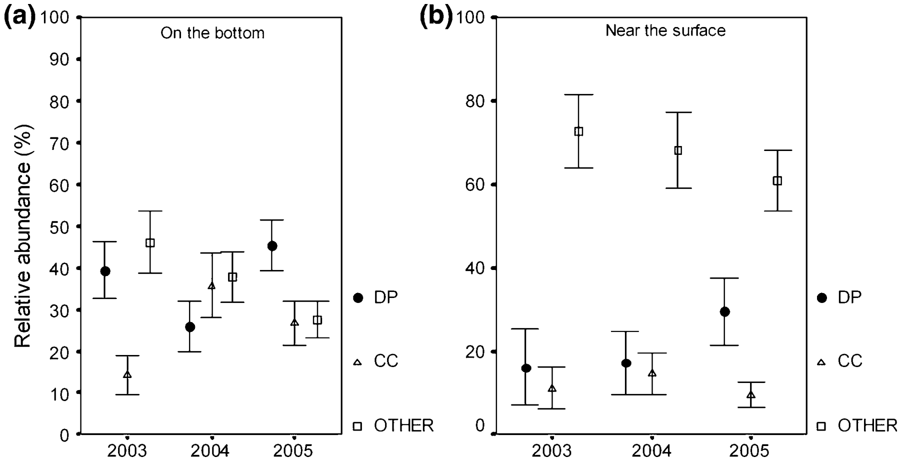


Fig. 2 The measured environmental parameters in 2003–2005. (**a**) conductivity, (**b**) temperature, (**c**) pH, (**d**) turbidity (NTU: Nephelometric Turbidity Unit) and (**e**) chlorophyll *a* concentration grouped according to sampling sites (Almádi: Balatonalmádi) in the different depths (position: bot—on the bottom, sur—near the surface). Boxplots show the medians, quartiles and interquartile range of the measured parameters

Fig. 3 The relative abundance of zebra mussels (Dp), *C. curvispinum* (Cc) and other animals in the different portions of the littoral zone (**a**) on the bottom and (**b**) near the surface in 2003–2005



dominated. In 2005, a large part of the mussel population consisted of mussels in the size range of 1 mm (Fig. 5).

The mussels grew over time, from May till October, but newly settled veligers were continuously appearing through till October (Fig. 4). A large

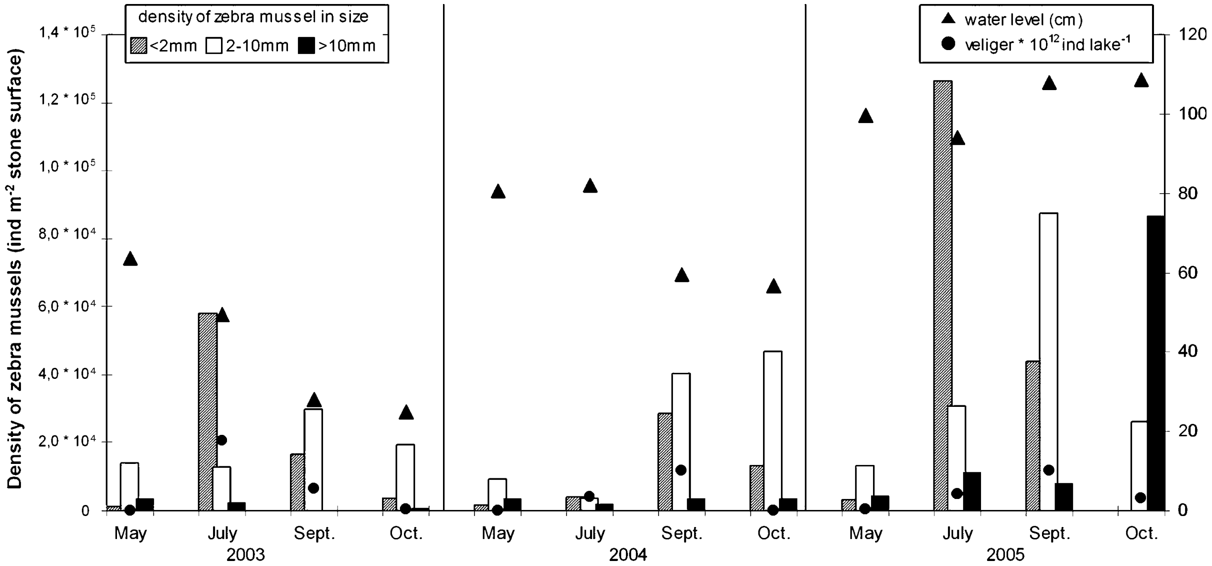


Fig. 4 The average density of zebra mussels grouped in different size ranges (smaller than 2 mm, between 2 and 10 mm and adult mussels and larger than 10 mm) at two positions and at all locations (left hand axis) as well as the current water level (cm) and the density of veliger larvae (individum Lake Balaton^{-1}), (right hand axis) in the open-water part of the lake at the current water level

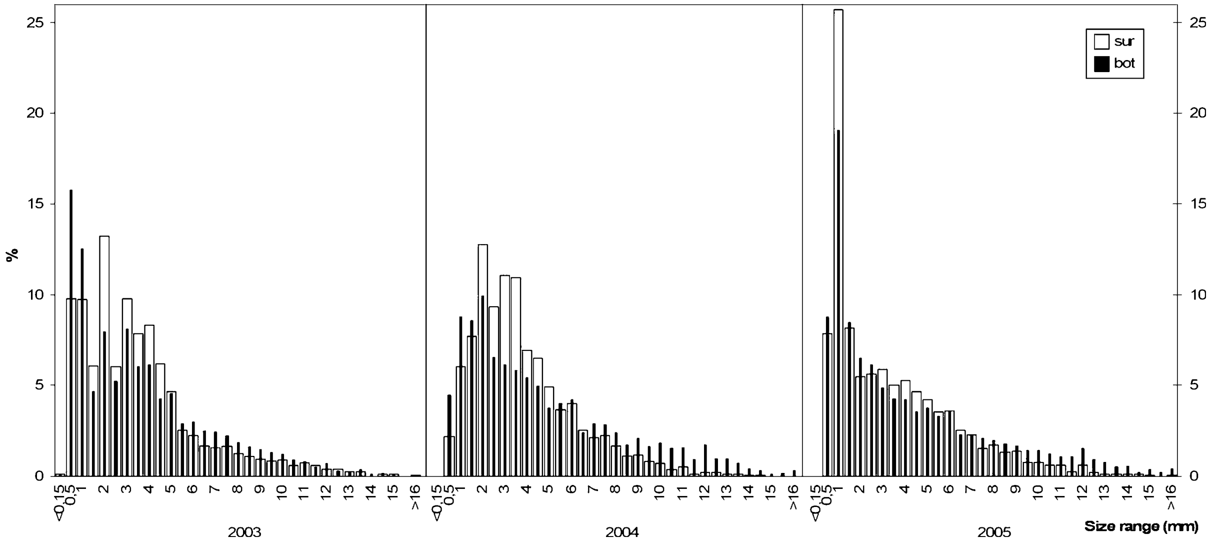


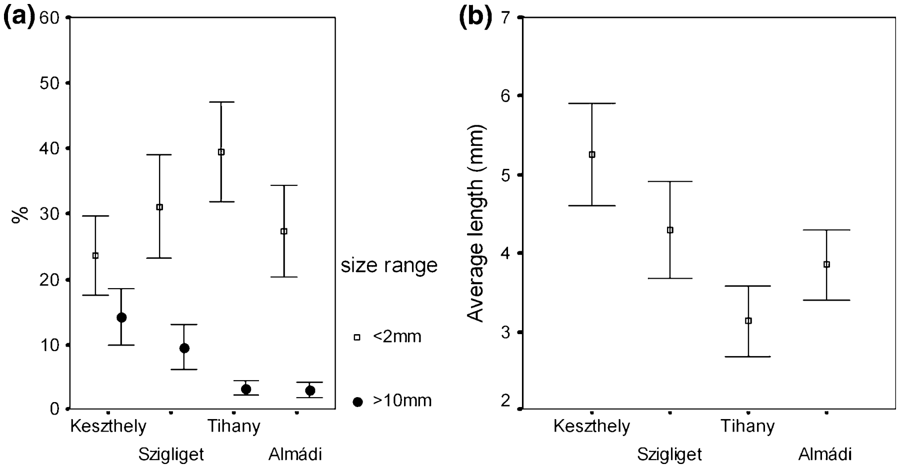
Fig. 5 The population structure of zebra mussels according to years in the different depths (position: bot—on the bottom, sur—near the surface)

amount of recruitment settled down in Tihany. However, in Tihany and Balatonalmádi, we found the fewest number of adults (Fig. 6a, size range: Ponyi, 1985).

The substrate size (the size of the stones on which the mussel settled down) and the abundance (%) of the newly settled mussels (<2 mm) correlated positively only in the upper portion of the rip-rap in July 2003 and 2005 (Pearson, $r = 0.797$, $r = 0.830$ respectively; $P < 0.001$), when there was an extremely high recruitment of settled larvae.

The density of *D. polymorpha* could reach 93,955 ind m^{-2} (stones surface) and the maximal biomass (dry mass with shell) was 714 g m^{-2} stone

Fig. 6 (**a**) the percentage of the newly settled (<2 mm) and the adult (>10 mm) zebra mussels at the different sampling sites (**b**) and their lengths at the different sampling sites (Almádi: Balatonalmádi)



surface. During the study, the maximal density of zebra mussel population was 220,000 ind m^{-2} lake surface, the biomass was 1,100 g m^{-2} lake surface and the length was 18.2 mm.

Mussel biomass and size were significantly greater (ANOVA and Tukey's test, $P < 0.05$; Table 1) on the bottom substratum than near the surface substratum (Figs. 5 and 7). In 2003, the density of the zebra mussels did not differ significantly from that in 2004 (Fig. 4) and was significantly higher in 2005 (ANOVA and Tukey's test, $P < 0.05$; Table 1, Fig. 4) than in the earlier years. The biomass also increased significantly by 2005 (ANOVA and Tukey's test, $P < 0.05$; Table 1, Fig. 7). The biomass of the zebra mussel grew (Fig. 7) while its relative abundance decreased from 2003 until 2004 (Fig. 3) on the bottom stones. By 2005, relative abundance of zebra mussel became higher at all depths (near the surface and on the bottom). In the beginning of 2005, this increase was significantly higher on the bottom than near the surface. Later in the year, this difference gradually diminished. The length of the zebra mussel was significantly (ANOVA and Tukey's test, $P < 0.05$; Table 1) higher in the Keszthely basin than in Szigliget, Tihany and Balatonalmádi (Fig 6b).

The dominant mussel-feeding waterbirds during the study period were *Fulica atra*, *Bucephala clangula* and *Anas platyrchynchos*, which occurred in high density (Fig. 8). The greatest number of diving ducks usually occurred in March, September, October and during the winter months. Only small number of the birds were present from mid spring and during the summer. Maximum number of all five species were recorded in October of 2003 and 2004. By autumn of 2005, the number of the birds had declined considerably.

Discussion

As a consequence of the water level decrease in Lake Balaton in the period of 2000 to 2003, 80% of the stony littoral zone dried out (G.-Tóth, 2005) and

Table 1 Results of ANOVA for the density, biomass, length of zebra mussel over time and distribution

Variables	Factors	Rank order	*F*-value	df	*P*-value
Density	Year	Y1 = Y2 < Y3	52,282	2	<0.0001*
Biomass	Year	Y1 = Y2 < Y3	22,701	2	<0.0001*
	Position	P1 > P2	44,948	1	<0.0001*
Length	Site	S1 = S2 > S3 = S4	19,384	3	<0.0001*
	Position	P1 > P2	28,471	1	<0.0001*

Rank order between years (Y1: 2003, Y2: 2004, Y3: 2005), positions (P1: on the bottom, P2: near the surface) and sites (S1: Keszthely, S2: Szigliget, S3: Tihany, S4: Balatonalmádi) was determined using a Tukey-HSD test

* Significant after sequential Bonferroni adjustment

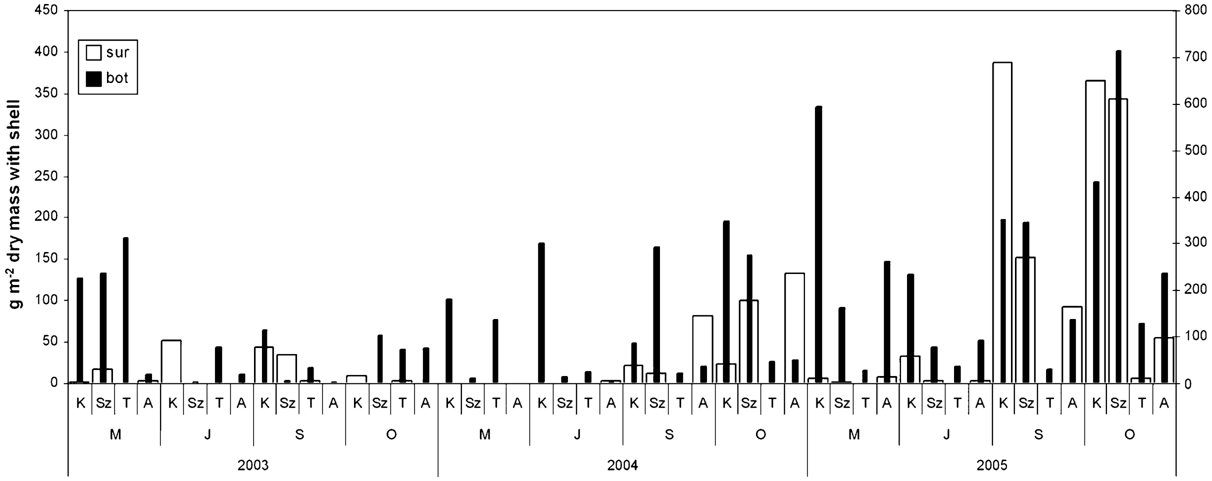


Fig. 7 The biomass of zebra mussels in Lake Balaton in 2003–2005. (position: bot—on the bottom, sur—near the surface). For further explanations, see Fig. 3

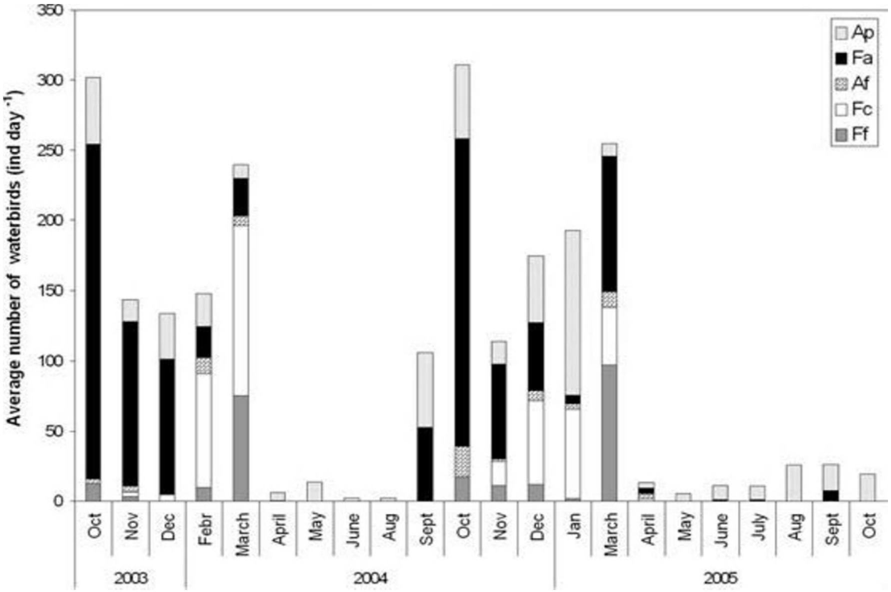


Fig. 8 Average number of the waterbirds feeding on zebra mussels at all locations of Lake Balaton in 2003–2005. Ff: *Fuligula ferina*, Bc: *Bucephala clangula*, Af: *Aythya ferina*, Fa: *Fulica atra*, Ap: *Anas platyrchynchos*

zebra mussel colonies perished. The electrical conductivity increased, while the water level decreased from 2000 to 2005 (Muskó & Bakó, 2005; Németh & G.-Tóth, 2004). In 2003, the higher electrical conductivity reflects a higher ion concentration similar to an earlier dramatic dry period of 1949 (Sebestyén et al., 1951).

According to the results, *D. polymorpha* reached 87% of the total abundance of all animals counted on the stones in the littoral zone in 2003. This clearly shows the permanent dominance of this invasive species after more than 70 years since initial invasion (Sebestyén, 1934).

The number of veliger larvae decreased yearly in 2000–2003, simultaneously with the water level decrease (Németh & G.-Tóth, 2004). The density of veliger larvae continually reduced until 2005, in spite of increasing water level. The animals settled later in 2004 than in 2003 and 2005 and the larvae occurred in larger numbers later. Most likely, the lower average water temperature in May of 2004 (16.7°C) than in 2003 and 2005 (21.4 and 20.3°C respectively) inhibited the settlement of larvae in 2004. It might also have been conducive to successful larval colonization of 2005.

The sampled submerged stones in 2003 were also covered with water in 2002. A water level recovery started in 2004; therefore in 2004 and 2005, large portions of the rip-rap (laid earlier for 2 or 3 years in dry conditions) were covered again with water. This suggests that the stones near the surface provided a potential new surface for the recruitment of zebra mussels, offering probably more suitable substrata in 2005 for the settlement than in 2003. On the stones that were out of the water in the dry period, there was a rapid colonization by zebra mussels beginning at the higher water level during the following year. The large number of 1-mm-long mussels on the surface portion in 2005 reflects the successful settling of the new generation there. The most intensive settlement of the new generations of zebra mussels during the study occurred at Tihany, but the fewest adults were found there. It is unclear which factors are responsible for the successful settling of this early stage there and the later mortality, but Tihany is an unique. It is the deepest sampling area with a long section of penetrable rip-rap, which might increase the fish predation (*Blicca bjoerkna*, *Rutilus rutilus*, *Cyprinus carpio*) and may decrease the mixing of the sediment there. More light penetration into the upper and the lower portions may cause better recruitment of zebra mussels (Bij de Vaate et al., 1992). Moreover, Mörtl and Rothhaupt (2003) showed that a large number of adult mussels negatively influenced the settlement of juveniles because of predation and food-competition pressure.

The density and relative abundance of zebra mussels decreased in September and October 2004 as a consequence of the existence and competition with the other Ponto-Caspian invasive species, especially *C. curvispinum*. The predation on zebra mussels by fish and the water-level fluctuation might also contribute to this process (Ponyi, 1985; Specziár et al., 1997). In 2005, the new substrata available may have encouraged better zebra mussel colonization, than the colonization of *C. curvispinum* (Muskó et al., 2003). Zebra mussels may be better competitors for new space as the earlier colonization study shows.

In Lake Balaton, diving ducks and coots intensively exploit *Dreissena polymorpha* (Ponyi, 1994). The northern shoreline might prove to be the only feeding area for the mussel feeding waterfowl, especially in 2003 and 2004, because the southern shore had already become dry. By 2005, the number of waterfowl on the northern shore decreased, which may have allowed the increase of mussel density and biomass there, due to reduced predation pressure.

Vertical stratification in the mussel density, biomass and length at each sampling was found in the littoral zone of Tihany, where the lake was deep enough for stratification. However, generally, more and larger mussels were found on the bottom than near the surface. The observed differences in the average length of the mussels on the western and eastern part of the lake reflects the existence of some trophic gradient between the sites. An earlier study showed this (Ponyi, 1985).

The density of zebra mussels in Lake Balaton is higher, on average, than in most other European lakes, but overall lower than the densities in the Great Lakes (Table 2). According to Werner et al. (2005), the density of newly settled zebra mussel population was up to 300,000 ind m^{-2} in Lake Constance, fourfold higher than earlier detected there; therefore the abundances at that time were similar to the Great Lakes and considerably higher than in Lake Balaton. Animals proved to be smaller in Lake Balaton than in other lakes (Bij de Vaate, 1991; Dermott et al., 2003). High densities of zebra mussels were observed on submerged macrophytes also in Lake Balaton (Muskó & Bakó, 2005), similar to the observations of Stanczykowska and Lewandowski (1993). However, a recent study in Lake Balaton indicates that mussels occurred in higher densities on stones than on submerged macrophytes in 2001–2002 (Balogh & Muskó, 2004), but considerably less than in 2000 (Muskó & Bakó, 2005). Their lengths and biomass were also greater on the stones.

By 2004 and 2005, new available substrata increased, due to the gradual recovery of the high water. Moreover, in 2005, the amplitude of the seasonal water-level fluctuation was small, and less waterfowl occurred in the northern shore. All the effects mentioned above contributed to a significant spread of the zebra mussel.

In this study, we showed how zebra mussel populations may react locally to yearly water-level fluctuation in Lake Balaton. Future studies will attempt to extrapolate our quantitative data together with other historical data concerning to the mussel (e.g. Sebestyén 1935, 1937, 1938; Entz & Sebestyén,

Table 2 Maximum average densities of *Dreissena polymorpha* in different lakes and rivers

Area	Density (ind m^{-2})	References
Lake Mikolajskie	2,200	Stanczykowska (1975)
River Rhine The Netherlands (1989)	21,000	Bij de Vaate et al. (1992)
Polish Lakes	6,720	Stanczykowska & Lewandowski (1993)
Lake Garda	20,000	Franchini (1978)[a]
Lake Constance	21,000	Walz (1975)
Lake Constance	~330,000	Werner et al. (2005)
Lake Zurich	30,000	Burla and Lubini-Ferlin (1976)[a]
Lake Dojran	4,000–5,000	Sapkarev (1975)[a]
Dneprodzerzhinsk Reservoir	25,000–36,000	Gaidash and Lubanov (1978)[a]
Szczecin lagoon	114,000	Wiktor (1963)[a]
Lake Erie (1989–1990)	342,000	Leach (1993)
Lake Huron	300,000	Nalepa et al. (1995)
Lake Ontario (2000)	38,865	Dermott et al. (2003)
Illinois River (1993)	100,000	Schloesser et al. (1996)

[a] Cited by Bij de Vaate (1991)

1946; Sebestyén et al., 1951; Bíró & Gulyás, 1974; Entz, 1981; Ponyi, 1981; Muskó & Russo, 1999; Lakatos et al., 2001; Muskó et al., 2003; Muskó & Bakó, 2005) and information concerning the metabolism of the mussels and density of the veligers. This study contributes to a better understanding of the effects of long-term water-level fluctuations on the population dynamics of the zebra mussel *D. polymorpha* in Lake Balaton.

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WATER-LEVEL FLUCTUATIONS

Patterns, origin and possible effects of sediment pollution in a Mediterranean lake

Nikolaos Skoulikidis · Helen Kaberi · Dimitrios Sakellariou

Abstract Vegoritis is a large, deep, mesotrophic, karstic lake in NW Greece, located in Ptolemais basin. Dramatic lowering of the lake's level has occurred during the last half century due to human pressures. The Ptolemais Basin and the lake itself are subjected to serious human pressures. Pollutants are carried into the lake through both, the atmosphere and surface runoff. In order to identify the levels, and assess the origin of heavy metals in surface lake sediments, 24 samples were collected and analyzed for their grain size, as well as for their mineral, organic matter, major element and heavy metal content. The origin of heavy metals has been attributed to specific geogenic and anthropogenic sources. Despite the anthropogenic disturbance, the levels of micropollutants were low, possibly due to the low retention time of lake water and the recent increase of sedimentation rates. Only Cr, Ni, Co As, and Ba were present in relatively high concentrations. Ba is derived from the erosion of acid silicate rocks, Cr primarily from mafic rocks and secondarily from pollution, whereas for Ni and Co the opposite is true, while As is primarily attributed to fly ash deposition. The lowering of the lakes' water level exposes sediments, which are then being oxidized. Mobilization of As and Cr could impair humans' and ecosystems' health.

Keywords Lake Vegoritis · Sediments · Heavy metals · Fly ash · Toxicity

Introduction

Pollutant levels in lake sediments can be a firm criterion for the evaluation of degradation in water bodies; sediments reveal higher pollutant concentrations than the overlying waters and stable surplus levels over time (Salbu & Steiness, 1995), while lake sediments are the final recipients of anthropogenic activities within the lake-basin, operating as pollutants storage tanks and reflecting long-term impacts (e.g., Maltby, 1992). Since lakes are essentially closed, or nearly closed systems with respect to sediment transport, metals are amassed through atmospheric deposition and/or watershed leaching and are then potentially adsorbed onto the organic or clay fraction in sediments (e.g., Salomons & Förstner, 1984). Through water-level fluctuations lake sediments are periodically either exposed to the

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atmosphere or inundated. In sediments that undergo periodic flooding there may be considerable variation of oxidation-reduction states, and as the oxidation condition of the sediments changes, redox-active inorganic constituents are affected (Maltby, 1992). Inorganic and/or microbially mediated redox reactions transform the physicochemical forms and valency of metals affecting their bioavailability and toxicity.

Due to water management practices, the water level of Vegoritis Lake experienced a gradual long-term diminishing (see Section "Hydromorphological aspects and sedimentation rates"). Due to the presence of significant pollution sources in the basin, the lake became subject for research concerning heavy metals in sediments (Katsanos et al., 1987; Fytianos et al., 1994; Skoulikidis, 2001a, b). This article present the levels and possible origin of heavy metals found in lake sediments and attempts an assessment of the environmental risk caused by water level change. The article is part of a greater research funded by the Prefecture of Florina and West Macedonia Region in order to assess the causes of the lakes' level drop and to evaluate the quality of lake sediments.

Materials and methods

Study area

The Vegoritis is a karstic lake in West Macedonia without any surface run-off. Apart from the southern flat part of its basin (1,853 km^2), where the Ptolemais plain extends, the lake is surrounded by high mountains, i.e., Mount Voras (2,524 m), at the northern and north-eastern boundary, and mounts Vermio (2,052 m) and Vernon (2,128 m) at the east and west respectively (Fig. 1). The geochemically important rock formations in the basin are acid metamorphic siliceous rocks (mica schist and gneiss) and calcareous formations (marbles/sipolines, limestones, and dolomites) of Mount Voras (Fig. 1). In the east and northeastern part of the catchment dominate marbles/sipolines, with schist and serpentinite intercalations, and ophiolites. The Ptolemais plain is filled with Holocene deposits (alluvium, lacustrine sediments, and peat), Pleistocene fluvio-lacustrine, lake-bog, and fluvial conglomerate sediments, with gneiss-schist material, as well as Upper-Pliocene lake/lake-bog deposits with lignite ores. The lake is supplied by the permanently flowing river Soulou (Pentavrisos), that crosses the Ptolemais plain, and the small temporary streams Panagitsa and Zervi, which drain the northern part of the basin. In addition, overflow waters from the lake system Zazari–Chimaditida–Petron (Fig. 1) enter the lake. Moreover, a great amount of karstic waters supplies the lake contributing to the low retention time of the lake's water (9.5 times/year) (Papakonstantinou et al., 1989). In Vegoritis basin, and especially in Ptolemais plain, urban development, extensive agriculture, and industrial activities (agro-industries and lignite mining and combustion) comprise major environmental pressures. Surface water flowing in the southern part of the lake is loaded with partly treated urban and hydropower plant wastewaters, wastes from agricultural manufacturing units, erosion effluents of lignite mines, agrochemicals, and leachates from landfills. In addition, atmospheric pollution from the hydropower stations heavily impacts the area making the city of Ptolemais one of the most-polluted cities in Europe. A heavy metal pollution source in the study area is the excavation and combustion of lignite. The combustion procedure releases particulates rich in heavy metals, such as As, B, Ni, Se, Cu, Cd, Cr, Pb, Hg, Mo, Fe, Mn, and Zn (Kagey & Wixson, 1983; Gerouki et al., 1997; Fytianos and Tsaniklidi, 1998; Zevenbergen et al., 1999; Samara, 2005). In the north part of the basin, agriculture and urban development are limited. As a result of intense human activity, a degradation of the terrestrial and aquatic status of Ptolemais basin is apparent. The Soulou River is highly mineralized due to elevated carbonate dissolution, caused by sulfuric acid that originates from lignite, and exhibits low oxygen levels and high nutrient concentrations (e.g., average $N–NH_3$ levels by 2 mg/l) due to the impact of organic effluents. Thus, the river reveals a moderate to bad biological status (Skoulikidis, 2001a). The waters of the lake show seasonally toxic ammonia levels (Diamandithis & Andonopoulos, 1984), which have probably caused massive deaths of fish (Fotis et al., 1984). The lake experiences summer stratification, with very low oxygen concentrations in the meta- and hypo-limnion (Diamandithis, 1984), while its trophic status changed from oligotrophic in 1977 to mesotrophic in 1983 (Nikolaidis et al., 1985).

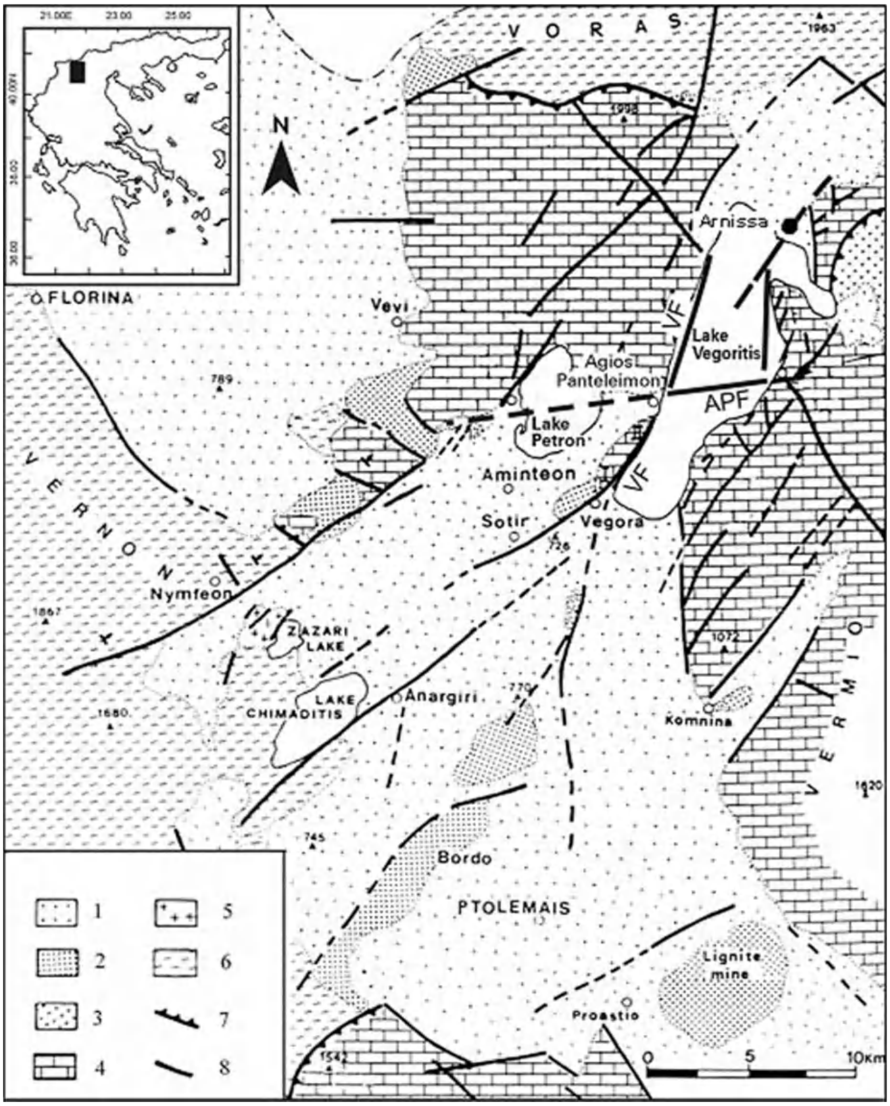

Fig. 1 Location and geological map of Vegoritis Lake basin (after Pavlides and Moundrakis, 1987; modified after Sakellariou et al., 2001). 1: Quaternary, 2: Neogene, 3: Ophiolites, 4: Marbles (Mesozoic), 5: Gneiss (U. Carboniferous), 6: Metamorphics (L. Palaeozoic), 7: Overthrust, 8: Fault, APF: Agios Panteleimon fault, VF: Vegoritis fault

Sampling and analysis

A sampling network was designed (Fig. 2), according to the distribution of active and potential pollution sources around the lake (villages, streams, agricultural areas, industrial units). 22 sediment samples were collected in September 2001 on a boat with the use of a VAN VEEN sampling device from depths ranging from 2 to 18 m and additional samples were taken from the river bed of Soulou and from the lignite field. All samples designated for chemical analysis were kept and maintained under low temperature (portable refrigerators). Grain-size analysis was carried out by wet sieving, for the sand fraction, while a SEDIGRAPH 5100 device was used for the resolution of silt and clay. Mineral composition was determined by a PHILLIPS X-ray diffraction (XRD) of CuNa radiation and 0.8 KW (40 KV–20 mA) maximum operation power. Concentrations of main elements (SiO_2, Al_2O_3, TiO_2, Fe_2O_3, K_2O, Na_2O, CaO, MgO, P_2O_5, MnO, and S) and heavy metals (V, Cr, Mn, Co, Ni, Cu, Zn, As, Rb, Sr, Mo, Ba, and Pb) were determined with the use of a PHILLIPS X-ray fluorescence (XRF) device. Total and organic carbon, total nitrogen and sulfur were determined with a Fisons Instruments CHN EA-1108-type element analyzer. Data were statistically processed with the use of multivariate statistical analysis (Principal

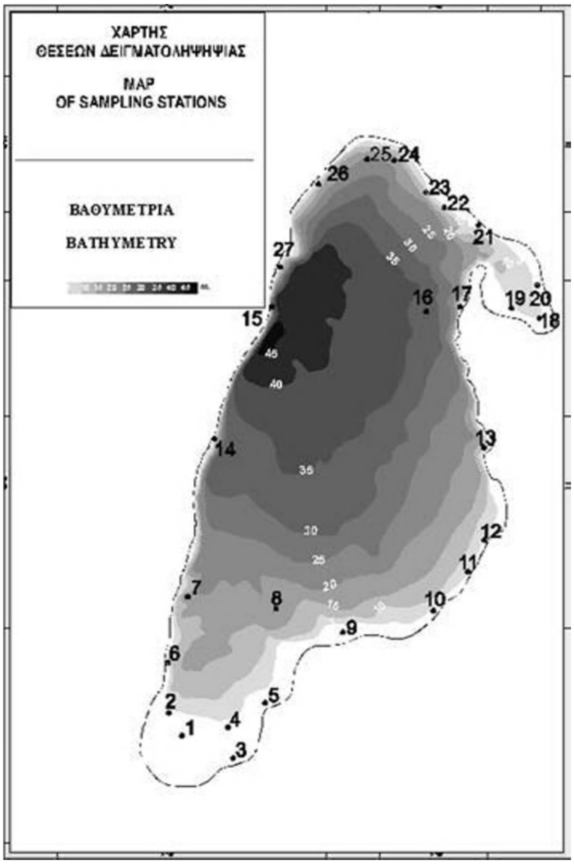

Fig. 2 Batymetric map of Vegoritis Lake with sampling sites (the sediment core is marked with triangle) (GIS Department of HCMR)

Component Analysis, Statistica Release 6.0). A 70 cm long core, recovered from the southern shallow part of the lake (which presents highest sedimentation rates and shows direct and more visible response to any changes in sedimentation processes) was used to calculate the actual sedimentation rate with the ^{210}Pb geochronological method. The core was collected from a water depth of 1.5 m, a few meters from the outflow of Soulou River. The corer, actually a 3-m long and 70 mm in diameter plastic tube with a core catcher at the lower edge, was pressed vertically into the lakebed and was pulled out by hand. The sediment core was sealed and transferred to the lab, where it was cut lengthways. 11 samples, every 1–2 cm from the upper part of the core and every 8–10 cm below 23 cm depth, were taken for XRD and XRF analyses. In addition, about 20 samples were taken every 1 cm until 10 cm depth and then every 5 cm to the lower end of the core. The down-core activity of ^{210}Pb was determined through the measurement of it's a-emitting granddaughter ^{210}Po, assuming secular equilibrium with ^{210}Pb. For the total dissolution of the dried-sediment samples the analytical method described by Sanchez-Cabeza et al. (1998) was followed, whereas the ^{210}Po activities were counted on a total a- counter (Ortec EG&C, Oak Ridge, TN, USA) (Radakovitch, 1995). The supported ^{210}Pb activity, which corresponds to sediment layers deposited earlier than the last 100–120 years, was determined in sediments old enough to accept that all the excess ^{210}Pb has decayed and assuming that parent-supported ^{210}Pb is constant.

Results

Hydromorphological aspects and sedimentation rates

In September 1999, when the present survey was conducted, the Vegoritis Lake level was at about 513–515 m asl. At that time, the area covered by the lake water was estimated to be approximately 50 km^2, with a maximum length of 12 km in NNE-SSW direction and maximum width of 5 km. The lake constitutes the northward prolongation of the southern flat part of the Ptolemais plain. Thus, the southern part of the lake, up to Agios Panteleimon village, is very shallow and characterized by the rapid accumulation of sedimentary material carried into the lake by the Soulou River. The lake-bed deepens gradually to the north and reaches a maximum depth of 48 m (about 465 m asl). The deepest part of the lake-bed is located at the base of the steep slope at the western lakeside, which is formed along the trace of Vegoritis fault. On the contrary, towards the east the lake-bed shallows very gently, indicating a significant morphological asymmetry.

Lake Vegoritis lacks any surficial outflow. Nevertheless, the strongly karstified Triassic-Jurassic marbles, which outcrop at the margins of the lake, allow the underground discharge of lake water to the Voda springs, a few kilometers NE of Arnissa village (Fig. 1). The lake level used to fluctuate normally, following climatic patterns, until 45 years ago (Fig. 3), and in 1956 it was measured at 542 m asl (Stamos, 1996). In this year, a water tunnel was set in

Fig. 3 Water-level fluctuations in Vegoritis Lake during the last century (Stamos, 1996)

operation at the NE side of the lake, through which huge quantities of lake water were abstracted to cover the needs of Agras hydro-electric power station. 34 years later (1990), the lake level was lowered by almost 30 m and fell below the operational level of the tunnel (515.5 m asl), which is abandoned since then, while the lake has lost about 65% of its water (Antonopoulos & Gianniou, 2003).

Figure 4 presents the vertical distribution of ^{210}Pb activity. From the sediment surface until 30 cm depth, the ^{210}Pb activity increases with depth, whereas from this depth to the lower end of the core the activity exponentially decreases, showing an almost theoretical pattern. The cause for this unusual distribution is attributed to the enormous lowering of the lake level since 1956. Hence, two separate sedimentation rates have been calculated. The CRS (Constant Rate of Supply) model was used (Appleby & Oldfield, 1978) for the calculation of the sedimentation rate in the lower part of the core. According to our assumption, this part of the core represents the period before 1956, and the apparent maximum sedimentation rate was calculated to about 0.4 cm/year. Consequently, the upper 30 cm of the sediment core have been accumulated during the last 45 years, after 1956, at a significantly higher sedimentation rate of 0.6 cm/year. Therefore, the rapid increase of the sedimentation rate in the upper 30 cm of the sediment core is attributed to the dramatic lowering of the lake level since 1956.

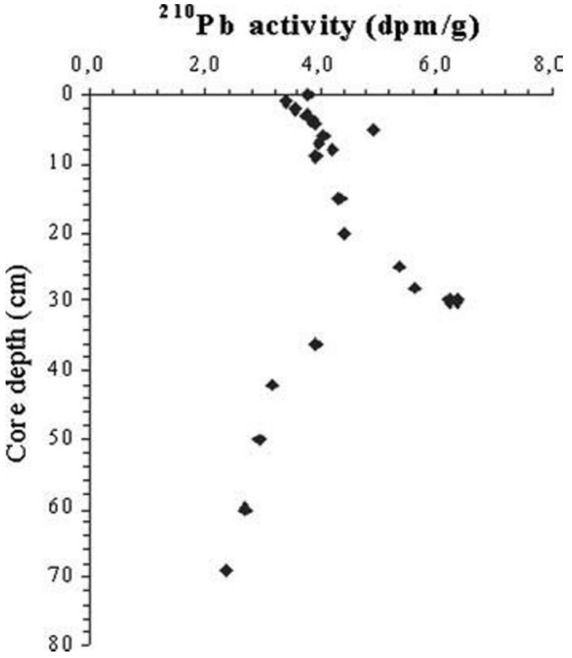

Fig. 4 ^{210}Pb distribution along the sediment core recovered from Vegoritis Lake bed. The depth of ca. 30 cm corresponds to year 1956 (for details see Section “Hydromorphological aspects and sedimentation rates”)

Physico-chemical characteristics of lake sediments

Tables 1 and 2 present the physical and chemical properties of the sediments in Vegoritis Lake and Soulou River and the metal concentrations in lignite. In average, lake sediments are composed by clayey silt, i.e., silt (51.7%), clay (33.6%) and sand (14.7%). The northern and, especially, the eastern parts of the lake reveal higher percentage in coarse grain material (33% and 15% sand, respectively), while the southern part is covered by finer grained material (96% silt/clay) as a result of fluvial inputs from the Neogene-Quaternary deposits of Ptolemais basin. The mineralogical assemblage of the sediments is made up by silica, calcite, dolomite, plagioclase, montmorillonite, illite, and chlorite. The north part of the lake is particularly enriched with illite. Organic carbon in lake sediments ranges between 0.65% and 2.26%, whereas Soulou River sediments are more enriched (3.76%). During the field study, a large part of lake sediments was covered by gas bubbles, indicating anaerobic decomposition of sediment organic matter (Sakellariou et al., 2001). The sediments' gray/black color and smell also indicate anoxic conditions.

Table A1 (Supplementary material) illustrates heavy metal concentrations in surface lake sediments, according to the present and previous research in Vegoritis Lake, and undisturbed lakes. It also includes heavy

Table 1 Concentrations of organic and total carbon, total nitrogen and sulfur and major elements in Lake Vegoritis and Soulou River sediments (28) and of major elements in lignite (29) (units in %)

Station ID	OC	TC	TN	TS	Sand	Silt	Clay	SiO_2	Al_2O_3	TiO_2	Fe_2O_3	K_2O	Na_2O	CaO	MgO	P_2O_5	MnO
1	1.05	3.83	0.14	0.029	0.8	58.5	40.7	40.25	12.63	0.68	7.05	1.95	0.7	13.81	4.59	0.17	0.11
2	1.2	4.28	0.16	0.04	1	68	31	40.14	11.6	0.67	6.56	1.79	0.87	15.25	4.53	0.16	0.11
3	0.89	3.33	0.12	0.017	11	53	36	42.81	12.9	0.72	7.32	1.96	0.83	12.39	4.52	0.16	0.11
4	0.99	3.71	0.14	0.035	0.35	55.85	43.8	39.5	13.02	0.71	7.47	1.95	0.69	13.5	4.57	0.16	0.11
5	1.75	4.7	0.21	0.095	0.54	64	35.5	38.28	12.32	0.68	7.06	1.84	0.71	14.49	4.58	0.17	0.11
6	1.47	5.43	0.19	0.058	4.25	48.8	47	33.64	11.44	0.59	6.34	1.73	0.48	18.9	4.47	0.18	0.09
7	1.46	5.84	0.18	0.038	11	42.3	46.7	31.9	10.86	0.55	5.95	1.71	0.44	20.69	4.51	0.18	0.1
8	1.91	4.84	0.21	0.493	1.3	52	46.8	36.78	12.26	0.65	7.58	1.84	0.51	14.4	5.06	0.16	0.12
9	1.77	4.28	0.19	0.087	3.8	61.6	34.6	42.46	11.44	0.65	6.77	1.73	0.74	12.75	5.42	0.16	0.11
10	0.65	3.59	0.07	0.026	55.7	30	14.3	51.27	7.35	0.66	4.24	0.97	0.88	13.96	5.34	0.13	0.08
11	0.95	4.32	0.1	0.025	53	32	15	46.05	7.81	0.54	4.28	1.07	0.87	15.82	5.2	0.14	0.08
12	1.74	5.36	0.21	0.056	15.3	53.4	31.3	40.33	9.57	0.58	5.26	1.58	0.71	16.52	5.34	0.16	0.09
13	2.2	6.33	0.26	0.175	8.6	50	41.5	32.99	10.24	0.55	5.88	1.49	0.47	19.28	5.21	0.18	0.09
18	1.88	5.69	0.22	0.178	3	52.5	44.5	36.15	10.86	0.52	5.33	1.85	0.55	18.66	3.97	0.18	0.09
19	1.63	5.59	0.2	0.093	11	48.2	40.8	33.79	11.16	0.52	5.44	2.01	0.64	19.71	3.87	0.19	0.08
20	2.26	5.55	0.28	0.241	2.3	65.5	32.2	38	12.47	0.53	5.16	2.49	0.88	15.81	3.96	0.18	0.09
21	1.74	4.3	0.23	0.195	7.2	64	28.7	43.1	14.34	0.55	5.09	3.32	1.31	12.04	3.56	0.19	0.09
22	1.32	2.36	0.09	0.054	40.8	44.6	14.6	51.89	17.88	0.54	4.88	4.73	1.93	4.43	3.12	0.18	0.08
23	0.96	3.08	0.1	0.066	13	51.5	35.5	45.79	15.24	0.59	5.44	3.43	1.42	10.25	3.49	0.18	0.09
24	0.95	2.66	0.11	0.09	32.7	51.7	15.6	48.47	16.08	0.56	5.22	3.99	1.7	8.98	3.14	0.19	0.09
26	1.51	5.39	0.18	0.076	6.3	55.7	38	34.79	12.01	0.55	5.35	2.25	0.82	18.12	4.28	0.17	0.09
27	1.65	8.92	0.21	0.086	40	35	25	20.87	6.15	0.32	2.84	1.06	0.63	31.38	5.49	0.14	0.07
Average	1.45	4.70	0.17	0.10	14.68	51.73	33.60	39.51	11.80	0.59	5.75	2.12	0.85	15.51	4.46	0.17	0.09
Median	1.49	4.51	0.185	0.071	7.9	52.25	35.5	39.82	11.805	0.57	5.44	1.845	0.73	14.87	4.525	0.17	0.09
% StDev	30.8	30.6	33.6	106.4	119.7	20.0	32.2	17.9	23.1	15.1	20.7	44.5	46.3	33.7	16.4	9.9	14.1
Max	2.26	8.92	0.28	0.49	55.7	68	47	51.89	17.88	0.72	7.58	4.73	1.93	31.38	5.49	0.19	0.12
Min	0.65	2.36	0.07	0.02	0.35	30	14.3	20.87	6.15	0.32	2.84	0.97	0.44	4.43	3.12	0.13	0.07
28	3.75	5.98	0.38	0.04	21.3	45.3	33.4	41.43	9.36	0.56	6.07	1.27	0.67	13.07	6.72	0.37	0.08
29								46.59	16.7	0.77	8.33	3.13	2.11	5.44	4.58	0.13	0.14

OC: Organic carbon, TC: total carbon, TN: total nitrogen, TS: total sulfur, % StDev: Standard Deviation * 100/average

metal concentrations estimated in fly ash of the area, background heavy metal concentrations in rock types found in the basin and recommended heavy metal limits in soils. As it is stemmed from comparisons with concentrations found in reference lakes, typical concentration levels of different types of rocks and soils and recommended thresholds in soils, only Cr, Ni, Co, As, and Ba exhibited relatively high concentrations in the lake.

A Principal Component Analysis (PCA) was performed on the parameters investigated in lake sediments in order to reveal their relationships (Table 3). Three principal components interpreting 75% of the total variability were distinguished. The first PCA component, which accounted for the one-thirds of the total variance, was more heavily weighted on V, Co, Ni, Cu, Mn, and Fe. The second component, which accounted for the $^1/_4$ of the total variance, was characterized by Rb, Ba, Ti, Si, Al, K (positive loadings) and Sr, Ca, and total C (negative loadings). Factor 3 (16.4% of the observed variance) involves Cu, Zn, As, Pb, clay, organic C, total N and total S (positive loadings) and Cr, sand (negative loadings).

A next PCA was performed on the 24 samples from the study area for major elements and heavy metals (Fig. 5) in order to differentiate groups of sites with similar composition, and thus, to allocate the main factors determining the differentiation of these groups. Three core groups of sites were distinguished,

Table 2 Heavy metal concentrations in the sediments of Lake Vegoritis and Soulou River sediments (28) and in lignite (29) (units in ppm)

Station ID	V	Cr	Mn	Co	Ni	Cu	Zn	As	Rb	Sr	Mo	Ba	Pb
1	118.9	323.1	897.7	33.9	309	42.6	97.5	10.5	116.7	170.9	1.7	412.7	24.4
2	111.7	297.8	947.1	30	260	40.6	87.6	12.4	104.1	196.9	2.2	387.6	23.3
3	124.9	324.4	910.8	31.8	283	44.1	97.1	13.4	113.2	164.4	1.8	426.1	23
4	127	318.2	896.9	33.6	292.5	46.7	100.9	12.1	116.6	165.1	1.7	422.5	23.9
5	116.6	308.6	977.4	31.6	271.8	44.7	98.6	8.5	111.6	187.7	2.2	417.3	25.6
6	114.4	262.7	825.6	28.1	247.5	42.6	93.5	11.8	111	199.6	2.4	403.3	25.7
7	109.2	241.5	863.3	26.3	233.5	42.3	86.8	12.1	110.4	212.1	1.5	423	26.7
8	124.7	348	1,018	33.1	306.7	48.2	102.6	13.5	114.3	161.9	3.4	404.8	26
9	113.1	380.4	933.3	33.2	321.9	40.9	93	12.4	99.7	159.7	2.3	374.7	23.2
10	88.7	706.1	713.3	25.5	261.4	16.4	51.9	8.5	47.3	227.9	2.2	231.3	11.6
11	87.1	424.3	712.3	23.8	255.4	22.1	58.5	9.5	59.8	238.9	2.3	263.9	14.2
12	99.5	299.5	832.1	26.7	244.5	34.3	76.7	11.6	87.1	201.6	2.2	332.8	19.6
13	109.9	291.3	838.2	29.1	257.1	43.3	82	13.6	94.5	223	2.1	372.3	23.4
18	99.1	207.5	754.5	23	201.5	41.2	85.2	13.3	118	228.6	2.1	410.4	27.3
19	99.6	210.1	716.2	25.2	203.8	39.9	87	13	124.1	256.5	3.6	443.8	28.2
20	93.6	164.3	795.2	21.3	156	37.7	90.8	15.6	152.8	242.3	1.6	513.4	32.5
21	92.5	139.9	754.9	20	121.6	33.3	97.2	12	188	241.8	3	605.4	33.4
22	90.6	61.7	692.5	14	37.7	29.8	111.2	11.9	256.3	204.7	2	963.6	40.3
23	96.7	149.4	738.3	19.4	135.4	30.4	99.1	10.4	195.5	218.5	2	610.4	32.5
24	90.7	114	736.2	16.2	97.8	23.7	98.2	8	214.7	221.3	2.1	667.4	29.7
26	101.3	176	792.2	22	162.4	39.7	93.6	10.9	139.9	246.5	2.5	485.1	33.4
27	68.3	104.1	681.6	13.3	86.4	21.4	49.8	15	67.9	345.3	3.9	365.2	20.6
Average	104	266	819	25.5	215.8	36.6	88.1	11.8	124.7	214.3	2.3	451.7	25.8
% StDev	14.3	51.8	12.2	24.9	37.3	24.6	18.2	16.9	40.4	19.5	27.5	34.0	25.0
Max	127	706	1018	33.9	322	48.2	111.2	15.6	256.3	345.3	3.9	964	40.3
Min	68.3	61.7	681.6	13.3	37.7	16.4	49.8	8	47.3	159.7	1.5	231	11.6
28	–	447	–	–	200	40	87.5	7	93.5	142	–	–	53
29	100.4	494.1	729.6	35.6	430.8	70.1	242.5	8.9	78.1	176.1	3	334.6	30.5

% StDev: Standard Deviation * 100/average

denoting that the distribution of metals in lake sediments follows a geographical pattern: sites in the south part of the basin (sites 1–9), sites in the east part of the basin (sites 10–13) and sites in the north part of the basin (sites 18–27). Sites in the south and east parts of the lake revealed stronger geochemical associations since they are closely located. Sites situated in the north part of the lake presented strong dissimilarities, possibly due to the heterogeneity of heavy metal sources. Especially site 27 differs greatly from the others since its composition depends on the erosion of carbonate formations of Mt. Voras. Soulou River sediments and lignite are obviously enriched in major elements and heavy metals; however, they present strong dissimilarities in their composition. This facilitates the heavy metal sources apportion. According to basic statistics in each one of the distinguished site-groups (Table 4), the following results can be depicted: (a) the south part of the basin is enriched in V, Mn, Co, Ni, Cu, Zn, (b) the east part of the basin is characterized by high Cr concentrations, (c) Pb, Rb, Sr, and Ba dominate in the north part of the basin and (d) As and M*o* present a, more or less, homogenous distribution.

Figure 6 presents a comparison of heavy metals levels in lignite and in the sediments of Soulou River and Vegoritis Lake. Cu, Zn, Cr, Ni, and Co exhibit maximum concentrations in river sediments, whereas

Table 3 The three main components of sediment quality in Lake Vegoritis according to a Principal Component Analysis carried out on the whole data set (bold numbers: significant loadings, italics numbers: significant negative loadings)

%	PC1 33.2	PC2 25.3	PC3 16.4
V	**0.230**	0.197	0.001
Cr	0.184	−0.074	*−0.276*
Mn	**0.221**	0.146	0.007
Co	**0.294**	0.067	−0.054
Ni	**0.288**	−0.007	−0.086
Cu	**0.230**	0.088	**0.215**
Zn	0.107	0.101	**0.158**
As	0.004	−0.072	**0.2419**
Rb	−0.197	**0.242**	0.136
Sr	−0.190	*−0.247*	0.091
Mo	−0.020	−0.182	0.148
Ba	*−0.208*	**0.214**	0.1326
Pb	−0.114	0.188	**0.298**
Si	−0.081	**0.201**	*−0.256*
Al	−0.110	**0.317**	0.092
Ti	0.170	**0.233**	−0.1969
Fe	**0.223**	**0.228**	0.0278
K	−0.208	**0.242**	0.0921
Na	*−0.236*	0.177	−0.065
Ca	0.049	*−0.295*	0.122
Mg	**0.206**	−0.197	−0.068
P	0.076	0.025	0.186
Sand	−0.162	−0.149	*−0.246*
Silt	0.074	**0.211**	0.184
Clay	0.193	0.039	**0.224**
Organic carbon	0.107	−0.077	**0.292**
Total carbon	0.064	*−0.285*	**0.226**
Total nitrogen	0.128	−0.098	**0.318**
Total sulfur	0.022	0.0191	**0.212**
φ	*−0.264*	−0.016	0.145
λ	*−0.211*	−0.0219	0.005

PC1, PC2, PC3: Components, φ/λ: coordinates

Mn, As, Pb, and Sr are maximum in lignite. Compared to the river and to lignite, the lake is enriched only with Ba and presents average concentrations of Cr, Mn, Co, Ni, As, Rb, Sr, and Mo and low concentrations of V, Cu, Zn, and Pb.

Elements in the sediment core did not differ substantially from those in surface sediments. Nevertheless, element concentrations derived from fly ash (Table A1—Supplementary material); show a slight increase in the upper ~30 cm (from 1956 up today) of the sediment core. The upper section of the sediments was enriched with sulfur, As, Mn, Sr, and Pb compared to the lower sediment section. Enrichment factors ranged between 1.12 and 1.36. However, the application of a *t*-test showed a statistically accepted variation only for Mn. Figure 7 shows the depth distribution of a selected example.

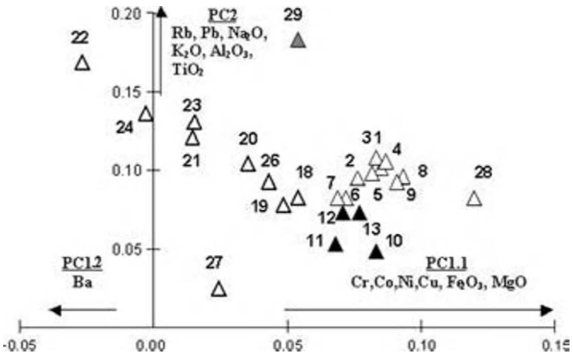

Fig. 5 Distribution of sampling sites according to the first and second axes of a PCA carried out on major elements and heavy metals (1–9: sites at the southern part of the lake, 10–13: sites at the eastern part of the lake, 18–26: sites at the northern part of the lake, 28: Soulou River, 29: lignite. For sampling site location see Fig. 1)

Discussion

The Soulou River comprises a significant source for lake organic matter of anthropogenic origin. In fact, organic carbon and total nitrogen are several times higher in river sediments compared with sediments of other Greek rivers, included polluted ones (Skoulikidis, unpublished data). On the other hand, sulfur concentration in river sediments is 2.5 times lower compared to the lake's average and similar to other Greek rivers, suggesting that lignite combustion is the main sulfur source for the lake. The association of V, Co, Ni, Cu, Mn and Fe in lake sediments, as derived from the PCA, suggests the adsorption of trace metals on Fe and Mn oxyhydroxides, as these minerals constitute significant sinks of trace metals through the effect of sorption/co-precipitation (Salomons & Förstner, 1984; Nikolaidis et al., 2004). The relationship of Rb–Ba with silicate, aluminum and potassium is due to the fact, that these metals are constituents

Table 4 Range, Median and Standard Deviation (S.D.) of heavy metal concentrations (ppm) in the sediments of the southern, eastern and northern parts of Lake Vegoritis (s: sampling site)

	South part (s. 1–9)			East part (s. 10–13)			North part (s. 18–26)		
	Min–Max	Median	S.D.	Min–Max	Median	S.D.	Min–Max	Median	S.D.
V	109–127	116.6	6.4	87–110	94.1	10.6	91–101	95.2	4.2
Cr	242–380	318	41.7	291–706	362	194	62–210	156.9	49.2
Mn	826–1,018	911	58.1	712–838	773	70.7	693–795	746	35
Co	26–34	31.8	2.6	24–29	26	2.2	14–25	20.7	3.6
Ni	234–322	283	29.9	245–261	256	7.2	38–204	145.7	55.1
Cu	41–48	42.6	2.6	16–43	28	12.1	24–41	35.5	6.2
Zn	87–103	97	5.5	52–82	67.6	14.4	85–111	95.4	8.2
As	8.5–13.5	12.1	1.5	8.5–14	10.6	2.3	8–15.6	12	2.2
Rb	100–117	112	5.7	47–95	73.5	22.3	118–256	170.4	48.3
Sr	160–212	171	19.5	202–239	225	15.6	205–257	235.2	17.2
Mo	1.5–3.4	2.2	0.6	2.1–2.3	2.2	0.1	1.6–3.6	2.1	0.6
Ba	375–426	412.7	17.4	231–372	298	64	410–964	559	176
Pb	23–27	24.4	1.4	12–23	16.9	5.3	27–40	32.5	4.1

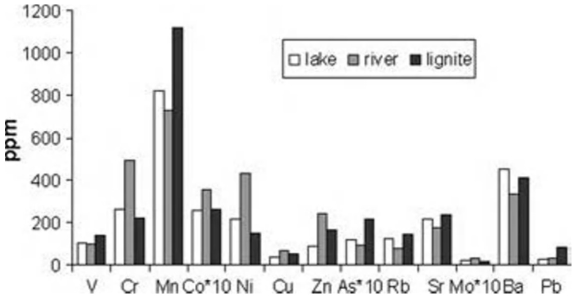

Fig. 6 Comparative concentrations of heavy metals in the sediments of Lake Vegoritis and Soulou River and in lignite

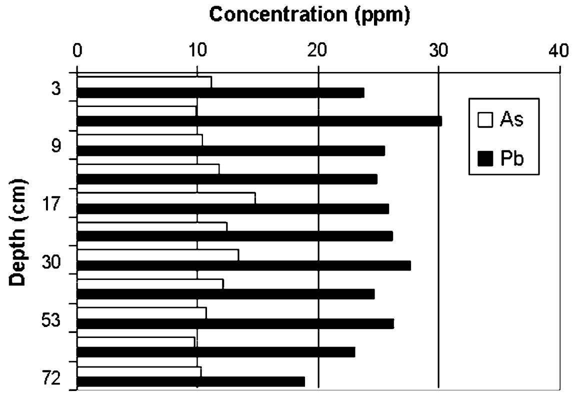

Fig. 7 Depth distribution of As and Pb in the sediment core

of potassium minerals, including illite [$KAl_3Si_3O_{10}(OH)_2$]. The association between calcium, total carbon and Sr is typical for calcite, where Sr replaces Ca since they present similar chemical behavior (Hem, 1985). The relation of Cu, Zn, As, Pb with clay, organic carbon, total nitrogen, and sulfur reveals metal adsorption on rich in organic matter clay material.

For the assessment of the origin of heavy metals in the lake, apart of the aforementioned associations, their spatial distribution in lake sediments and their relative concentrations in lake and river sediments and in lignite were used. Ba and Rb reach maximum concentrations in the north part of the lake as a result of the presence of metamorphic rocks and the dominance of illite in the mineralogical fraction of the sediments. Sr shows highest levels at the north and east parts of the lake due to the predominance of carbonate geology. In the south part of the lake, lignite may account as an additional source for Rb and Sr. The latter may also be derived from fly ash (Table A1—Supplementary material). The main source of Cu, Zn, Ni and Co for the lake is Soulou, which carries, partly treated, industrial and municipal wastewaters, agrochemicals, landfill leachates and geogenic material. Solid and liquid wastes resulting from urban areas are enriched with Cu, Pb, Zn, and Ni (DVWK, 1998), while Cu, Pb, Zn, Cr, Ni, and Co are constituents of agrochemicals (Förstner & Wittmann, 1981). High Pb and Zn concentrations at the north part of the lake are attributed to metal sulfides found in metamorphic rocks. Maximum Ni concentrations in the southern part of the lake suggest a prevalence of anthropogenic Ni-sources over geogenic ones, i.e., ophiolites found at the eastern part of the lake. In contrast, mafic rock erosion is the dominant Cr source for lake sediments, since Cr is associated with sand and maximum Cr concentrations occur at the eastern part of the lake. The east part of the lake illustrates minimum concentrations of Mn, Cu, Zn, As, and Pb probably due to the lack of important pollution sources, and minimum Rb and Ba levels, due to the low abundance of K-minerals (Skoulikidis, 2001a). Mn and V, which show higher concentrations at the southern part of the lake, may be derived from lignite weathering/erosion and combustion. The As distribution in lake sediments does not facilitate the partition of its sources. Application of arsenical compounds as pesticides and herbicides are band. Fly ash from Ptolemais area contains high As concentrations (Table A1—Supplementary material), while river sediments revealed lower concentrations than lake sediments. Therefore, it is assumed that the main As source in Lake Vegoritis is fly ash.

Despite the prolonged anthropogenic pressures on the lake, the majority of metal concentrations in sediments are below the health standard limits. Only arsenic and chromium will be considered hereafter, since their concentrations in the lake may pose toxic hazards to the environment and to humans. Concerning As, the concentration in lake sediments did not exceeded the limits for undisturbed soils, according to Eikmann & Kloke (1993) and VROM (1988). Nevertheless, over 80% of the samples surpassed the 10 ppm threshold for residential areas according to the State of Connecticut regulations (1996). Regarding Cr, all, except one, sites exceeded 100 ppm, indicating disturbance. The State of Connecticut (1996) sets distinct limits for Cr(III) and Cr(VI). The Cr(VI) limit for residential areas soils is 100 ppm.

As described before, the water level of the lake underwent a dramatic diminishing in the past half century. Only between 1981 and 1993, the surface area of the lake reduced by 13 km^2 (Antonopoulos & Gianniou, 2003). As a result, huge sediment amounts were exposed to the atmosphere. Although there is an incomplete understanding of the biogeochemical controls on arsenic transformation among reservoirs (sediment—aqueous—atmosphere) (Nicholas et al., 2003), an attempt will be made to assess its toxicity in exposed sediments. Arsenic is a toxic and well known human carcinogen (IARC, 1987). In environmental media, arsenic exists as As(III) (arsenite) or As(V) (arsenate). Arsenite is considered as more toxic (Morton & Dunnette, 1994; Yamauchi & Fowler, 1994). Human exposure to As, includes ingestion of food and water and inhalation of airborne particulates. As sediments shift to anoxic sulfidic environments, a repartition of bound arsenic from iron and manganese compounds to the sulfide phase is possible (Moore et al., 1988). Anoxic sediments can, therefore, become an arsenic sink. The likelihood for arsenic to appear as sulfide in the lake is high, since waters inflowing to the lake are rich in sulfate (average sulfate concentration of Soulou river amounts 245 mg/l), lignite combustion cause high SO_2 emissions and sediment conditions are anoxic. Moreover, there is an association between As and sulfur in the sediments of the lake (Table 3). Exposure of the sediments due to the lake level drop results in the re-establishing of oxic conditions and sulfides can be oxidized releasing arsenic. In that case, arsenic could pass in the trophic chain of the terrestrial ecosystem. The microbial activity of soils alters causing hazards to biota (Luh et al., 1973). Arsenic could also be transported with dust and, acting cumulatively to fly ash, may pose adverse effects to humans, e.g., cardiovascular disease, peripheral vascular disease, developmental effects, neurologic and neurobehavioral effects, diabetes, hearing loss, portal fibrosis of the liver, lung fibrosis, hematologic effects and carcinogenic effects (Chen & Linn, 1994).

The stable forms of chromium are the trivalent Cr(III) and the hexavalent Cr(VI) species. Cr(VI) is a potent, extremely toxic carcinogen (SRC, 1993), 10–100 times more toxic than Cr(III) (Katz & Salem, 1994). Human exposure to chromium includes ingestion of food and water and inhalation of airborne particulates. Under oxic conditions, Cr(III) may be oxidized to Cr(VI), which can lead to serious environmental consequences (Bartlett, 1991). What happens when wetted sediments gradually dry out? Masscheleyn et al. (1992) found out that Cr(III) in floodwater may be oxidized to Cr(VI) by iron and manganese oxyhydroxides, while if any Cr(VI) is present in floodwater it will not be reduced to Cr(III). However, the oxidation of Cr(III) to Cr(VI) is restricted by the availability of mobile Cr(III)

(Bartlett, 1991), it is a very slow process (Eary & Rai, 1987) and is expected to decrease when sediments dry out (Zayed & Terry, 2003). Hence, when sediments are exposed to the atmosphere, it is assumed that if any Cr(VI) is present it will remain as that, while only a small part of Cr(III) will be oxidized to Cr(VI). Only if over one-thirds of chromium concentration found in lake Vegoritis sediments is present as Cr(VI), could pose hazards to humans (e.g., lung carcinogenesis, toxicity through oral or dermal exposure) and to the environment, e.g., toxic effects in terrestrial and aquatic plants (Dirilgen, 1998; Shanker et al., 2005) and amphibians (Calevro et al., 1998).

Conclusions

In the late 1950s, the area started to develop industrial and agricultural activity, which gradually became intense. At the same time the first thermal power stations started operating. Since the lakes sediments were ~30 cm below their present level, it was expected that this sediment fraction should be more impacted with anthropogenic elements. Nevertheless, it was found that there was only a slight enrichment in the upper section of the sediments for selected elements (S, As, Mn, Sr, and Pb). In addition, heavy metal levels in surface sediments are generally low compared to concentrations found in reference lakes, typical concentration levels of different types of rocks and soils and recommended thresholds in soils. It is assumed, that the increase of the sedimentation rate during the last half century, in combination with the low retention time of the lake water, cause a "dilution" of pollutants, and positively affects the environmental state of the lake. Only Cr, Ni, Co, As, and Ba exhibited relatively high concentrations in lake sediments, whereas only As and Cr presented concentrations that could be regarded as toxic. The main source for arsenic is considered to be fly ash, while chromium mainly derives from mafic rocks. Since 1956, when lake water started to be used for hydropower production, the lake level was lowered by almost 30 m and large lake sediment surfaces were exposed to the atmosphere. Exposure of sediments results in re-establishing of oxic conditions causing oxidation of As-sulfides and of Cr(III) to Cr(VI). These metals may then pass in the trophic chain of the terrestrial ecosystem or may be transferred with dust particles. Regarding chromium, it is estimated that only when over one-thirds of Cr found in lake sediments is present as Cr(VI), could pose hazards to the environment and to humans. In order to secure humans and ecosystem health, future research should focus on the valency of chromium and arsenic, their bioavailable fraction, as well as the biogeochemical processes that control their mobility.

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WATER-LEVEL FLUCTUATIONS

Temporal scales of water-level fluctuations in lakes and their ecological implications

Hilmar Hofmann · Andreas Lorke · Frank Peeters

Abstract Water-level fluctuations (WLF) of lakes have temporal scales ranging from seconds to hundreds of years. Fluctuations in the lake level generated by an unbalanced water budget resulting from meteorological and hydrological processes, such as precipitation, evaporation and inflow and outflow conditions usually have long temporal scales (days to years) and are here classified as long-term WLF. In contrast, WLF generated by hydrodynamic processes, e.g. basin-scale oscillations and travelling surface waves, have periods in the order of seconds to hours and are classified as short-term WLF. The impact of WLF on abiotic and biotic conditions depends on the temporal scale under consideration and is exemplified using data from Lake Issyk-Kul, the Caspian Sea and Lake Constance. Long-term WLF induce a slow shore line displacement of metres to kilometres, but immediate physical stress due to currents associated with long-term WLF is negligible. Large-scale shore line displacements change the habitat availability for organisms adapted to terrestrial and aquatic conditions over long time scales. Short-term WLF, in contrast, do not significantly displace the boundary between the aquatic and the terrestrial habitat, but impose short-term physical stress on organisms living in the littoral zone and on organic and inorganic particles deposited in the top sediment layers. The interaction of WLF acting on different time scales amplifies their overall impact on the ecosystem, because long-term WLF change the habitat exposed to the physical stress resulting from short-term WLF. Specifically, shore morphology and sediment grain size distribution are the result of a continuous interplay between short- and long-term WLF, the former providing the energy for erosion the latter determining the section of the shore exposed to the erosive power.

Keywords Water-level fluctuation · Waves · Remobilisation of particles · Shore formation · Habitat conditions · Littoral zone

Introduction

Water-level fluctuations (WLF) and their ecological and socio-economic consequences have been investigated in large lakes, e.g. Aral Sea (Usmanova, 2003; Zavialov et al., 2003), Lake Chad (Guganesharajah & Shaw, 1984; Coe & Foley, 2001), Great Salt Lake (Stephens, 1990) or Salton Sea (Bourne et al., 2005) and also in small lakes and reservoirs, e.g. (Hunt & Jones, 1972; Coops et al., 2003; McGowan et al., 2005; Naselli-Flores & Barone, 2005). The reasons

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Ecological Effects of Water-Level Fluctuations in Lakes

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and causes of WLF can be various: Hydrologically induced WLF are connected to climatic changes, changes in the constellation of large atmospheric pressure systems (North Atlantic and Southern Oscillation), or, most frequently, to seasonal variations in meteorological conditions. They can also be the result of anthropogenic use of water resources, as in the case of the Aral Sea (Usmanova, 2003). Hydrologically induced WLF are the result of a change in the water budget and, therefore, depend on the amounts of precipitation and evaporation, catchment size and characteristics, and on the discharge conditions (inflow versus outflow) of the basin. Prominent examples are Lake Constance (Luft & van den Eertwegh, 1991; Jöhnk et al., 2004) or Lake Issyk-Kul (Brennwald et al., 2004). The time scales of the hydrologically induced WLF range from days to centuries (and even up to geological time scales) and will be referred to as long-term WLF throughout this paper. Wind forcing and ship traffic affect the surface-wave field and cause WLF on time scales on the order of seconds to hours. These hydrodynamically driven WLF are classified throughout this paper as short-term WLF.

Here, we present examples for WLF at different temporal scales from a physical oriented perspective and discuss their implication on the lake ecosystem with specific emphasis on the littoral zone. WLF are presented in an order of decreasing time scales, beginning with a time scale of centuries and ending with a time scale of seconds. Examples are taken from different lakes: Lake Issyk-Kul (Kyrgyzstan) for century scales, the Caspian Sea for decadal scales and Lake Constance for shorter time scales spanning years to seconds.

Long-term WLF and their ecological impacts are subject of a number of papers throughout this special issue. Here, we will put special emphasis on the discussion of short-term WLF. Often, the latter are not considered in the context of WLF, although they can have a major impact on the abiotic and biotic processes in the littoral zone. Several studies have investigated the impact of short-term WLF on coastal and shelf regions (Clark, 1997; Eriksson et al., 2004; Soomere, 2005; Erm & Soomere, 2006). Only a few investigations, however, have focused on lake-littoral zones (Luettich et al., 1990; Eggleton et al., 2004; Scheifhacken, 2006). Information on short-term WLF are required for the understanding of shore formation, which is the result of the interaction between short- and long-term WLF. Furthermore, short-term WLF impose physical stress on aquatic and riparian plants and organisms. This stress varies with the properties of the substrate (e.g. sand or stones), which, in turn, is altered by long-term WLF moving the boundary of the aquatic habitat up or down the shore. Hence, short-term WLF are important for an understanding of the ecological consequences of long-term WLF for aquatic organisms living in the littoral zone.

In the following sections, we first provide information on the materials and the methods used in this study. Then we present data on long-term and on short-term WLF at the example of Lake Constance. The subsequent discussion is focused on the impact of long- and short-term WLF on the littoral ecosystem, and specifically emphasises the importance of the combined effect of both. In the final section we summarise the main conclusions of the paper.

Materials and methods

Daily readings of water levels at gauge Konstanz for the time period 1817–2005 were provided by the State Institute for Environment, Measurements and Nature Conservation Baden-Württemberg (LUBW). The water levels are measured relative to the reference level of the gauge (391.89 m a.s.l., level Amsterdam). The water level time series was corrected for reading errors between 1817 and 1825 (Jöhnk et al., 2004). Note that between 1817 and 1876 the resolution of water level readings was only 3 cm, thereafter 1 cm.

Short-term WLF were measured using a pressure sensor with a resolution of 0.1 mbar, corresponding to about 1 mm water level. Measurements were carried out in the western part of Upper Lake Constance at a site called Littoral Garden (LG; 47°41′29″ N, 09°12′11″ E). The pressure sensor was deployed 1 m above the sediment at 2.0–2.5 m water depth and measured at a sampling frequency of 16 Hz throughout the entire year 2005. Pressure is a direct measure of water level only under hydrostatic conditions. However, the assumption of hydrostatic conditions is valid only if the wave length of the WLF exceeds a critical wave length of about 20 times the local water depth. WLF generated by surface gravity waves usually have a wave length that is significantly shorter than this critical wave length. Hence, the calculation of water level and WLF from pressure measurements requires a correction for pressure attenuation that depends on the water depth, the depth of the sensor and the wave length (Kundu & Cohen, 2002; Hofmann et al., 2008). In the procedure wave length was calculated from wave frequency using the approximation to the dispersion relation of surface gravity waves by Fenton & McKee (1990).

Maximum near-bottom current velocities generated by surface waves, $u_{\max}$ (m s^{-1}), were estimated using (Brown et al., 2005):

$$u_{\max} = \frac{\pi \cdot H}{T \cdot \sinh \frac{2 \cdot \pi \cdot h}{\lambda}} \quad \left(\mathrm{m\ s^{-1}}\right) \qquad (1)$$

where H denotes the wave height (m), h the water depth (m), λ the wave length (m) and T the wave period (s). The remobilisation of particles is related to $u_{\max}$ and can be determined from empirical equations. For non-cohesive sediments with a mean grain size d_{50} between 0.063 and 2 mm (sand fraction) the formulation by Hallermeier (1980) was used to estimate the remobilisation of particles at 1 m water depth in the littoral zone of Lake Constance.

An Acoustic Doppler Velocity Meter (ADV) was deployed close to the pressure sensor at the site LG throughout the entire year 2005. The instrument measured the 3-dimensional current velocity 0.05 m above the sediment (at 1–2 m water depth) with a sampling frequency of 8 Hz. Current velocities associated with distinct frequencies (e.g. 54.6 min for the first-mode surface seiche in Lake Constance; see Table 1) were estimated using spectral analysis (Emery & Thomson, 2001).

Results

Long-term WLF

In the following we analyse long-term WLF from Lake Constance, the second largest prealpine lake in Europe with a surface area of 536 km^2 and a maximum water depth of 254 m (Braun & Schärpf, 1990). Lake Constance and its main tributary, the river Rhine, are almost unregulated and the lake level shows a strong seasonal cycle. The level declines during winter and typically reaches the annual minimum at the end of February, when precipitation in the catchment area is, to a large extent, stored as snow. The lake level typically reaches an annual maximum in June/July due to increased snow melt in spring (Luft & van den Eertwegh, 1991; Jöhnk et al., 2004). Long and intense precipitation in the catchment area in combination with snow melt can result in extreme floods with rapidly increasing water levels. Some examples of major flood events are marked in Fig. 1a. The relative height in the figure indicates the

Table 1 Temporal scales of WLF with the corresponding amplitudes and estimated maximum near-bottom current velocities. Whereas long-term WLF are generated by meteorological and hydrological processes, short-term WLF are generated by hydrodynamic processes

Example		Temporal scale	Amplitude (m)	Near-bottom velocity (m s^{-1})
Issyk-Kul	Long-term WLF	~2,000 yr	~250	≪10^{-3}
Caspian Sea		20–100 yr	~2.5–4	
		1–10 yr	1–3	
		1 yr	0.5	
		0.5 yr	1–4	
		1 day	0–0.5	
Lake Constance	Short-term WLF	54.6^{a} min	0.02–0.05	10^{-3}
		6.3^{b} s	~0.04	10^{-2}
		3.3^{b} s	0.1–0.5	10^{-1}
		2^{b} s	0–0.8	10^{-1}

[a] Surface seiching and [b] surface waves generated by fast catamaran ferries (6.3 s), passenger ships or ferries (3.3 s) and wind (2 s) measured at Lake Constance

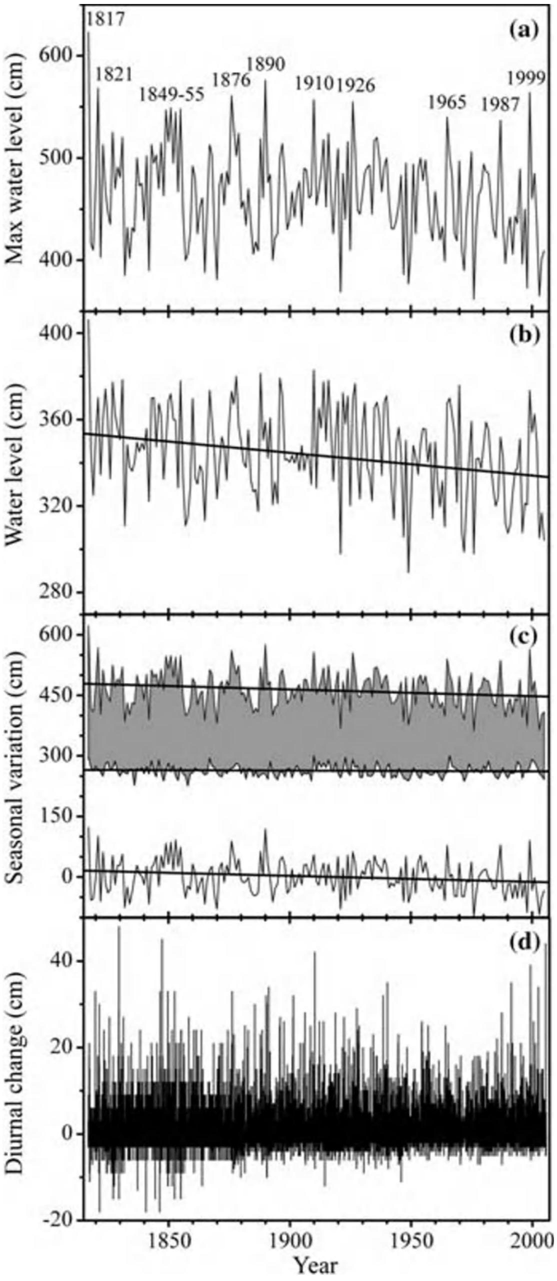

Fig. 1 Lake-level time series at gauge Konstanz (Lake ▶ Constance) based on daily measurements from 1817 to 2005. (**a**) Annual course of the maximum water levels. Major floods are marked by the individual year or period, whereas the height corresponds to the importance of the flood. (**b**) Mean annual water levels with linear regression line. (**c**) Seasonal variations within a single year (filled grey surface) determined as the difference between the maximum and minimum water level of the respective year. Linear regression lines emphasise the trend of the maximum and minimum water levels. The solid line fluctuating around zero shows the annual deviation from the mean of the seasonal WLF (over the whole time series) with its linear regression line. (**d**) Diurnal change of the water level shown as the difference between the daily mean values

importance of the events (Luft & van den Eertwegh, 1991; Jöhnk et al., 2004). The greatest flood within the time period considered here was observed in 1817 with 623 cm above reference level. Other floods between 525 and 575 cm occur more frequently with an average recurrence time period of about 12 yr. Maximum water levels between 400 and 500 cm seem to be a regular range within the gauge Konstanz time series (Fig. 1a).

Linear regression reveals that the annual mean water level shows a significant long-term trend and declined by about 21 cm between 1817 and 2005 (slope: -0.11 ± 0.03 cm yr^{-1}, $P < 0.01$; Fig. 1b). From 1817 to 1940 the annual mean water level shows no significant trend (slope: -0.008 ± 0.05 cm yr^{-1}, $P = 0.87$), but from 1941 to 1980 the level started to decrease (slope: -0.12 ± 0.14 cm yr^{-1}, $P = 0.40$). This decrease is even more pronounced during the last two and a half decades (slope: -0.41 ± 0.57 cm yr^{-1}, $P = 0.48$) and is mainly caused by decreasing maximum water levels in summer. The reasons for the obvious break point around 1940 and the ongoing decline in water level has been widely discussed and was explained by changes in hydraulic discharge conditions and climatic changes in the catchment area (Luft & Vieser, 1990; Jöhnk et al., 2004).

Inter-annual WLF, determined from the difference between the annual mean water levels of consecutive years (Fig. 1b), are about 20 cm ± 17 cm (SD) on average. The maximum of the inter-annual WLF was 75 cm between 1921 and 1922.

Seasonal WLF can be quantified by the difference of the minimum and maximum water level with respect to the mean water level of the particular year (Fig. 1c). Extreme seasonal WLF reach up to more than 300 cm and occur in years with unusually high maximum water levels. The linear regressions of the annual maximum (slope: -0.17 ± 0.06 cm yr^{-1}, $P < 0.01$, ± 45 cm yr^{-1} SD) and minimum (slope: -0.02 ± 0.02 cm yr^{-1}, $P = 0.33$, ± 14 cm yr^{-1} SD) water level indicate a significant decline in the seasonal WLF from about 215 cm at the beginning of the 19th century to about 185 cm at the beginning of the 21st century (Fig. 1c). The long-term decline is caused by the decrease in the annual maximum water level, where in contrast the annual minimum water level remained constant. This also explains the observed trend of the annual deviation from the mean of the seasonal WLF (slope: -0.15 ± 0.06 cm yr^{-1}, $P < 0.01$, ±42 cm yr^{-1} SD; Fig. 1c) which is mainly stated by the deviation of the annual maximum water level and, thus, shows the same significant decline. The decrease in the seasonal WLF especially during the last decades can be partly explained by the construction of hydropower reservoirs in the catchment (Luft & van den Eertwegh, 1991; Jöhnk et al., 2004).

Over a single day, the water level can change by up to 40 cm (Fig. 1d). Such rapid increases in water level are always caused by extreme discharge events of the river Rhine resulting from intense precipitation in the catchment. Large water level increases continuing over several consecutive days can lead to major flood events (Luft & van den Eertwegh, 1991). However, the typical daily decrease or increase in water level is much smaller than the extreme case mentioned above and typically ranges only from -5 to 10 cm (Figs. 1d, 2a).

Short-term WLF

Short-term WLF, at scales from seconds to hours, are mainly caused by hydrodynamic processes. In the following section we analyse high-frequency and high-resolution data of surface water level (estimated from pressure measurements) and current velocity from the littoral zone of Lake Constance. Single-day time series were chosen to explain the temporal variability of hydrodynamic processes on 17 and 26 January 2005 (Fig. 2a, b). Both days differ considerably due to different surface forcing generated by strong on-shore wind on 26 January 2005 and no wind on 17 January 2005.

A very prominent feature of enclosed water bodies are basin-wide oscillations of the surface level, often referred to as surface seiching (Mortimer, 1974; Lerman et al., 1995). The periods of such basin wide oscillations, called "modes", are determined by the morphology of the basin. The first-mode surface seiche in Lake Constance has a period of 54.6 min and can be seen in the running average applied to the surface level time series shown in

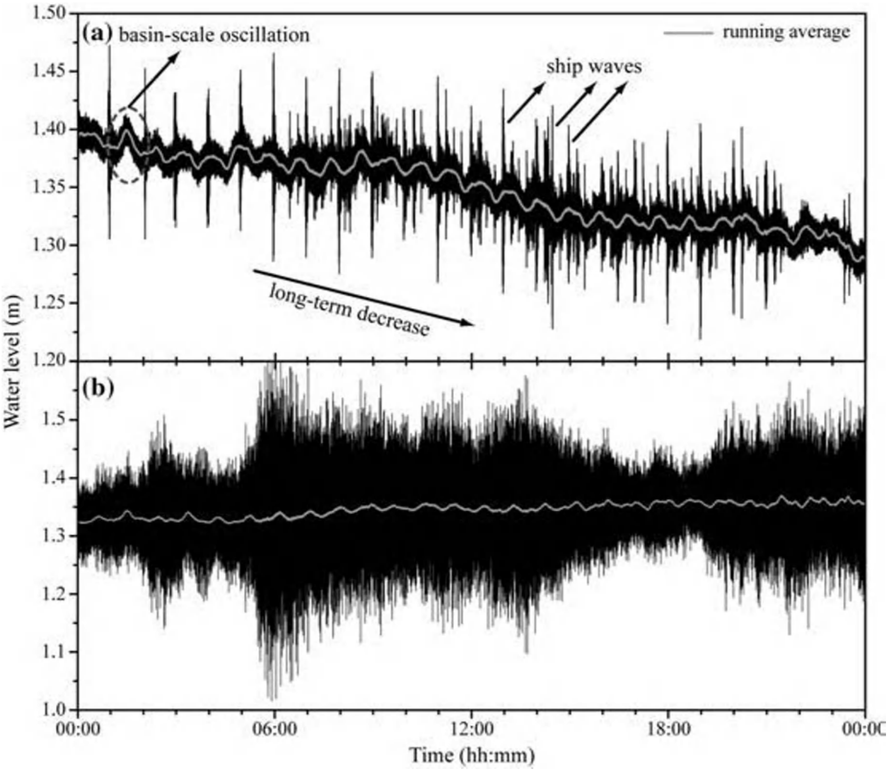

Fig. 2 High-frequency (16 Hz) and high-resolution (1 mm) measurements of the water level over a single day. (**a**) On 17 January 2005 under a no wind situation. (**b**) On 26 January 2005 under a strong (wind speed was about 9–10 m s^{-1}) on-shore wind. The different arrows point out examples of different temporal scales of WLF, e.g. long-term decrease in water level (diurnal change), basin-scale oscillation and short-term WLF generated by ship waves. The 1 min running average highlights the basin-scale oscillation with a magnitude of about 2 cm (emphasised by the dashed grey ellipse with arrow)

Fig. 2a, b, although the period may differ slightly depending on the actual water level of the lake (Hollan et al., 1981). The vertical displacements of the water surface associated with the first-mode surface seiche are only a few centimetres and were measured to be about 2 cm at the measuring site LG (Fig. 2a, b). These lake level oscillations are excited by wind forcing at the water surface or due to atmospheric pressure gradients. Power spectra of high-frequency pressure time series show several spectral peaks with periods between minutes and one hour. Numerical calculations suggest that these peaks correspond to level fluctuations due to second-, third- or even higher-order modes of basin-scale surface oscillations of Lake Constance (Bäuerle, pers. comm.).

From an ecological perspective, travelling surface gravity waves are probably the most important short-term WLF. Such waves are generated by wind or by ships and are usually classified as wind waves and ship waves. Both types of waves were measured, characterised and analysed at Lake Constance (Fig. 2a, b; Hofmann et al., 2008). Ship waves cause very harmonic and regular surface oscillation and their periods are determined by their excitation, which is characteristic for each individual ship. The frequency of occurrence and the wave heights of ship waves are highly predictable in time for Lake Constance. They are controlled by the regular sailings of various ferry lines throughout the year with each individual wave group identified as a distinct signal (Fig. 2a; Hofmann et al., 2008). Wind waves in contrast are irregular and are determined by the length of the effective wind fetch and the wind speed, which changes from site to site. Ship waves generated by ferries, passenger ships, or by the recently introduced fast catamaran ferries have wave periods of 2.9–6.3 s, characteristic wave heights of 0.04–0.5 m and wave lengths of 13–50 m (assuming deep-water waves); whereas the wave periods, heights and lengths of wind waves are 1.5–2.3 s, up to 0.8 m, and 2–8 m, respectively (Fig. 2a, b; Hofmann et al., 2008). If no wind is present, the wave field is dominated by ship waves (Fig. 2a), which are masked by the higher wind waves during periods of strong on-shore wind (Fig. 2b). Depending on the duration of wind forcing, wind waves can dominate the wave field for hours or even days (Fig. 2b).

Discussion

Impacts of long-term WLF

Since long-term WLF are associated with large shore line displacements, the major impact of long-term WLF on lake ecosystems is a change in habitat. Long-term WLF flood formerly dry shore areas or expose submerged sediment surfaces to the atmosphere. Thus, long-term WLF play a role in the selection of sessile species adapted to dry or wet conditions. In addition, long-term WLF result in a change of the properties of the sediment surface in the littoral zone, because the grain sizes in the shore region are not homogeneously distributed but change from large to small towards deeper regions of the lake. In the following we provide examples for the range and consequences of long-term WLF.

Based on noble gas concentrations in sediment pore water Brennwald et al. (2004) concluded that the water level of Lake Issyk-Kul, one of the largest and deepest lakes in the world (volume: 1,740 km^3, max. depth: 668 m) located in Kyrgyzstan, has been at least 250 m lower during the mid-Holocene than today. As Lake Issyk-Kul is a closed basin lake, its water level is very sensitive to changes in the meteorological conditions. The drop in water level by 250 m during the mid-Holocene implies a shore line displacement of 20–60 km and a reduction of water volume by more than 40%. During low water level the salinity was more than twice its present value of 6‰ as indicated by noble gas data from the pore water (Brennwald et al., 2004). WLF induced salinity changes between 6‰ and above 12‰ can be expected to have had severe effects on the species composition, because most freshwater animals cannot survive in waters with salinities of more than 10‰ (Wetzel, 2001). This long-term WLF had clearly visible consequences for the basin morphology. During low water level, rivers caused large gully erosion especially in the eastern shallow region, which was dry at this time, resulting in channels of 100 m depth (Tsigelnaya, 1995). Today, these ancient shallow regions are 20 m below water level and the flooded channels play an important role in the renewal and the oxygenation of the deep water in Lake Issyk-Kul (Peeters et al., 2003). Hence, today's high oxygen levels in the deep water can be considered as an indirect consequence of the long-term WLF.

Long-term WLF on decadal time scales have been recorded for the Caspian Sea, the largest inland water body (with respect to surface area and volume) on earth. Between 1880 and 1978 the level of the Caspian Sea decreased by 4 m and then rose again by 2.5 m within 20 yr. According to Rodionov (1994) the sea level fluctuations of the Caspian Sea are caused by variations in the inflow, which resulted from natural fluctuations of the North Atlantic Oscillation (NAO) and, to a minor extend, by anthropogenic influences, e.g. the use of Volga water for irrigation (Klige & Myagkov, 1992). The vertical amplitudes of the WLF of the Caspian Sea are small compared to those mentioned above for Lake Issyk-Kul, but the associated change in surface area is much higher with about 50,000 km^2. The inflow of freshwater related to the water level increase during the 1980s and 1990s caused a significant reduction in vertical mixing, which resulted in nearly anoxic conditions in the deep water (Peeters et al., 2000). The consequence of a long-term increase in water level for internal mixing processes is particularly important in saline lakes, e.g. Mono Lake (Romero & Melack, 1996) or Caspian Sea (Peeters et al., 2000), because a change in water level is usually associated with freshwater inflow that leads to an increase in water column stability, and thus, hinders convective mixing processes. In freshwater lakes and reservoirs long-term WLF have an impact on vertical mixing only if the level is altered substantially, e.g. if the level is reduced sufficiently that wind forcing or nocturnal convection reaches down to the lake bottom of a formerly dimictic or monomictic lake.

The above examples demonstrate that long-term WLF can influence the oxic state of saline lakes, which in turn affects sediment–water exchange and the chemical composition of the deep-water. Long-term WLF have also implications on socio-economic circumstances. The Aral Sea is a very drastic example (Usmanova, 2003). However, in the Caspian Sea the comparatively small decline until 1978 caused rapidly decreasing ground water levels, which resulted in a drastic reduction of agricultural production (Kosarev & Yablonskaya, 1994). The rising sea level in the 1980s and 1990s destroyed infrastructure built along the shore line during the period of low water level (Dumont, 1995). Furthermore, the strong decline in the abundance of sturgeon in the Caspian Sea during the last decades has been explained by the reduction of appropriate spawning grounds (Khodorevskaya & Krasikov, 1999). Impacts of long-term WLF on fish reproduction have been demonstrated in Lake Constance as well as in other lakes. The temporal variability of seasonal WLF affects the fish specific substrate availability for spawning, and hence determines egg mortality and breading success (Gafny et al., 1992). Also water birds are affected by long-term WLF at Lake Constance (Werner, pers. comm.). Especially low water levels in spring reduce the availability of appropriate breeding-sites, and hence increase the mortality due to predation. Seasonal or even longer-lasting WLF also cause shifts and variations of the riparian plant community, e.g. diversity, abundance and structure (Kotowski & Pioŕkowski, 2005). In contrast, flood events as specifically drastic long-term WLF can have severe effects on a former established plant community. Schmieder et al. (2004) has documented the degradation of reed belts after early spring floods at Lake Constance.

Impacts of short-term WLF

Since short-term WLF do not induce large horizontal shore-line displacements but are accompanied by high current velocities near the sediment (Table 1), their major impact on the lake ecosystem is the imposition of hydrodynamic stress on organisms living in the shore region and on the sediment surface. The hydrodynamic stress affects ecological processes such as competition between individual organisms, short-term production and losses in biofilms and erosion of sediments. The impact of the short-term WLF is, however, variable in strength and time.

Wind and ship waves can be observed throughout the entire year and at any lake shore as long as no ice cover exists. However, wave heights and frequencies can vary substantially due to the different exposure to wind or ship traffic (see section "Short-term WLF"). Particularly affected by short-term WLF are the shallow littoral zones of lakes, even if wave heights are small. Note that the littoral zone is of specific importance to the entire ecosystem because they are characterised by high species diversities and abundances and are important for the reproduction and the life cycle of many fish species.

The availability and intensity of light, as an indispensable resource for primary production of

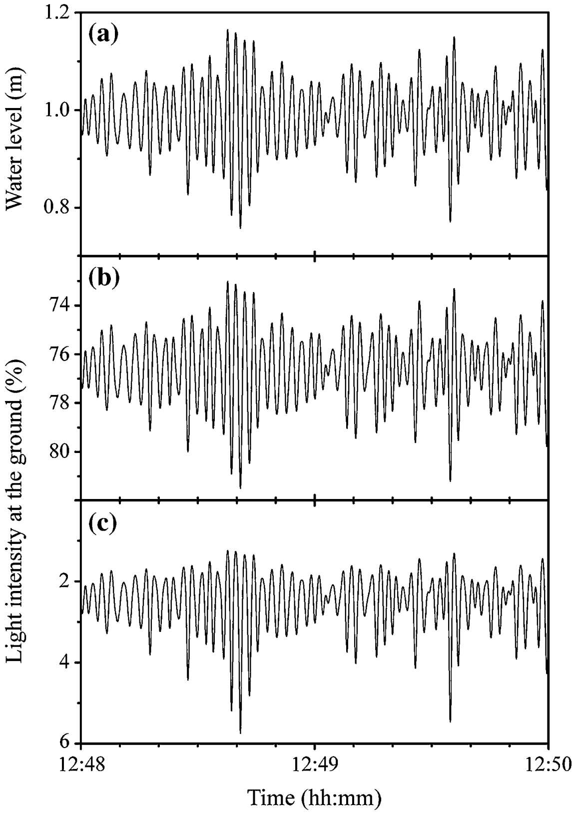

Fig. 3 Wave-generated high-frequency water level and light fluctuations. (**a**) Water-level fluctuations measured in Lake Constance on 18 September 2005 during a period of strong on-shore wind. Light intensity fluctuations at the ground are given as percents of the incoming light intensity at the water surface. (**b**) For clear water. The light intensity was calculated for an exponential decay of light with depth using an average extinction coefficient (K_d) of 0.27 m^{-1} representative for pelagic waters (IGKB, 2002). (**c**) Considering the additional shading effect due to resuspended particles in the shallow littoral ($K_{dss} = 0.27 + 0.025*C_{ss}$) (van Duin et al., 2001). The particle concentration C_{ss} was measured to 140 mg l^{-1} during the time of measurement

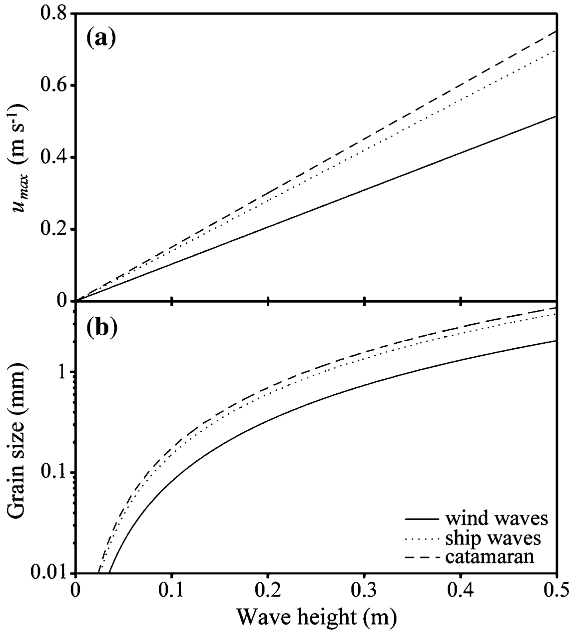

Fig. 4 Potential forcing of short-term WLF in the littoral zone. (**a**) Maximum wave-generated near-bottom current velocity (u_{max}) at 1 m water depth as a function of wave height and wave period (T) for wind-generated ($T = 2$ s) and ship-generated ($T = 3.3$ and $T = 6.3$ s) waves, respectively. (**b**) Minimum wave heights required for the remobilisation of particles of different grain sizes as a function of wave period (as under (**a**)) at the water depth of 1 m

phytoplankton in the water column or of periphyton on stones and on the sediment surface, is affected by short-term WLF. Fluctuations of the under water light intensity associated with short-term WLF due to wind waves are exemplified in Fig. 3. During on-shore wind on 18 September 2005, short-term WLF (wind waves) with a period of about 2 s and wave heights between 0.1 and 0.4 m were observed (Fig. 3a) and caused light intensity fluctuations at the ground of 2–8%, based on exponential light decay with an average extinction coefficient (K_d) of 0.27 m^{-1} representative for pelagic waters (Fig. 3b; IGKB, 2002). The remaining mean light intensity at 1-m water depth is then about 77% of the incoming light at the water surface. Fluctuations of the under water-light intensity can be further amplified by wave focussing which increases the light intensity within milliseconds up to five times of the mean value (Dera & Gordon, 1968; Stramski & Legendre, 1992; Schubert et al., 2001; Hofmann et al., in press). In the shallow littoral the observed surface waves induce resuspension of particles with grain sizes up to 1 mm at 1-m water depth (Fig. 4b). The increased back-scatter of light due to suspended particles leads to intense shading and reduces dramatically the light intensity at the sediment surface down to 2–3% of the incoming light at the water surface (Fig. 3c; van Duin et al., 2001). During an individual wind event, which can last for more than one day, primary production can be reduced or even inhibited (van Duin et al., 2001). In the aftermath of such events the remobilised and suspended particles settle down and cover biofilms and periphyton on stones. The frequency of

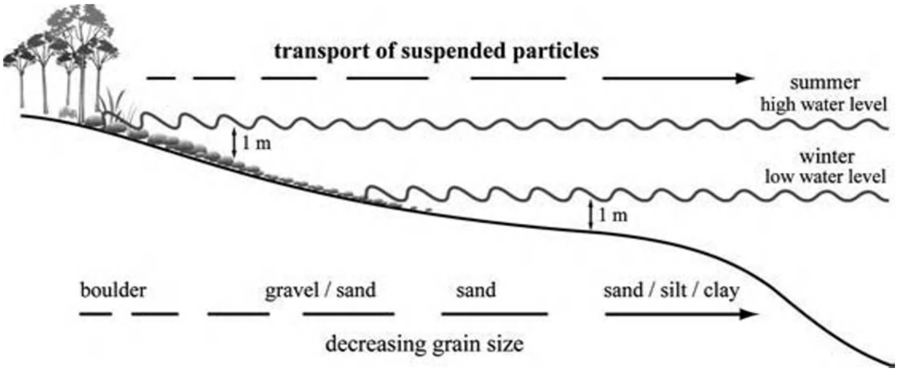

Fig. 5 Sketch of a typical prealpine shore line for different water levels. The sketch indicates the interactions and impacts of long-term versus short-term WLF on remobilisation, resuspension, transport and distribution of particles in the littoral zone

occurrence of strong wind events determines the density and appearance of periphyton in the shallow littoral, and hence indicates the habitat exposure to hydrodynamic disturbances (Cattaneo, 1990; Airoldi & Cinelli, 1997; Francoeur & Biggs, 2006).

Also higher developed organisms are influenced by hydrodynamic stress due to waves. The comparison of zoobenthos and fish communities at surface wave exposed and non-exposed shores revealed the different sensitivity, selectivity and species composition of these communities in many studies (Clark, 1997; Abdallah & Barton, 2003; Eggleton et al., 2004).

The high productivity of the shallow littoral zone results in intense microbial decomposition rates of organic material (Wetzel, 2001). The sequence of production and decomposition is forced by boundary conditions as nutrient availability or the renewal of diffusive gradients for deoxidisation of organic material to carbon dioxide and methane. High current velocities and strong turbulence associated with shoaling surface waves enhance solute diffusion across the sediment–water interface (Lorke et al., 2003), lead to remobilisation of particles and reallocation of sediment layers (Fig. 4b), and hence reset the adjusted gradients due to increased pore-water exchange (Precht & Huettel, 2003; Precht et al., 2004). An important implication is the rapid release of recycled nutrients and methane (Li et al., 1997; Asmus et al., 1998; Heyer & Berger, 2000; Schulz et al., 2001).

Interacting long- and short-term WLF

The discussion above exemplifies the impacts of WLF on abiotic or biotic processes at very different temporal scales. In the following we demonstrate that the interaction between different time scales, i.e. the interaction between long-term and short-term WLF, has important ecological consequences.

With respect to WLF, Lake Constance can be considered to represent natural conditions typical for prealpine lakes before their regulation. The seasonal change in water level is about 2 m. During summer, the entire shore region up to the very shallow littoral is covered with water, whereas in winter the littoral is reduced to a very narrow zone along the steep slope of the lake (Fig. 5). At low water levels the shallow littoral is not submersed, and hence widely exposed to atmospheric decomposition, weathering and deflation. These processes change the former sediment composition, where rock will break up and fine particles will be blown away or deposited.

Waves impose hydrodynamic shear stress on the lake bottom and initiate sediment remobilisation, resuspension and transport due to background currents in cross- or along-shore direction. Remobilisation of particles at the sediment surface depends on water depth, grain size, wave height and wave period. The maximum near-bottom wave-generated current velocity $u_{\max}$ at the sediment surface at 1-m water depth was estimated for wave heights of 0–0.5 m and for wave periods of 2, 3.3 and 6.3 s (Eq. 1, Fig. 4a). These represent typical values at Lake Constance for wind waves, for ship waves generated by permanent ferries or passenger ships and for ship waves generated by fast catamaran ferries, respectively (Hofmann et al., 2008). Long-periodic ship waves induce much higher velocities at the ground and remobilise much larger particles in comparison to wind waves with the same height (Fig. 4a, b). For example, with a wave height of 0.2 m, wind waves remobilise particles of grain sizes up to 0.3 mm, whereas ship waves are able to remobilise particles with grain sizes up to 0.6 mm. This demonstrates the importance of ship waves for sediment remobilisation at exposed shores. Although wind and ship waves occur throughout the whole year, they develop their main impact at different sections of the littoral zone due to seasonal, long-term WLF (Fig. 5). Due to the shore line displacement by seasonal WLF the substrate at the ground at shallow depths varies substantially over the year. During summer, when the water level is high, the substrate consists mainly of boulders, cobbles, gravel and sand. In winter, the substrate at low water levels is formed by much smaller particles like fine sand, silt and clay (Fig. 5). Therefore, the same wind and ship waves result in much higher rates of remobilisation, resuspension and transport into the pelagic zone during winter than during summer (Figs. 4b, 5). The interaction between seasonal WLF (long-term WLF) and waves (short-term WLF) is a permanent process leading to a continuously decreasing grain size distribution from boulders to clay in off-shore direction (Fig. 5). Over the decades, small particles that can be remobilised by waves, are transported to deeper zones. At the site LG the lake floor falls off gently from the shore line towards the open water. At a water depth of about 1–2 m below the average annual minimum water level, the slope of the lake floor increases significantly, thus, forming the so-called "Haldenkante". The location of the "Haldenkante" and the presence of the fine-grained sediments at this location reflect the combined action of long- and short-term WLF in Lake Constance.

The export of fine particles from the littoral zone to the pelagic, and thus, erosion is expected to increase with the decreasing mean water levels observed during the recent past. In combination with the increasing exposure of the shore region to ship waves due to increasing ship traffic on Lake Constance, i.e. due to passenger ships and the recently introduced fast catamaran ferries, erosion of the shore region may be even more dramatic. Observations of divers investigating oak poles in the context of maritime archaeology suggest that many historic and archaeologically important under water heritages like pile dwellings are more and more threatened by the interaction between surface waves and long-term WLF, i.e. previously sand covered sites became uncovered by erosion and are now directly exposed to oxygen rich water, and thus, faster biological decomposition (Bürgi & Schlichterle, 1986; Körninger, 2005).

Conclusions

WLF in lakes exist on temporal scales from seconds to even hundreds of years (Table 1). The ecological impact of WLF depends on the time scale of the level fluctuation and can be amplified by the combined action of long- and short-term WLF. In this paper, WLF are classified as long- and short-term WLF based on the generation mechanism of the WLF with long-term WLF being the consequence of changes in the hydrologic conditions and short-term WLF being the result of hydrodynamic processes, namely waves and basin-scale oscillations.

Long-term WLF can have large amplitudes and induce a slow shore-line displacement of metres or even kilometres, whereas the immediate physical forcing due to currents is negligible. Although the physical forcing of long-term WLF is low, the impacts on the entire ecosystem can be versatile: long-lasting changes in habitat availability for organisms adapted to terrestrial and aquatic conditions, lake salinity, vertical mixing, deep water renewal, or oxygen supply to the deep water. In the case of Lake Constance, the annual mean water level has changed only very little over the last 189 yr and also the inter-annual variation of the annual mean water level did never exceed 0.75 m. However, seasonal changes in water level can reach up to more than 3 m, and thus, cause shore-line displacements of up to hundreds of metres. Hence, seasonal WLF are probably the most important component of long-term WLF affecting competition and survival of species in the littoral zone.

Compared to the seasonal WLF, short-term WLF have much smaller amplitudes and do not significantly displace the boundary between the terrestrial and aquatic habitat but provide high amounts of mechanical energy to abiotic processes, e.g. remobilisation and resuspension of particles, sediment transport, release of nutrients and methane and abrasion of biofilms. The change in abiotic habitat conditions is often followed by changed biotic processes, e.g. resuspended and settled particles reduce the availability of light for photosynthesis, which then result in a decreased growth of phytoplankton and biofilms.

Although the forcing of long- and short-term WLF is different the interaction of both can cause additional consequences to those resulting from the individual process themselves. Long-term WLF change the habitat exposed to the physical stress provided by short-term WLF. Specifically, shore morphology and sediment grain size distribution are the result of a continuous interplay between short- and long-term WLF, the former providing the energy for erosion the latter determining the section of the shore exposed to the erosive power.

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WATER-LEVEL FLUCTUATIONS

Effects of water-depth and water-level fluctuations on the macroinvertebrate community structure in the littoral zone of Lake Constance

**Daniel Baumgärtner · Martin Mörtl ·
Karl-Otto Rothhaupt**

Abstract In a 2-year field study, abundance, biomass and community structure of benthic macroinvertebrates and their seasonal dynamics were assessed along the depth gradient in the stony littoral zone of Lake Constance, Central Europe. The macroinvertebrate community patterns differed significantly between the depth zones, partly because of species turnover, but mostly as a result of different dominance structures. These distinct differences should be considered when designing surveys of benthic invertebrates also for applied purposes, since sources of variation should be kept small and particularly on hard substrates, extensive efforts are required to obtain sufficient data for a powerful statistical analysis. A large seasonal variability in the macroinvertebrate communities of the eulittoral zone indicates a strong influence of physical disturbances, particularly of water-level fluctuations. The community pattern of the drift line samples was influenced by the previous development of the water level. The cumulated water-level fluctuations and their net tendency accounted for three quarters of the variation in a PCA. Since Lake Constance is the only large pre-alpine lake whose water level is not extensively regulated, the uniqueness of the littoral community should have implications for nature conservation measures.

Keywords Benthos · Vertical gradient · Ordination · *Dreissena polymorpha*

Introduction

The organisation of the macroinvertebrate community in the littoral zone of lakes has been subject to a number of studies since the early days of limnology. They range from commented species lists and descriptions of faunal assemblages (Wesenberg-Lund, 1908; Muckle, 1942; Ehrenberg, 1957) to quantitative studies involving productivity (Hayne & Ball, 1956) and effects of habitat variables and biotic interactions on the invertebrate community (Macan, 1966; Gilinsky, 1984; Diehl, 1992; Cobb & Watzin, 1998).

However, the relative importance of biotic and abiotic processes in the structuring of macroinvertebrate communities of littoral habitats is largely unknown (Johnson & Goedkoop, 2002). Compared to the large research effort in studying the water

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Ecological Effects of Water-Level Fluctuations in Lakes

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column of lakes or the benthos of streams, relatively little is known about the stony littoral zone of lakes (Harrison & Hildrew, 1998a). Part of the difficulty arises in the large variation in replicate samples. Extensive efforts are required to obtain sufficient statistical data to detect changes in the fauna. Spatial heterogeneity in the littoral zone, the patchy distribution of benthic organisms and sampling bias overlap with potential impacts of changes in the environment or experimental perturbations. It is therefore crucial to optimise sampling precision and to take into account other sources of variation. In field studies of the impact of single factors and mechanisms, it is necessary to consider habitat gradients and seasonal changes in the community since they add to the "noise" of the data structure by overlapping with the biological signal if their impacts are not known or not considered (Reid et al., 1995; Johnson, 1998).

The presence or absence of organisms in a lake might depend on large-scale factors, such as climate, geology, or colonisation history (Johnson & Goedkoop, 2002). Comparisons of fauna of the littoral zones of lakes have pointed to the importance of environmental variables. Lake morphometry, productivity and water chemistry (Jackson & Harvey, 1993; Bailey et al., 1995), and biotic factors, e.g. the presence of fish and the extent of predation exerted on the macroinvertebrate community have proven to be good predictors in comparisons of invertebrate communities among lakes (Jackson & Harvey, 1993; Wong et al., 1998).

Within a lake, biotic factors, such as predator–prey interactions, competition and life-history traits, play a major role for the community structure (e.g. Gilinsky, 1984; Johnson et al., 1996; Harrison & Hildrew, 1998b, 2001).

However, the importance of single factors in the interplay of biological interactions and physical characteristics for the benthic community is not yet clear. Particularly in the littoral zone of large lakes, a multitude of abiotic gradients can influence biotic interactions differently depending on water depth: Hydraulic stress on organisms caused by wave action is lower in deeper water. Habitat stability, substrate particle size and with that the availability of shelter for macroinvertebrates change with water depth. Radiation attenuates and the light spectrum becomes narrower with depth, and the epilithic algal community—a food resource for grazers—is altered. Temperature and daily temperature ranges vary depending on water depth, season and with the degree of internal seiches (Dall et al., 1984; Winnell & Jude, 1987; Death, 1995; Tolonen et al., 2001).

Fluctuations in water level do not only provide additional dynamics in the littoral zone, e.g. by limiting the temporal scale of succession in the upper littoral zone or by determining the available settlement area, but they also shift the locations of vertical gradients and affect their quality.

The aim of this study was to explore changes in the macroinvertebrate community structure along a vertical habitat gradient. We did not include other possible abiotic parameters or biotic interactions in order to keep the model simple and to focus on the influence of water depth (and correlated factors) and of water-level fluctuations on the macroinvertebrate community in the stony littoral zone of Lake Constance.

Methods

Study area

Upper Lake Constance (47°39′ N, 9°18′ E) is a large pre-alpine lake (500 km^2) in Central Europe with a maximum depth of 254 m. At mean water level, about 12% (57 km^2) of the lake's total area is shallow water less than 10 m deep and is therefore classified as the littoral zone (IGKB, 1994). The average water-level fluctuation is about 2 m annually, with a minimum in February and a maximum in the summer, triggered by melting water runoff in the Alps (Fig. 1).

The sampling was conducted on the south-western shore of the Überlingen Basin, a part of Upper Lake Constance, on a leeward erosion bank with a wide boulder shore. The littoral sediment there consists mainly of silty sands with a loosely packed stony overlay, a habitat that occurs frequently in the littoral zone of Lake Constance (Fischer & Eckmann, 1997).

Sampling design

Starting in September 1999, benthic invertebrates were sampled every 3 months over a period of

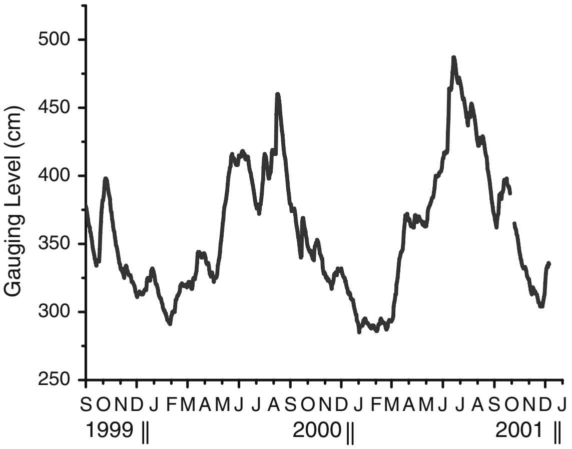

Fig. 1 Course of the gauging level of Lake Constance, station Constance Harbour. Long-term average low-water level: 262 cm. Gap: no data available

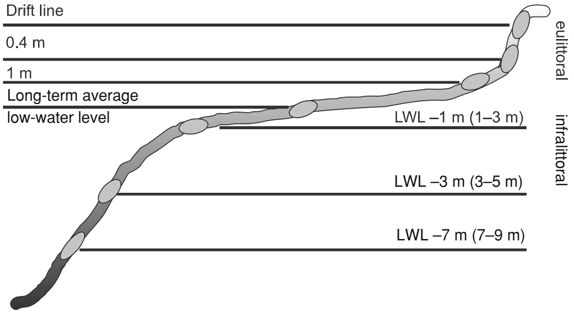

Fig. 2 Vertical zonation of sampling stations

2 years from up to 7 depths; the number of depth zones sampled depended on the water level (Fig. 2). Sampling dates were September 23, 1999, December 14, 1999, March 14, 2000, June 20, 2000, September 29, 2000, December 18, 2000, March 20, 2001 and June 26, 2001. To observe temporal changes on a monthly basis, an additional sampling was carried out on April 12, 2000.

Five replicates from each depth zone were taken randomly in a shoreline of 30–50 m, three of which were counted. Four fixed depth zones were sampled: the zone of the average low-water level (LWL), which is equivalent to a gauging level of 262 cm measured at Constance harbour; and three infralittoral depths, 1, 3 and 7 m below the LWL (−1, −3, and −7 m). At these zones, water depth changed according to the water level.

In the eulittoral zone, up to three shifting depths were sampled; the water depth was invariable, but the location depended on the water level: the drift line (surf zone), 0.4 m and 1 m water depth. Shifting sampling depths in the eulittoral zone were chosen since the actual water depth should have a considerable influence on the macroinvertebrate community and should therefore be kept fixed. The eulittoral sampling depth in 1 m water depth was only present in the June samples when the water level was high.

To see whether colonisation from the interstitial was possible during the rising water level in summer, a quantitative interstitial sampling was carried out on March 18, 2001, by sampling a defined area (25 × 25 cm^2) at a distance of 3, 5 and 7.5 m from the drift line. These sampling locations had been dry for at least the previous 24 weeks.

Sampling devices

For benthos sampling, two different suction samplers were used. The eulittoral zone down to the average LWL was sampled using the Eulittoral Suction Sampler (ESS) with a sampling area of 30 × 40 cm^2; the infralittoral zone was sampled using the Infralittoral suction Sampler (ISS, sampling area 25 × 25 cm^2) and SCUBA diving. A detailed description of these samplers and a comparison of their sampling precision and accuracy are given in Baumgärtner (2004). Drift-line invertebrates were sampled with a frame (25 × 25 cm^2) and a hand net. Mesh size was always 200 μm.

Sorting and sieving

The benthos samples were brought to a climate chamber (4°C) on the same day and processed in the laboratory on the same or next day. Stones were rinsed and brushed gently to remove all organisms. Fine sediments were stirred up repeatedly, and the floating organisms and debris were collected on a 200-μm sieve. The remaining sediments were sorted by hand and searched for dense animals such as molluscs and caddisflies. Each sample was then preserved in 70% ethanol.

Biomass estimation

Invertebrate biomass was estimated using length–dry mass regressions (Baumgärtner & Rothhaupt, 2003). Each taxon was grouped into three size classes. For each taxon, the sampling date was recorded and size class and body length parameters of 10–20 individuals were determined. From the median of each size class, the average dry mass was determined, and the population biomass was calculated by extrapolating the weighted means of these size classes. Average dry mass values were used for several taxa for which body size measurements are not useful, such as hydrozoa, oligochaeta and hirudinea. For molluscs and caddisfly larvae, dry mass was calculated for the soft body without shells or cases.

Statistical analyses

Multivariate community measures were used to include information on the occurrence, abundance and biomass of as many taxa as possible in the evaluation, while at the same time to reduce the complexity of the data. For the graphic representation of community relationships, non-metric multidimensional scaling (NMDS) was applied (Kruskal & Wish, 1978). NMDS is an iterative ordination method and uses the ranks of similarities between samples for a low-dimensional ordination. In contrast to the analogous principle component analyses (PCA), the underlying similarity matrix can be chosen freely and is not restricted to Euclidean distances. This is an advantage in the evaluation of community data, because the nature of species-sample matrices with a high prevalence of zero entries causes major problems in fulfilling assumptions for parametric statistics, such as normal distribution of data. The use of ranks between samples for the ordination makes it clear that the distances in an NMDS plot are relative. Relative distances in a plot reflect the relative dissimilarity between samples. NMDS plots can be arbitrarily rotated, scaled etc. and do not posses defined axes.

For computing similarity between samples, the Bray-Curtis coefficient was used. An important advantage of the Bray-Curtis coefficient is that it is not influenced by joint absences of species in two samples, a condition that many other coefficients fail (Clarke & Green, 1988).

Similarity was measured on matrices with absolute numbers of biomass and abundance per m^2. To balance the contribution of common and rare species, the biomass and abundance data were square-root transformed prior to calculating sample similarities.

The reliability of the two-dimensional picture of the multidimensional relationship between the samples is indicated by a stress value (Kruskal & Wish, 1978). Stress values <0.05 give excellent representation without the prospect of misinterpretation (Clarke, 1993), stress values <0.1 correspond to a good representation of the similarities between the samples and stress values >0.2 indicate that not too much reliance should be placed on details. However, this is a simplified guideline since, for example, stress tends to increase with increasing sample numbers. All NMDS plots in this study were produced with PRIMER 5.0, and the algorithm was restarted ten times for each plot.

Similarities between the drift line samples and other depth zones were analysed with the ANOSIM procedure in PRIMER (Clarke & Green, 1988), which compares the ranked similarities for differences within and between previously defined groups. This test is somewhat comparable to ANOVA/MANOVA, but, like NMDS, it makes few, if any, assumptions on data and is calculated by permutation applied to the underlying similarity matrix. While the resulting *R*-values in theory lie within the range of -1 to $+1$, R is approximately 0 if the null hypothesis is true, and it usually lies between 0 and 1 (but see Chapman & Underwood, 1999). *R*-values close to 1 indicate separation of the groups; values close to 0 imply little or no segregation. For the ANOSIM tests in this study, the same matrices as for the NMDS plots with square-root transformed data and Bray-Curtis similarity were used.

The contribution of species to average dissimilarity between the depth zones was elucidated using the SIMPER routine in PRIMER (Clarke, 1993). The Bray-Curtis similarities between samples were disaggregated by computing average dissimilarities between all pairs of inter-group samples and then breaking down this average into separate contributions from each species to dissimilarity.

The ratio of the average dissimilarity and standard deviation is given as a measure of how consistent the species contributes to the characterisation of differences between groups. We focused on differences between the drift line samples (0 m) and LWL and infralittoral (LWL -7 m), respectively.

Correlations between water-level fluctuations and macroinvertebrate drift-line samples were assessed with the BIO-ENV routine in PRIMER (Clarke & Ainsworth, 1993). This procedure is an exploratory tool for species–environment relationships, using separate similarity or dissimilarity matrices for biological and environmental data. First, a correlation-based PCA on abiotic variables was calculated: water-level fluctuations of the previous 3, 7, 14 and 28 days, their net tendency (sinking or rising water level), and the number of days on which the drift line had been flooded were included (Fig. 7). In the BIO-ENV routine, similarity matrices with subsets of these abiotic variables, based on Euclidean distance, were then compared with the Bray-Curtis similarity matrices of square-root transformed abundance and biomass data of the drift line samples, maximising rank correlations expressed as weighted Spearman rank correlation ρ.

Results

Community patterns

In 173 benthic samples, 48 taxa were distinguished. A total of 27 taxa occurred in more than half of all samples. In general, the ordination of samples by NMDS revealed similar patterns for abundance and biomass (Figs. 3 and 4). The largest space in the plot is occupied by the drift-line samples, which are responsible for the most pronounced differences.

The ordination of the highly variable drift-line samples was estimated separately (Figs. 5 and 6) and correlated with water-level variables. The ordination of samples according to fluctuations in the water level by PCA is shown in Fig. 7. PC axis 1 is mainly influenced by absolute cumulated water-level fluctuations prior to the sampling, with positive values representing small fluctuations and negative values representing larger variation, while axis 2 represents the net tendency of the water level, with negative values indicating rising water level (Table 1). The single variable that grouped the drift-line samples best, in a manner consistent with the faunal patterns based on biomass, was the cumulated water-level fluctuation of the previous 3 days (BIO-ENV,

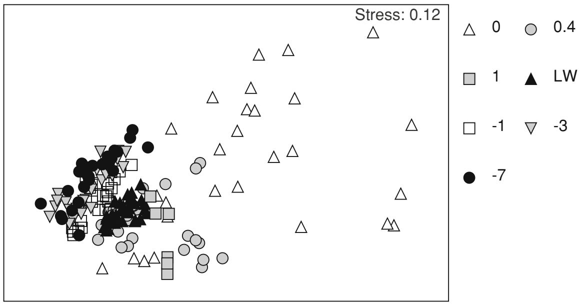

Fig. 3 NMDS plot of invertebrate abundance, including drift-line samples, grouped over depth zones (m). The data were square-root transformed. LW: low-water level

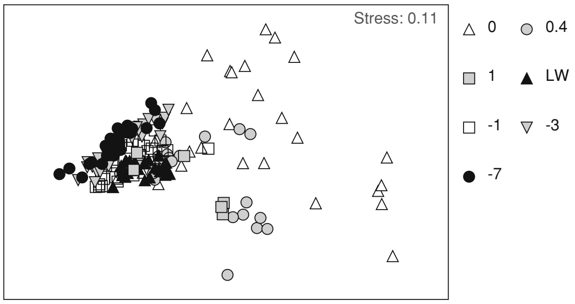

Fig. 4 NMDS plot of invertebrate biomass including drift-line samples, grouped over depth zones (m). The data were square-root transformed. LW: low-water level

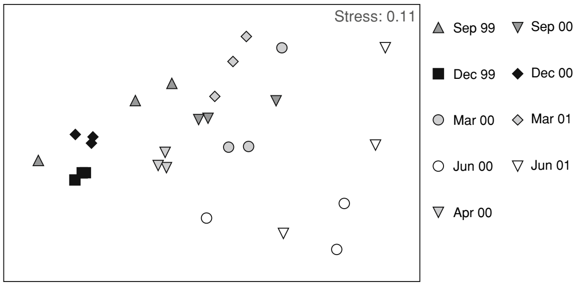

Fig. 5 NMDS plot on invertebrate abundance of drift-line samples, grouped over sampling dates. The data were square-root transformed

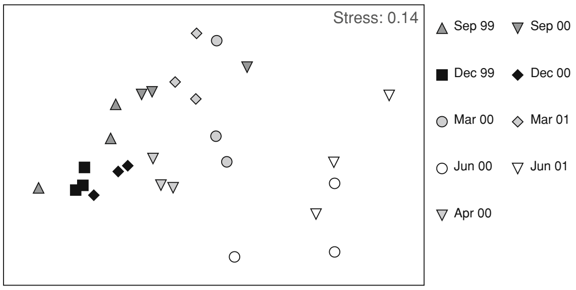

Fig. 6 NMDS plot on invertebrate biomass of drift-line samples, grouped over sampling dates. The data were square-root transformed

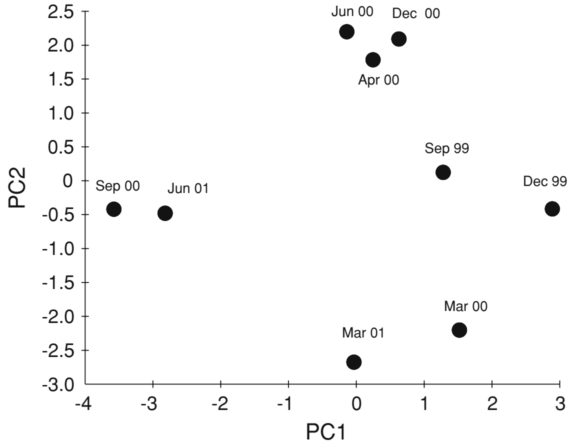

Fig. 7 PCA ordination of the sampling dates based on gauging level variables

weighted Spearman rank correlation $\rho = 0.53$). Considering ordination by abundance, a combination of four factors delivered the best correlation: the number of days that the drift line had been flooded, the cumulated water-level fluctuations 3 and 28 days prior to the sampling and the net tendency of the previous 2 weeks (BIO-ENV, weighted Spearman rank correlation $\rho = 0.51$).

Differences in multivariate community structure between depth zones were tested with ANOSIM tests on abundance and biomass. Global differences were significant for abundance and biomass between depth zones (Table 2). As seen in the NMDS plot, drift-line samples proved to be very different from all other samples, with $R > 0.88$ except for the 0.4-m samples, where the difference is somewhat smaller, but still pronounced ($R = 0.77$ for abundance and 0.67 for biomass).

Table 2 ANOSIM test for differences in abundance or biomass between surf zone samples and other depth groups (averaged across all month groups)

Test	Abundance		Biomass	
	R	*P*	*R*	*P*
Global	**0.632**	<0.001	**0.581**	<0.001
0, 0.4	**0.774**	<0.001	**0.665**	<0.001
0, 1	**0.926**	0.002	**0.933**	0.002
0, LWL	**0.895**	<0.001	**0.885**	<0.001
0, −1	**0.912**	<0.001	**0.889**	<0.001
0, −3	**0.945**	<0.001	**0.913**	<0.001
0, −7	**0.896**	<0.001	**0.887**	<0.001

Pronounced differences are in bold. LWL: low-water level

Species analyses

The dominant species *Dreissena polymorpha* contributed most to the differences between the examined depth groups (0, LWL, −7 m) with regard to abundance (Table 3) and biomass (Table 4); the latter was more pronounced. The zonation of the chironomid subfamilies also accounts for a

Table 1 PCA on gauging level variables

	PC 1	PC 2	PC 3	PC 4	PC 5
Eigenvalues	3.87	2.88	1.18	0.70	0.22
% Variation	43	32	13.1	7.8	2.5
% Cumulated variation	43	75	88.1	95.9	98.4
Eigenvectors					
Number of days flooded	0.358	0.285	0.061	0.575	0.047
3-Day fluctuation	−0.339	0.285	−0.427	−0.044	−0.671
3-Day tendency	0.333	−0.409	0.029	0.259	−0.096
7-Day fluctuation	−0.463	−0.088	0.316	0.179	−0.031
7-Day tendency	0.047	−0.452	0.491	−0.245	−0.510
14-Day fluctuation	−0.435	−0.210	0.233	0.288	0.221
14-Day tendency	0.167	−0.447	−0.398	0.396	−0.286
28-Day fluctuation	−0.453	−0.128	−0.165	0.400	0.059
28-Day tendency	−0.083	−0.446	−0.482	−0.330	0.378

Table 3 Results of the SIMPER routine: contribution of taxa to average dissimilarities between depth zones based on abundances

Species	Average abundance (ind. m^{-2})		Average dissimilarity	Dissimilarity/SD	Species contribution (%)	Cumulative (%)
	Group 1	Group 2				
Groups 0 and LWL						
Average dissimilarity = 67.64						
Dreissena polymorpha	6676.2	8415.8	8.96	1.76	13.25	13.25
Chironominae	978.4	6221.0	7.81	2.00	11.54	24.79
Caenis spp.	122.2	4273.0	6.92	1.95	10.23	35.02
Tinodes waeneri	39.1	2277.1	5.45	1.77	8.06	43.08
Tanypodinae	41.5	1322.0	4.11	2.85	6.08	49.16
Oligochaeta	422.5	1288.1	3.25	1.51	4.81	53.96
Centroptilum luteolum	0.6	610.2	3.02	2.86	4.46	58.42
Orthocladiinae	2055.7	1317.4	2.95	1.36	4.36	62.78
Pisidium spp.	30.8	362.6	1.89	1.86	2.80	65.58
Polycentropus flavomaculatus	12.4	278.2	1.86	2.10	2.76	68.34
Bithynia tentaculata	30.2	286.3	1.64	1.38	2.43	70.77
Gammarus roeseli	218.1	384.7	1.63	1.34	2.41	73.18
Hydroptila sp.	33.2	226.9	1.47	1.36	2.18	75.36
Groups 0 and −7						
Average dissimilarity = 71.37						
Dreissena polymorpha	6676.2	18778.7	13.55	1.42	18.98	18.98
Chironominae	978.4	4867.0	7.85	1.65	11.00	29.98
Oligochaeta	422.5	2564.2	5.22	1.32	7.31	37.29
Pisidium spp.	30.8	1588.7	5.14	2.35	7.20	44.50
Tanypodinae	41.5	1536.6	4.94	1.96	6.92	51.42
Caenis spp.	122.1	1775.4	4.46	1.56	6.25	57.66
Orthocladiinae	2055.7	89.5	4.12	1.25	5.78	63.44
Potamopyrgus antipodarum	1.2	730.7	3.29	1.60	4.61	68.05
Acari	1.2	557.6	3.08	1.73	4.31	72.37
Mystacides azurea	7.1	235.9	2.01	2.22	2.82	75.19

Cut-off at 75%. SD: standard deviation; LWL: low-water level

considerable part of the differences: In drift-line samples, Chironominae and Tanypodinae occurred rarely, while Orthocladiinae reached highest abundances there. With regard to abundance, the Tanypodinae were a good taxon for discriminating between the depth zones examined: the relatively high ratio between dissimilarity and standard deviation of approximately 2 indicated a frequent contribution to differences in comparisons of samples between depth groups. Other good discriminators between the drift line and the LWL with regard to abundance and biomass were the mayflies *Caenis* spp. and *Centroptilum luteolum* and the caseless caddisfly larvae *Polycentropus flavomaculatus* and *Tinodes waeneri*.

Larvae of the mayfly *Ecdyonurus dispar* and of the stonefly *Leuctra* sp. occurred only in the eulittoral samples in June at high water level, but not in any other of the lake bottom samples. However, in the interstitial sampling in March 2001, we found early instars of *Ecdyonurus dispar* and *Leuctra* sp. larvae inhabiting the upper centimetres of the dry eulittoral zone in abundances of 96 (±16) ind./m^2 and 1328 (±961) ind./m^2, respectively (mean ± SE).

Table 4 Results of the SIMPER routine: contribution of taxa to average dissimilarities between depth zones based on biomass

Species	Average biomass (mg m^{-2})		Average dissimilarity	Dissimilarity/ SD	Species contribution (%)	Cumulative (%)
	Group 1	Group 2				
Groups 0 and LWL						
Average dissimilarity = 70.26						
Dreissena polymorpha	5928.2	38247.2	25.97	1.99	36.96	36.96
Tinodes waeneri	5.3	527.6	3.94	2.32	5.61	42.57
Chironominae	43.4	578.1	3.58	2.17	5.09	47.67
Bithynia tentaculata	137.6	640.6	3.45	1.62	4.91	52.58
Centroptilum luteolum	0.1	326.1	3.05	2.00	4.34	56.92
Gammarus roeseli	416.1	589.5	2.96	1.54	4.22	61.13
Radix ovata/peregra	327.7	462.9	2.76	1.17	3.93	65.07
Caenis spp.	4.9	195.5	2.17	2.32	3.08	68.15
Goera pilosa	6.1	158.8	1.93	1.34	2.74	70.89
Polycentropus flavomaculatus	10.1	146.8	1.86	1.90	2.65	73.54
Orthocladiinae	239.4	152.5	1.57	1.27	2.23	75.78
Groups 0 and −7						
Average dissimilarity = 73.53						
Dreissena polymorpha	5928.2	77378.6	38.09	2.08	51.81	51.81
Radix ovata/peregra	327.7	1081.4	4.67	1.37	6.35	58.16
Pisidium spp.	8.1	419.1	3.52	2.16	4.78	62.94
Chironominae	43.5	342.9	2.72	1.41	3.70	66.64
Gammarus roeseli	416.1	40.2	2.48	1.09	3.38	70.02
Bithynia tentaculata	137.6	153.2	2.05	1.26	2.79	72.81
Orthocladiinae	239.4	9.1	1.86	1.08	2.53	75.35

Cut-off at 75%. SD: standard deviation; LWL: low-water level

Discussion

Species patterns

The neozoon *Dreissena polymorpha* dominated the invertebrate fauna and was the most important species in the sample ordinations with regard to both abundance and biomass, although the data were square root transformed to downplay the role of this dominant species. *Dreissena polymorpha*, when present, is also the dominant species in Danish lakes (Brodersen et al., 1998). *Dreissena polymorpha* was first recorded in Lake Constance in 1965 (Siessegger, 1969) and since then has become distributed throughout the lake. The seasonal dynamics of *Dreissena polymorpha* is regulated by settlement of the larvae in summer and subsequent somatic growth (Wacker & von Elert, 2003) and predation by waterfowl, which induces a decrease in abundance and biomass in winter (Werner et al., 2005). Apparently, the eulittoral zone is colonised each year by recruits of deeper settling mussels. The lack of mobility, particularly of the larger mussels, makes it unlikely for the zebra mussel to respond to the water-level fluctuations in the eulittoral zone with appropriate depth movements (Toomey et al., 2002).

The high abundance and small biomass of *Dreissena polymorpha* at the drift line illustrate the lack of older individuals in the eulittoral zone owing to predation and water-level fluctuations.

Nymphs of the mayfly *Ecdyonurus dispar* and of the stonefly *Leuctra* sp. occurred only in the eulittoral samples in June. The presence of early instars of these taxa in the interstitial can be a competitive advantage when the water level rises and covers the formerly dry eulittoral habitats because larvae from the interstitial can settle promptly. Short-term variations in species arrival can influence the outcome of interspecific interactions (Morin, 1999). Hence, the seasonal water-level fluctuations seem to facilitate the occurrence of these species.

Community patterns

The epibenthic macroinvertebrate community at the sampling site exhibited a gradual transition in the community structure with water depth. Like a distance map, the NMDS plots illustrate the littoral zone with the infralittoral zone on the left side and the eulittoral zone on the right side of the plot. The stress value for all configurations is, particularly considering the large sample number, sufficiently low to view the two-dimensional plot as a useful representation of the multidimensional picture. Pronounced similarities of samples within a depth zone and differences between adjacent zones support the hypothesis that water depth is a key factor in structuring the littoral macroinvertebrate community.

With regard to depth, the largest differences in the community structure occurred between drift-line samples and the other samples, and the variation was largest within the drift-line samples. Here, the extent of variation was not only caused by the differences in season, but was also correlated with water-level fluctuations prior to the sampling. Although the course of the water level has a basic seasonal pattern, season and water-level fluctuations are not necessarily correlated because of variations from year to year (Fig. 7). The colonisation of the drift-line habitat during sinking water levels differs from that during rising water levels, and the macroinvertebrate assemblage depends partly on the duration of the flooding of the habitat. This is probably connected with the availability of food resources for non-predatory invertebrates, e.g. the lack of epilithic algae at the drift line when the water level is rising or the presence or absence of allochthonous coarse particulate organic matter (CPOM).

Abiotic disturbances are strong and frequent in the eulittoral zone: The sheer stress caused by wave action is higher in the eulittoral zone and leads repeatedly to extensive movements of the substrate, depending on wind exposure. Water-level fluctuations create and destroy new habitats, facilitating pioneer species (Hofmann et al., 2008).

Although the invertebrate data were square-root transformed to downplay the influence of the most abundant species and the species with the highest biomass, differences and grouping in the ordination were influenced more by changes in the dominance structure than by an exchange of species. This indicated that different zonation is not merely due to different physiological capabilities of a species, but is also the result of competition and predation effects (Connell, 1961).

The difference between autumn 1999 and 2000 is probably the consequence of the exceptionally high gauging level that had occurred in June 1999. Owing to the high water level, the available settlement area for invertebrates in the eulittoral zone was increased dramatically. Unusually high abundances correlated with a large settlement area support the hypothesis that space is a limited resource in the littoral zone, at least for some invertebrates (Quinn et al., 1998), e.g. the zebra mussel *Dreissena polymorpha*, which had an extremely high abundance and biomass in September and December 1999 following the high water level compared to in the same months of 2000.

There is evidence that global climate change leads to increasing rainfall on the northern sides of the Alps and in the same time temperature rises and therefore snowmelt is shifted to earlier periods. Both effects in combination lead to the assumption, that the occurrence of extreme flood peaks in Lake Constance will be earlier in future (Joehnk et al., 2004). This shift in the occurrence time of flood peaks may change the dominance structure in the macroinvertebrate community of the eulittoral zone. Juveniles of *Dreissena polymorpha* and associated species may have advantages, while it is unclear how pioneer species with early instars in the interstitial of the dry eulittoral zone such as the stonefly *Leuctra* sp. will respond.

The water-level fluctuations have become a special feature of Lake Constance, which is the only large pre-alpine lake that is not subject to extensive regulation of the water level and therefore has a distinctive eulittoral zone. A detailed comparison of the community with those of the stony littoral zone of other pre-alpine lakes would be of interest, particularly with regard to the importance of the dynamically flooded eulittoral zone for pioneer species, which could have implications for nature conservation measures.

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WATER-LEVEL FLUCTUATIONS

Flooding events and rising water temperatures increase the significance of the reed pathogen *Pythium phragmitis* as a contributing factor in the decline of *Phragmites australis*

Jan Nechwatal · Anna Wielgoss · Kurt Mendgen

Abstract *Pythium* species are economically significant soilborne plant pathogens with worldwide distribution, causing seedling damping-off or root rot diseases. *Pythium phragmitis* is a newly described pathogen of common reed (*Phragmites australis*), widespread in the reed-belt of Lake Constance, Germany. It is highly aggressive towards reed leaves and seedlings, but obviously does not affect roots. In the context of 'reed decline' phenomena, *P. phragmitis* infection of reed inundated during flooding events may be of particular significance. We could show that flooding itself is not necessarily detrimental for reed plants. In the presence of the pathogen, however, most submerged leaves and plants were killed within several weeks. Clipped plants did not show regrowth in the *Pythium* infested treatments. Significant losses in assimilating leaf area of reeds could, thus, be the result of *Pythium* infection rather than of flooding alone. Therefore, we suggest that the combination of extended flooding and the presence of *P. phragmitis* might considerably contribute to 'reed decline' at Lake Constance. In parallel, we could show that pathogenicity and spread of this species are considerably favoured by rising temperatures. Since an increase in average water temperature has been found for Lake Constance, we propose that *P. phragmitis* could be an important factor in the dieback of reed stands likely to be promoted by predicted climate change phenomena.

Keywords Flooding · Global change · Oomycetes · *Phragmites australis* · *Pythium* · Zoospores

Introduction

Common reed (*Phragmites australis* [Cav.] Trin. ex Steud.), a large perennial grass with worldwide distribution is a major component of wetland and littoral plant communities of many freshwater ecosystems. It usually forms large natural monocultures at the land–water interface with several important ecological functions (Haslam, 1972). Within the last decades, dieback of reed stands has been a periodically recurring threat to littoral ecosystems of many European lakes (Ostendorp, 1989; van der Putten, 1997; Brix, 1999). In general, adverse effects of lake water eutrophication, organic acid toxicity, wave action, water level regulation, insect attack, algal mats and low genetic diversity have been repeatedly discussed as possible reasons for the decline (e.g. Ostendorp, 1989; Armstrong et al., 1996; Brix, 1999;

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Ecological Effects of Water-Level Fluctuations in Lakes

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Koppitz & Kühl, 2000). Lake Constance, a large prealpine lake and one of Europe's largest inland water bodies, is also affected by the decline, and its reed belt dynamics have been investigated in great detail (e.g. Ostendorp et al., 2003; Dienst et al., 2004). Currently, the negative impact of extreme floods on reed stand health due to impaired oxygen supply of rhizomes and submerged shoots seems to be accepted as one major factor in reed dieback events of Lake Constance (Koppitz, 2004). Thus, the term 'flood-induced reed-dieback' has been introduced by several authors (Ostendorp et al., 2003; Dienst et al., 2004). It is now under discussion in the context of global warming, and of subsequent environmental changes on a more regional scale (Jöhnk et al., 2004). However, other as yet unknown factors have been postulated to account for the damage observed (Ostendorp et al., 2003).

Pythium species are economically significant plant pathogens that cause damage to a large array of different host plants. Grasses and cereals are among the major hosts of this genus (Hendrix & Campbell, 1973). Being oomycetes, *Pythium* species are strongly dependent on the presence of water for zoospore dispersal and host plant infection. *Pythium phragmitis* is a newly described water-borne pathogen of common reed (Nechwatal et al., 2005). It was consistently isolated from soils in permanently flooded parts of Lake Constance reed stands, as well as from other German lacustrine and riverine systems (J. N., unpublished). In in vitro and field assays it proved to be highly aggressive towards seedlings as well as mature leaves of reed. It has been postulated that due to its potential as an aggressive leaf pathogen, *P. phragmitis* might play a significant role in the aetiology of Lake Constance reed decline, in particular under flooding situations (Nechwatal et al., 2005). The aim of this study was to demonstrate in artificial flooding experiments with young *P. australis* plants whether submergence of reed would cause more damage in the presence of the pathogen than would have been caused by flooding alone. Since *P. phragmitis* is known to have a relatively high optimum temperature for growth (Nechwatal et al., 2005) we also wanted to investigate whether warmer temperatures, anticipated consequences of human activity on earth, could possibly favour development and spread of the pathogen. The possible impact of *P. phragmitis* on reed stands, as exemplified by the situation at Lake Constance, is discussed in the light of predicted climate change phenomena and their potential consequences.

Materials and methods

Flooding experiments

Reed plants for flooding experiments were grown from commercially available reed seeds (Jelitto Staudensamen, Schwarmstedt, Germany) in autoclaved standard potting soil. After germination, seedlings were transferred singly to plastic pots (5 cm diameter), and grown for 6–8 weeks in a greenhouse under natural light. By that time plants were approximately 20–30 cm in height, and were beginning to develop additional shoots from their rhizomes. For the tests, plants were chosen, so that within each experiment only largely uniform plants were used. For each treatment within a single experiment, 25 plants were selected. Plants were placed with their pots in 2,000 ml plastic beakers (height approximately 20 cm) for subsequent flooding with tap water and *Pythium* infestation. *Pythium phragmitis* isolate UKN P40, originally isolated from reed rhizosphere soil of the Lake Constance littoral was grown on V8 agar (Nechwatal et al., 2005) in 90-mm Petri dishes for one day prior to each experiment. Each plant in the *Pythium* infested treatments received one agar disc (15 mm diameter) from the growing margin of the *P. phragmitis* culture, spiked on a wooden, autoclaved toothpick which was fixed to the inner wall of the beaker with adhesive tape. Agar discs were mounted so that they were hanging just below water level. Controls received plain agar discs only. In Experiment 1, all plants were fully submerged, i.e. all leaves were in contact with the water. Occasionally, this was achieved by bending leaves down below water level. In Experiment 2, two partial flooding treatments were tested, with approximately 6 and 12 cm water level, respectively, as measured from the soil surface, corresponding to 50% and 75% of the number of plant leaves (2 of 4, or 3 of 4, respectively). Plant performance and damage was recorded after 4 weeks of inundation, with evaporated water being refilled regularly. All shoots were harvested, measured, and plants left for another 2 weeks to monitor regrowth from the rhizomes. In Experiment 3, all plants were clipped right above soil line before the beginning of the test, and subsequently subjected to flooding of approximately 6 and 12 cm above soil line. Number and length of regrown shoots was recorded after 8 weeks. All experiments were repeated twice.

Pathogenicity test

Pathogenicity tests on mature reed leaves under different temperature regimes were performed as described earlier (Nechwatal et al., 2005). In short, mature leaves from greenhouse grown reed plants were inoculated with *P. phragmitis* by placing a disc (4 mm diameter) from an actively growing V8 agar culture onto the leaves, and incubated on moist filter paper in Petri dishes at 15, 18, 20 and 25°C. Control leaves received plain V8 agar discs. After 5 days, lesion length was measured. In each test, three different isolates of *P. phragmitis* were used (UKN P13, P42, P52; Nechwatal et al., 2005), with six leaves per isolate. The tests were repeated thrice for each isolate and temperature combination.

Zoospore test

The influence of temperature on zoospore production of *P. phragmitis* was tested in a bait assay with young reed leaves. Discs from actively growing V8 agar cultures of each of three *P. phragmitis* isolates (UKN P13, P42, P52) were flooded with 60 ml soil extract water (1 l of water, 10 g soil, filtered through filter paper) in 100 ml glass beakers. Ten young reed leaf sections (approximately 0.5 × 0.5 cm) were floated on the water surface as baits. Beakers were then incubated at room temperature for approximately 5 h for initial mycelial growth and sporangia production. Afterwards, they were transferred to 15, 20 and 25°C chambers and incubated for 24 h in the dark. Reed baits were removed, and, separately for each isolate and temperature treatment, carefully transferred to Petri dishes containing sterile distilled water, where they were incubated for another 24 h at room temperature. Number and activity of zoospores present under the different temperature regimes was rated from the number of baits showing signs of infection, i.e. necroses developing from the cut ends of the leaves. For each bait, both cut ends were counted separately, resulting in a maximum number of 20 possible infection sites. The test was repeated thrice for each isolate and temperature combination.

Statistical analysis

Unpaired *t*-tests or one-way ANOVA were performed to test for significant differences among mean values for each treatment in the different experiments. Non-parametric data were log-transformed before analysis. Tukey's Multiple Comparison Test was used as a post-test if one-way ANOVA revealed significant differences between treatments. All statistical analyses were performed using GraphPad Prism 3.00 (GraphPad Software, San Diego, USA).

Results

In Flooding experiment 1, with full submergence, all shoots of the *Pythium* infested plants were dead after 4 weeks, while no shoot death occurred in the control plants. Accordingly, shoot dry weight was significantly higher in the control plants (Table 1). None of the *Pythium* plants showed any regrowth from the rhizomes after two more weeks under non-flooded conditions, indicating complete plant death in the *Pythium* infested trial. In contrast, all of the control plants showed normal shoot regrowth from the rhizomes, with a mean shoot length of 6.8 cm.

In Experiment 2, plants were only partially flooded, and water levels corresponded to 50–75% of the number of leaves present at the beginning of the experiment. Plant and shoot mortality, although at a low degree only, was found only in the *Pythium* infested trial. While no difference in mean live shoot length could be observed within the control and *Pythium* infested plants irrespective of the water level, the latter were significantly shorter as compared to the controls at both 50% and 75% submergence (Table 2). The number of live shoots was similar in all treatments, as was mean shoot dry weight (data not shown). Regrowth after 2 weeks of re-exposure was markedly more pronounced in control plants, where 60% or 75% of the plants sprouted, as opposed to 42% and 30%, respectively, in infested plants (Table 2).

When plants were clipped right above soil level before the beginning of the flooding period (Experiment 3), shoot regeneration from the rhizomes after 8 weeks was markedly stronger in control plants which

Table 1 Flooding experiment 1. Reed plant performance after 4 weeks of full submergence, and two more weeks of regeneration, in the presence or absence of *Pythium phragmitis*

	Pythium phragmitis infested[a]	Control[a]
% Dead shoots	100	0
Shoot dry weight, original shoots (g)	0.096a (0.01)	0.175b (0.02)
% Plants with regenerative shoots	0	100
Shoot length, regenerative shoots (cm)	0 (0.0)	6.8 (0.8)

[a] Means and—if applicable—standard error (SE) of two replicate experiments are given (2 replications × 25 plants). Significant differences ($P \leq 0.01$) are indicated by different letters (unpaired *t*-test)

Table 2 Flooding experiment 2. Reed plant performance after 4 weeks of partial submergence (50% or 75%), and two more weeks of regeneration, in the presence or absence of *Pythium phragmitis*

	P. phragmitis		Control	
	50%[a]	75%[a]	50%[a]	75%[a]
% Dead plants	2	10	0	0
No. of live shoots	2.78a (0.10)	2.40ac (0.14)	2.38bc (0.07)	2.52c (0.10)
No. of dead shoots	0.38a (0.10)	0.46a (0.10)	0b	0b
Total no. of shoots	3.16a (0.10)	2.86ac (0.12)	2.38b (0.07)	2.52bc (0.10)
Shoot length (live shoots) (cm)	37.3a (1.1)	35.8a (1.3)	42.2b (1.2)	42.7b (1.4)
% Plants with regenerative shoots	42	30	60	75
Shoot length (regenerative shoots) (cm)	6.6a (1.0)	5.1a (1.0)	6.9a (1.0)	8.4a (0.8)

[a] Means and—if applicable—standard error (SE) of two replicate experiments are given (2 replications × 25 plants). Significant differences ($P \leq 0.05$) are indicated by different letters (one-way ANOVA, Tukey's Multiple Comparison Test)

produced significantly more shoots (Table 3). While some of the control plants even reached above water level from both 6 and 12 cm depth, none of the infested plants managed to reach this height. Shoots developing from *Pythium* infested plants were extremely small, and approximately 40% of the plants were dead (Table 3, Fig. 1). In contrast, none of the control plants had died after 8 weeks of submergence.

Pythium phragmitis proved to be increasingly aggressive to reed leaves with rising temperatures (Fig. 2). Leaf necroses developed fastest at 25°C, with growth rates similar to those on malt extract agar plates (data not shown). No necroses developed on control leaves.

Similarly, zoospore release rates, and/or zoospore activity of *P. phragmitis* were favoured by warmer temperatures. Reed bait infection was significantly increased at 20 and 25°C, as compared to 15°C (Fig. 3). In none of the tests reed bait infection occurred via vegetative hyphae from the inoculum, as judged from the length of the hyphae emerging from the agar discs.

Discussion

Morphologically, *Phragmites australis* is considered a terrestrial plant that secondarily developed specific morphological structures (aerenchyma) to withstand periods of submergence and low oxygen supply (Jackson & Armstrong, 1999). However, it is generally accepted that reed plants will not be able to tolerate complete flooding for longer periods of time (Mauchamp et al., 2001; Koppitz, 2004). The term 'flood-induced reed dieback' has, therefore, been introduced by several authors to stress the role of flooding events and their consequences like anoxia in the aetiology of reed decline phenomena, in particular at Lake Constance (Ostendorp et al., 2003; Dienst et al., 2004). Our results show that under laboratory conditions, reed plants are able to tolerate periods of major flooding for up to eight weeks, and even will be able to regrow above water level from depths of up to 12 cm (Table 3), i.e. after being "top submerged" (Mauchamp et al., 2001). Although there still might be some negative effect of submergence on plant

Table 3 Flooding experiment 3. Clipped reed plant regeneration after 8 weeks of submergence, at two different water depths, in the presence or absence of *Pythium phragmitis*

	P. phragmitis		Control	
	6 cm[a]	12 cm[a]	6 cm[a]	12 cm[a]
% Dead plants	36	40	0	0
No. of shoots (live plants)	1.81a (0.26)	1.60a (0.22)	3.72b (0.26)	3.80b (0.35)
No. of shoots above water level	0a	0a	0.80b (0.16)	0.12a (0.07)
Shoot length (live plants) (cm)	2.36a (0.55)	1.88a (0.81)	11.07b (1.62)	11.02b (1.31)

[a] Means and—if applicable—standard error (SE) of two replicate experiments are given (2 replications × 25 plants). Significant differences ($P \leq 0.01$) are indicated by different letters (one-way ANOVA, Tukey's Multiple Comparison Test)

Fig. 1 Flooding experiment 3. Shoot regeneration from reed rhizomes 8 weeks after plants were clipped and flooded to ca. 12 cm above soil line. Left: uninoculated control, right: *Pythium phragmitis*-inoculated

vitality as compared to non-flooded conditions, as has been reported by Mauchamp et al. (2001), in none of our flooding experiments any of the control plants died, and most plants were able to return to normal growth after being re-exposed to non-flooded conditions. Similarly, in the experiments of Mauchamp et al. (2001), plant mortality was low, and occurred only in permanent and full submergence treatments. In contrast, in the presence of the reed pathogen

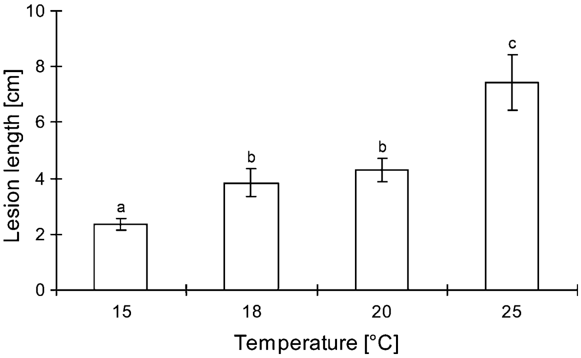

Fig. 2 Lesion size caused by *Pythium phragmitis* on reed leaves at different temperatures. Means and standard error of three replicate experiments (3 replications × 3 isolates × 6 leaves) are given. Different letters above bars indicate significant differences ($P \leq 0.01$, One-way ANOVA, Tukey's Multiple Comparison Test)

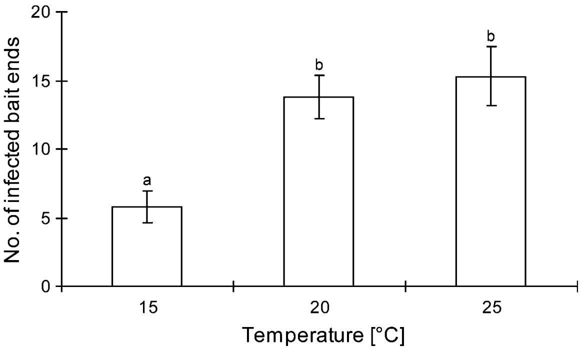

Fig. 3 Zoospore release/activity of *Pythium phragmitis* as expressed as the number of infected reed leaf bait ends (of a maximum of 20). Means and standard error of three replicate experiments are given (3 replications × 3 isolates). Different letters above bars indicate significant differences ($P \leq 0.01$, One-way ANOVA, Tukey's Multiple Comparison Test)

Pythium phragmitis, plant death was common in our tests, in particular when plants were completely submerged, or large parts of the vegetative organs were in contact with water (Table 1). Even only partial submergence occasionally led to plant and shoot mortality, and significantly decreased mean shoot length and regrowth (Table 2). As *P. phragmitis* obviously is not a root pathogen (J. N., unpublished), and root systems in our tests were usually symptomless (data not shown), infection of reed will generally occur through the leaves. Therefore, we agree on the role of flooding events as an important factor in reed dieback, since only in these situations *Pythium* zoospores will be able to come into contact with major parts of the susceptible plant organs. However, the hypothesis of 'flood-induced reed dieback' at Lake Constance of Ostendorp et al. (2003), involving low oxygen supply, and anaerobic metabolism under submerged situations as the primary causes for reed plant death is not supported by our data. A direct detrimental effect of flooding on reed plant health could not be observed in our study, supporting the finding that, apart from the presence of aerenchyma, reed shows a certain degree of tolerance to anoxic conditions due to physiological reasons (Brändle & Crawford, 1987). Indeed, other as yet unknown factors such as insect damage or sediment differences have been postulated to account for the patterns and dynamics of reed damage (Ostendorp et al., 2003). We propose that the observed decline symptoms like stand thinning, change in shoot class composition and stand dieback are in part due to the loss of assimilating leaf area after *Pythium* infection. Reduced photosynthesis rates might lead to decreasing carbohydrate storage in the rhizomes, and reduced shoot numbers and sizes in the next growing period, as discussed by Nechwatal et al. (2005). In addition, seedling losses due to the pathogen's activity might prevent the re-colonisation of stand gaps, as well as the establishment of new reed stands (Nechwatal et al., 2005). Since *P. phragmitis* has now been isolated from other lakes and riverine systems in Germany (J. N., unpublished), its impact on reed stand dynamics might not be regionally restricted to Lake Constance.

Up to now, inoculum densities of *P. phragmitis* in natural habitats (i.e. zoospore densities in littoral lake water) are not known. Hallet & Dick (1981) found up to 400 propagules of *Pythium* spp. with swollen lobulate sporangia (the group which *P. phragmitis* belongs to) per litre lake water in Great Britain. Although *P. phragmitis* does not abundantly sporulate under laboratory conditions (Nechwatal et al., 2005), densities in our tests were most likely higher as compared to natural conditions. However, natural *Pythium* loads obviously are sufficient to cause infection during natural water level rises even in mature reed leaves in the field. These leaves, even though much more sclerophyllous than those of the seedlings used in our tests, were readily infected with *P. phragmitis* under natural conditions (Nechwatal et al., 2005).

As a consequence of rising mean temperatures on a global scale, an increase in average water temperature of approximately 0.017°C year^{-1} has been found for Lake Constance since the 1960s (Straile et al., 2003). Similar trends were observed in other alpine and prealpine lakes (e.g. Thompson et al., 2005). In parallel, dieback of reed belts also has been reported from many European lakes for about five decades (Ostendorp, 1989; Van der Putten, 1997; Brix, 1999; Ostendorp et al., 2003). Since *P. phragmitis* has an optimum growth temperature of around 30°C (Nechwatal et al., 2005), the species might be considerably favoured by higher mean water temperatures in long-term considerations, thus causing a higher incidence of reed damage. Our results indeed show that zoospore production and virulence of *P. phragmitis* on mature reed leaves significantly increases with rising temperature. Leaf infection exhibited spread rates similar to the pathogen's growth rates on agar media (Fig. 2), indicating that a maximum will be reached at 30°C, with a subsequent decline to 40°C, the maximum temperature for growth (Nechwatal et al., 2005). Zoospore production and release, although generally considered to be favoured by chilling in many *Pythium* spp. (Martin, 1992), also increased with rising temperature (Fig. 3). The potential bias brought about by faster growth of germinating zoospores and subsequent secondary hyphal infection of baits at higher temperatures was counteracted by our experimental setup. Thus, our results indicate that differences in leaf bait infection in the tests were basically due to the influence of temperature on zoospore production and release.

Continuous temperature measurements in the eulittoral zone (water/sediment) of Lake Constance indicate that optimum infection temperatures above 20°C will be reached during summertime from June to September (J. N., unpublished). Since Lake Constance is a largely unregulated lake with natural water regimes, flooding events will most likely occur during summertime, after snow melt in the Alpine region, and thus, coincide with optimal temperatures for zoospore production and infection. It, therefore, can be concluded that global change phenomena via rising mean water temperatures potentially promote *Pythium* infection of *P. australis* during summer flooding events, since the pathogen is considerably favoured by higher temperatures within the range of 20–30°C. A similar promotion of the important oomycete root pathogen *Phytophthora cinnamomi* by rising mean temperatures in Europe has been suggested by Brasier & Scott (1994).

Remarkably, out of 17 oomycete species isolated during 2003 from Lake Constance littoral sites, nine had temperature optima of 30°C and above (J. N., A. W. & K. M., unpublished), among them another new species of *Pythium* and a previously undescribed *Phytophthora* sp. (Nechwatal & Mendgen, 2006a, b). In contrast, in a large-scale field study from the late 1960s and early 1970s from The Netherlands (van der Plaats-Niterink, 1975) only 3 out of 19 identified *Pythium* spp. from similar sites had an optimum growth temperature of $\geq 30°C$. Although nothing is known about the past composition of oomycete communities at our sites, these findings could point at a recent gradual shift in community composition towards high-temperature species, possibly brought about by recent climate change phenomena.

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WATER-LEVEL FLUCTUATIONS

Leaf litter degradation in the wave impact zone of a pre-alpine lake

Simone Pabst · Nicole Scheifhacken · John Hesselschwerdt · Karl M. Wantzen

Abstract Contrary to streams, decomposition processes of terrestrial leaf litter are still poorly understood in lakes. Here, we examined the decomposition of two leaf species, beech (*Fagus sylvatica*) and poplar (*Populus nigra* '*italica*') in the littoral zone of a large pre-alpine lake at a wave exposed site. We focussed on the shredding impact of benthic invertebrates in a field experiment and on the effects of wave-induced disturbances under field and mesocosm conditions. In contrast to our expectations, benthic shredders did not reveal an important role in leaf processing under the conditions of the field experiment (early spring time, wave impact zone). Strong wave turbulence during storm events significantly reduced leaf mass, FPOM and invertebrate densities at field conditions. Several reasons can explain the low importance of shredders in our field study: (a) phenology of the shredder species, (b) feeding preferences and alternative food sources for gammarids, (c) generally low abundance of the native gammarid species due to the recent occurrence of an invasive predator, (d) disturbance of shredder activity due to high wave impact and (e) relatively low food value of the offered leaves. We suggest that leaf litter decomposition in lakes occurs in specific process domains, which largely depend on the hydraulic characteristics and on water-level fluctuations.

Keywords Decomposition · Leaf hardness · Benthic invertebrates · Aquatic fungi · Hydrodynamics · Mesocosm · Littoral · Ergosterol

Introduction

In running water ecology, leaf litter is generally accepted to represent an important allochthonous carbon source for canopy-shaded streams, e.g. in the northern temperate zone (Wallace et al., 1997). In lakes, this situation may be different. Litter inputs vary considerably with the type of aquatic-terrestrial linkages. Little is yet known about allochthonous litter inputs via the littoral zone, about the organisms using the carbon deriving from these inputs and about the fate of the degraded leaves. Studies from oligo-mesotrophic lakes in SE Sweden have shown a very intensive input of leaf material, the carbon of which is then transferred to the bacteria (Bohmann & Tranvik, 2001) and benthic invertebrate shredders (Bjelke et al., 2005). Similar to northern temperate streams (Grubbs & Cummins, 1996; Wantzen & Wagner, 2006), aquatic insects, especially

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Ecological Effects of Water-Level Fluctuations in Lakes

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Limnephilidae (Trichoptera), were the most important shredders in these lakes, and they showed an apparent temporal pattern of winter and summer growing species that were specialised on different litter types (Bjelke et al., 2005). The "winter shredders" began their life cycle during the autumnal leaf fall and used the freshly fallen leaf material of fast-degrading species as food source, while the "summer shredders" used a mixture of processed, more recalcitrant leaves and additional food sources.

In the same Swedish lakes, the natural decomposition rate of the most common leaf litter types (*Betula pendula* and *Quercus robur*) were rather fast and the leaves were processed after 3–6 months (Bohmann & Hermann, 2006). Although the shredding activity released little dissolved organic matter (DOM) in addition to the passive initial leaching, the bacterial production in the water was enhanced by shredders (Bohmann & Tranvik, 2001).

In a study on a small eutrophic lake in Wisconsin, USA, Gasith & Hasler (1976) suggested that in oligotrophic and small eutrophic lakes, about 10% of the organic carbon budget were derived from airborne litter, and more than 80% of the litterfall consisted of leaves. They pointed out that the density of terrestrial vegetation along the shore and the shore length strongly determine the magnitude of transport of the airborne litterfall into lakes. For similar lacustrine systems, Gasith & Hasler (1976) estimated a maximum annual transport of airborne litterfall of 500 g C per m shoreline. In a study in Lake Stechlin (NE Germany), Casper (1987) calculated a dry-mass input from beech trees that cover nearly the whole lake shore to 1,111 g C per m shoreline and year. Considering that most of the leaves become sedimented in the upper littoral of Lake Stechlin, this amount increased the sedimentation rate from 30 to 152 mg C m^{-2} d^{-1} (not considering macrophytes). Interestingly, the decomposition rate of beech leaves did not vary between Lake Stechlin and acidic or eutrophic lakes (Casper, 1990). Gasith & Lawacz (1976) also investigated the breakdown rate of five different leaf species in a eutrophic lake and found similar leaf processing rates in lotic and lacustrine systems for some species. They concluded that the efficiency of the two systems in decomposing leaf litter is comparable even though the contribution of the biotic and abiotic factors affecting the breakdown may be different.

In pre-alpine lakes of Europe, most decomposition studies have focussed on reed, *Phragmites australis*, which contributes to large parts of the primary production and organic carbon budgets of the littoral zone (Gessner et al., 1996; Gessner, 2000, Kominkova et al., 2000). It is currently unknown to which degree allochthonous leaf litter from trees contributes to the carbon budget, neither do we know which factors influence the decomposition process in these lakes. A large variability of these processes can be expected. Reed belts are known to be efficient mechanical filters for lateral coarse particulate organic matter (CPOM) inputs, and many shore areas have been colonised and deforested, and therefore, tree litter inputs occur only in selected areas. The morphology of the littoral zone varies greatly between shallow and vertical slopes, with a wide range of hydraulic conditions and substrate types, including the respective benthic invertebrate assemblages (Scheifhacken et al., 2007). Moreover, species-specific characteristics of the leaves (e.g. leaf hardness and plant secondary compounds) influence the microbial attack and shredding by invertebrates (Wantzen et al., 2002).

Natural pre-alpine lakes have water-level fluctuations (due to freezing of the tributaries in winter and snowmelt and rain inputs in early summer) that completely change the hydraulic situation in the upper littoral zone where most of the decomposition is supposed to take place. The wave impact zone and the layer where the strongest shear stress occurs move along the aquatic-terrestrial transition zone (ATTZ) during the annual water-level fluctuations. Contrary to streams, the direction of the water movement is hard to predict in the wave zone of the littoral as it changes with water level, internal seiches, wind impact, thermal currents and waves caused by ships. The impact of water movement on the mechanical destruction of organic matter in the lake littoral is currently unknown.

In the present study, we examined, for the first time, the decomposition of terrestrial leaf litter in the littoral zone of a large, deep pre-alpine lake, Lake Constance (47°39′N, 9°18′E). We focussed on the natural processing of the leaf litter under field conditions and in standardised mesocosm experiments with controlled wave impact. We used leaves of two tree species that are common at European lakeshores and have different leaf characteristics. Beech (*Fagus sylvatica*) is more recalcitrant to decomposition than poplar (*Populus nigra* '*italica*') in streams. Studies in lotic ecosystems reported $-k$ values of 0.0018 for beech and 0.0091 for poplar (Baldy et al., 1995;

Dangles & Guérold, 1998). Therefore, we hypothesised that poplar leaves would be processed faster than beech in the lake, too, and we expected that the colonisation process by benthic invertebrates and the importance of shredders for leaf decomposition would vary according to leaf type. We further expected that the underlying hydrodynamic conditions of the lake littoral zone, i.e. wave action, are important to break up the leaves and therefore to accelerate decomposition. Effects of wave action on the decomposition rates of the leaves were studied under natural exposure conditions and in mesocosms that allowed to compare a defined wave action with a no-wave-control treatment.

Methods

Site of the field experiment

The field experiment was performed in the 'Littoral garden', a leeward erosion bank with a wide boulder shore on the south-western shore of the Überlingen Basin, a part of Upper Lake Constance (Fig. 1). Lake Constance is an oligotrophic pre-alpine lake (10 μg P l^{-1} during spring circulation) with a surface of 473 km^2, a mean depth of 101 m and a maximum depth of 254 m. The water level normally fluctuates by about 2 m every year, with a minimum water level in the winter and a maximum in the summer months, triggered by melting water runoff in the Alps (Luft & Vieser, 1990). At mean water level, about 15% of the area is shallow water less than 10-m deep and is therefore classified as a littoral zone (IGKB, 2004). Westerly winds prevail throughout the year, with a second less-dominant peak of easterly winds especially in winter (Bäuerle et al., 1998). Along the 186-km shoreline of Upper Lake Constance, the littoral zone varies greatly in width, sediment composition and wind exposure. The study site is characterised by regular wave action caused by ferries and leisure boats. The littoral sediment of this place consists mainly of siltish sands with a more-or-less packed stony overlay (Schmieder et al., 2004). The shore vegetation contains mainly native trees such as beech, poplar and oak.

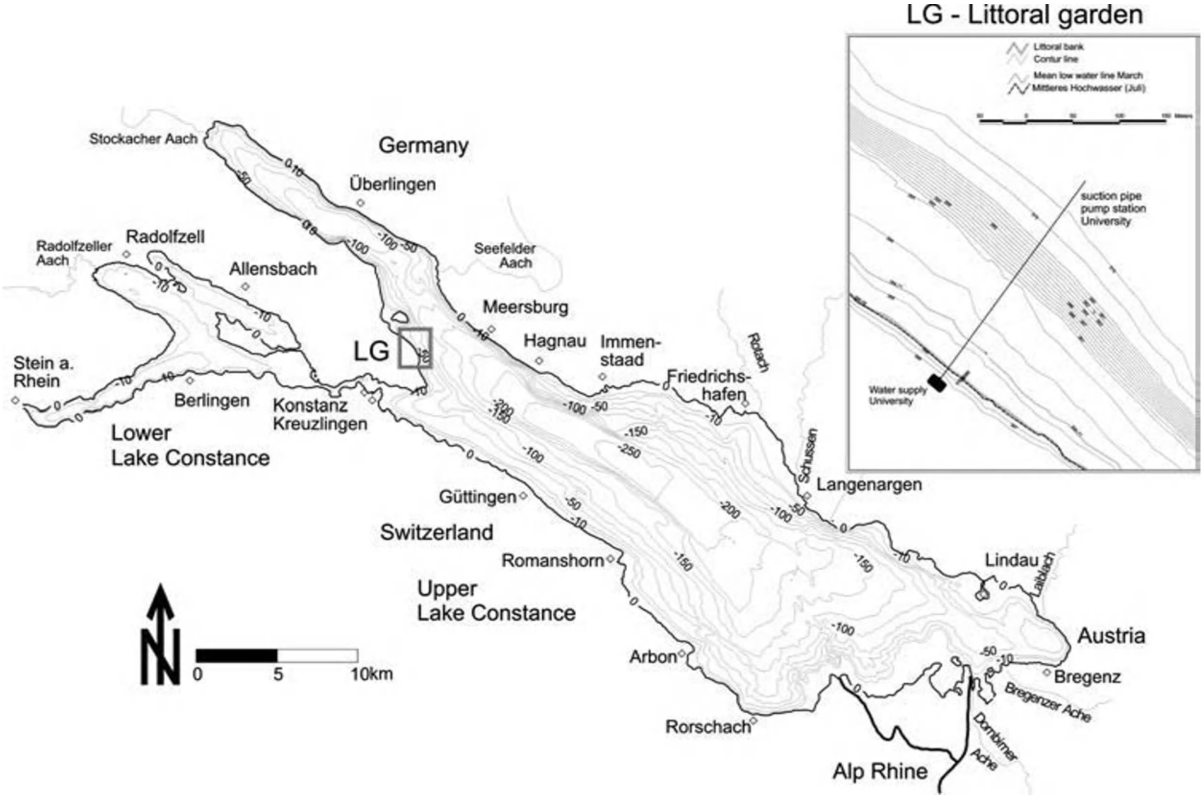

Fig. 1 Experimental field site 'Littoral garden'—LG at Upper Lake Constance

Litterbags

Both field and mesocosm experiments were conducted with leaves of beech (*Fagus sylvatica*) and poplar (*Populus nigra* '*italica*'), collected with an aboveground mounted nylon net near the study site just after abscission in October/November 2004. The leaves were air-dried and stored at room temperature until the beginning of the experiments in winter/spring 2005. For the field experiment, leaves were placed in nylon litterbags of 15 × 15 cm and 4-mm mesh size. The bags were filled with 5 ± 0.01 g leaf air-dried weight. The mean correction factor of leaf weight loss was calculated for precise weight loss analysis from air-dried to oven-dry weight (105°C, 15 subsamples per tree species).

At field, all litterbags of beech and poplar leaves were fixed randomly at a metal square cage (1 × 1 × 0.5 m, mesh width 4 cm). In order to avoid sedimentation on the litterbags, they were tethered about 15 cm above the sediment surface, and access by crawling invertebrates from the bottom was possible as the lower end of the bags touched the ground. The cage was tightly anchored in the sediment with 40-cm pegs at each corner to withstand wave action at the site. All litterbags were exposed in February 2005 at 0.4-m water depth. Due to severe storm events, some beech litterbags were lost. Three to five randomly chosen samples per leaf species and date were retrieved after 1, 2, 7, 14, 27, 42, 55 and 84 days for the determination of weight loss, accumulation of FPOM and status of colonisation with benthic invertebrates. Loss of invertebrates and FPOM during sampling was avoided by placing the litterbags into plastic bags before detaching them from the metal cage. Another three replicates per date were taken for ergosterol analysis from separate litterbags, which were filled with double amount of leaves (10 g dry weight) to ensure sufficient material even after several weeks of decomposition.

Abiotic parameters

Wind speed and wind direction were obtained from the nearby weather station in Constance-Egg. The maximum wave height and wave period were continuously measured using an acoustic doppler velocity meter (ADV meter) in 2-m water depth at the study site (Hofmann et al., unpublished data). In order to compensate the methodological constraints of ADV in very shallow water depths, we used the dissolution rate of gypsum spheres to characterise the hydrodynamic turbulences near the litterbags, following a standardised procedure (Scheifhacken 2006, Scheifhacken et al., 2007). This method was successfully used in a variety of aquatic environments (e.g. Petticrew & Kalff, 1991; Angradi & Hood, 1998; but see also Porter et al., 2000 and cited references therein). The weight loss of five gypsum spheres was determined weekly, thereby integrating overall wave exposure of the site for the given time period. Water temperature was continuously recorded using Minilog data loggers (Vemco, Canada) next to the litterbags. In addition, conductivity, pH and dissolved oxygen were measured in situ weekly using a portable WTW logger (Multiline F/SET 3, Weilheim, Germany).

Wave mesocosm experiment

The impact of hydrodynamics on leaf processing was studied under standardised mesocosm conditions without adding invertebrates. Two treatments (wave and control) were tested in concrete basins (10-m length, 1-m width, 1-m height). Each basin was equipped with an artificial littoral zone at one side that was made of a metal grid, covered with aquarium foil and a thin layer of substrate coverage (10 cm, cobble stone) to mimic natural field conditions (slope, substrate roughness, wave shear stress), as described in Scheifhacken (2006), Scheifhacken et al., 2007). The water level was maintained at 0.8-m depth by adding water (2–2.5 $l\ min^{-1}$) to compensate for evaporation loss.

Wave action in the 'wave mesocosm' was generated by pneumatically moved paddles (0.9 × 0.5 m) by employing a specifically designed and self-constructed pneumatic wave machine (Scheifhacken 2006; Stoll et al., 2008). The 'control mesocosm' lacked waves. Wave duration was regulated through a time switch gear at regular intervals adjusted to the intervals of current ferry timetables at Lake Constance. In the field site of our study, waves caused by ferries are the most important hydraulical impact. During the day (6 am to 9 pm), wave intervals of 2.5-min duration were followed by a 5-min pause (8 times per hour). During the night, the frequency of wave occurrence was reduced to half of the daytime.

The two mesocosms were filled with filtered lake water (300 µm mesh). Abiotic water quality parameters were measured in the same way as in the field experiment. In the control and wave mesocosm, 120 separately weighed (± 0.1 mg) and marked leaves, 60 per species (beech and poplar), were arranged in two baskets. These baskets contained four identical compartments (25 × 15 × 15 cm) filled with a gravel layer of the same grain size as found in the littoral sediment. The front and back sides of these units were covered with a wide mesh (4-mm mesh size, polyester, 0.8-mm fibre) to allow maximum wave action but to hinder leaves from floating within the whole mesocosm. In both mesocosms, the baskets were exposed in 0.4-m water depth. The mesocosm experiment was conducted from mid-May to the end of June to avoid freezing periods. Similar to the field experiment, the leaves were retrieved in the time series of 1, 7, 14, 21, 27 and 42 days (five replicates). A longer exposition was not possible due to the tight time schedule for the use of the mesocosms.

Sample processing

The content of the litterbags was wet-sieved with a set of sieves (6,300; 250; 63 µm) using 50-µm filtered lake water. The remainder of the 6,300-µm mesh sieve were defined as "whole leaves". The broken leaf parts of the 250-µm fraction was later added to the leaf fraction for dry weight analysis. We designated the remaining fraction smaller than 250 µm and larger than 63 µm as FPOM. All benthic macroinvertebrates were collected from 250-µm mesh size fraction and preserved in 70% ethanol. Additionally, the tiny invertebrates (mainly dipteran first instar larvae), were picked out of the finest fraction using a dissection microscope (Zeiss, Stemi DV4) when possible. In the samples of the last date, there were too many individuals so that about 2/3 of them were left in the FPOM fraction. All invertebrates were identified to the species level if possible, and otherwise, to the nearest taxonomic level, and counted. The assignment of invertebrate taxa to functional feeding groups (FFG) was made according to Moog (2002). All taxa, which at least partly feed on coarse organic matter, were classified as shredders.

Determination of leaf degradation

The dry weight (DW) of all leaf samples and the FPOM fraction was obtained using drying chambers (105°C). One aliquot of 250 mg from the coarse leaf fraction was pulverised and combusted in a muffle furnace at 550°C for 5 h to determine the ash-free dry weight (AFDW), the FPOM fraction was completely combusted. Further, five leaves of each litterbag were air-dried for leaf hardness determination, but afterwards added to the leaf fraction and treated as described above (DW, AFDW).

Leaf hardness was determined from re-moistened air-dried leaves in a water saturated atmosphere. The penetrometer that we used to measure the hardness of leaves was developed by the Max–Planck-Institute for Limnology in Plön, by adapting a piercing device to a commercial mechanical pressure meter (Hahn+Kolb GmbH, Stuttgart). The leaf hardness is measured as the maximum counter-force (measured in Newton, N) of a leaf opposing and withstanding a small penetrating metallic bolt (Ø 5 mm), see Graça & Zimmer (2005) for a current review on the method.

The litter breakdown was determined by calculating a decay coefficient k_{day} for both leaf types using the exponential regression formula $M_t = M_0{*}\mathrm{e}^{-kt}$ according to Petersen & Cummins (1974).

Ergosterol concentrations

The decomposed leaf material was frozen at −30°C after sampling until measurement. Determination of ergosterol was done by high-performance liquid chromatography (HPLC, see Gessner (2005) and Gessner & Schmitt (1996) for a detailed description). For analyses, the leaf material was lyophilised and ground. The extraction was done in alkaline methanol at 80°C. Solid-phase extraction through C18 cartridges was used for purification. Dry, unprocessed leaves were used for blank values. This material was stored dry at room temperature. In addition to ergosterol concentration, we calculated the biomass of hyphomycetes at the peak time with the conversion factor of 5.5 mg ergosterol g^{-1} fungal biomass according to Gessner & Chauvet (1993).

Data treatment

Effects of sampling date and leaf species on remaining leaf mass or leaf hardness were analysed with two-way ANOVA (Bonferroni corrected) using SPSS 11.0 (SPSS, Chigago, IL) software. Variances were stabilised with $\log(x + 1)$ transformation and tested for homogeneity with the Levene test; normality was tested with Kolmogorov–Smirnov test (Lozán &

Kausch, 1998). Tukey HSD post-hoc tests were applied when significant effects were detected. Nonmetric Kruskal–Wallis-test and Mann–Whitney-*U*-test were applied when assumptions of variance homogeneity failed after transformation, e.g. for ergosterol and FPOM data. The colonisation process of leaf litterbags by invertebrates was analysed with nonparametric tests using abundance data, number of taxa as well as the Margalef species richness and Pielou's eveness (mean ± SD) as diversity parameters. In order to detect the dependences of species richness and eveness in terms of exposure time, we used the Spearman rank correlation coefficient (Köhler et al., 1996). Further, benthic community composition was examined with non-metric multidimensional scaling (nMDS) using the PRIMER 6 software (Clarke & Warwick, 2001). Abundance data (non-transformed) were displayed in nMDS plots using Bray–Curtis index for similarity calculations. A priori defined groups (leaf taxa, sampling date) were tested with ANOSIM (analysis of similarities) permutation statistics against random distribution (Clarke & Warwick, 2001).

Results

Abiotic parameters

The mean wave height during the field experiment was 0.07 m (±0.06 m SD). However, two distinct storm events were recorded in the end of February (days 11–13 after exposure) and in mid-May (days 54–55; indicated by arrows in Fig. 2), both occurring from eastern directions with maximum wave heights of 0.64 and 0.55 m, respectively. The gypsum dissolution method also registered these events as highly significant (ANOVA: $F_{10,44} = 532.66$, $P < 0.001$), however, in different magnitudes (see Fig. 2c). The daily mean water temperature (±SD) ranged from 3.1 ± 3.1°C to 13.6 ± 1.3°C (Fig. 2d). Mean conductivity was 327 ± 8 µS/cm (mean ± SD) and mean pH was 8.5 ± 0.1. The water was always saturated with oxygen (12.7 ± 0.9 mg/l).

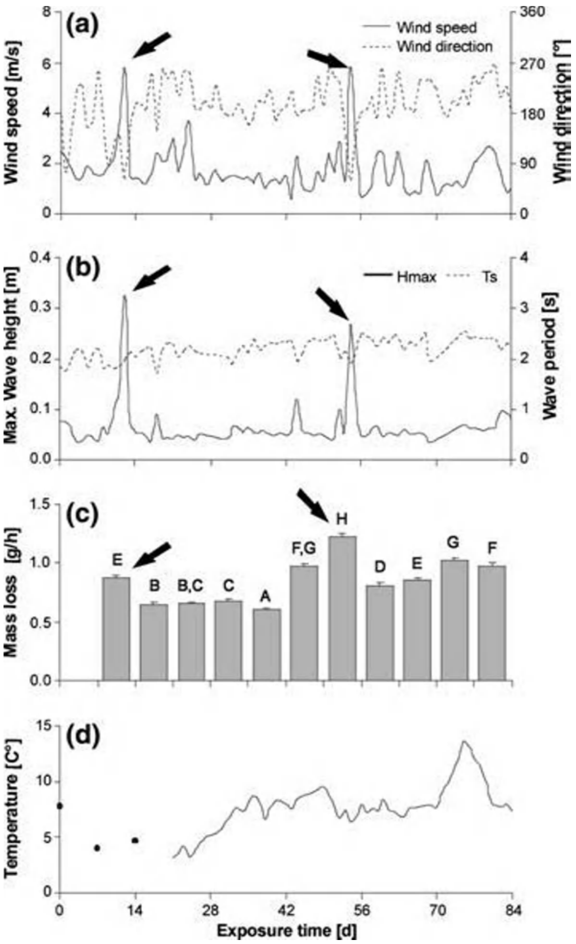

Fig. 2 Measurement of water temperature, hydrodynamic and wind parameters—daily means (**a**), (**b**) and (**d**) weekly means (**c**). (**a**) Wind speed (m/s) and wind direction (0° = N, 90° = E, 180° = S, 270° = W). (**b**) Maximum wave height ($H_{\max}$) and wave period (T_s), both measured with an ADV meter. (**c**) Mean mass loss of plaster balls exposed in the littoral of Lake Constance (g/h), vertical bars denote positive standard deviation (SD), $n = 5$. Values with the same capital letter are not significantly different (Tukey HSD post-hoc test). Arrows mark the two extraordinary incidents of storm events from NE directions. (**d**) Daily mean water temperature (°C). During the first 3 weeks, temperature was measured only once a week (symbols)

Mass loss, FPOM accumulation, ergosterol content and leaf hardness

After the storm events (Fig. 3a, arrows), the mass loss of poplar was significantly higher than during the other periods (Fig. 3a). The mass loss of beech was only higher after the first storm event although the differences were not significant (Tukey HSD post-hoc test, see Fig. 3a). The littoral process of leaf decay revealed a first short phase with rapid mass loss (leaching) and a second longer phase with a moderate decay (Fig. 3a). In the first 24 h, poplar lost 16%, whereas beech only lost 5% of the initial AFDW. The

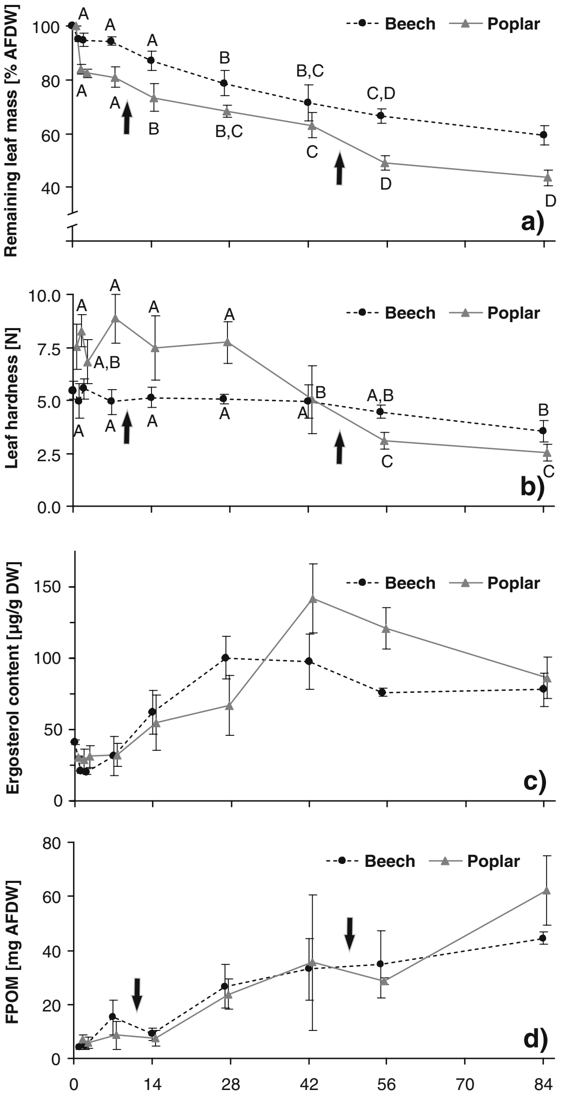

Fig. 3 Degradation rates of leaf mass, leaf hardness and FPOM-accumulation over exposure time. Arrows mark the two extraordinary incidents of storm events. (**a**) Average leaf decay expressed as remaining mass of leaves in % AFDW referring to initial leaf mass. (**b**) Mean change in leaf hardness (N). (**c**) Mean change in ergosterol content of the leaves (µg/g DW). (**d**) Mean change in FPOM accumulation (mg AFDW) in litterbags. Symbols and vertical bars indicate mean ± SD, $n = 3$–5 (beech) and $n = 5$ (poplar). For ergosterol content, $n = 3$. Values with the same small letter (beech) and capital letter (poplar) are not significantly different (Tukey HSD post-hoc test)

decomposition process revealed significant differences between the two leaf species ($F_{1,56} = 235.45$, $P < 0.001$, ANOVA).

The exponential breakdown coefficients k_{day} was −0.0065 for beech and −0.0089 for poplar. According to the classification of Petersen & Cummins (1974), the exponential decay coefficients were intermediate for both species ($-0.01 > k_{\text{day}} > -0.005$), meaning that only resistant leaf material (e.g. petioles) would be present a year after submersion. Visible changes of the leaves occurred only in case of poplar leaves. After 42 days of submersion, we recognised distinctive fenestrate feeding patterns and other damages in poplar leaves, whereas beech leaves remained intact during the experimental time.

The ergosterol content (Fig. 3c) was significantly dependent on the exposition time in the lake ($F_{8,35} = 46.52$, $P < 0.001$, ANOVA). The maximum concentration of ergosterol was 100.30 µg g^{-1} DW after 28 days in beech and 142.05 µg g^{-1} DW after 42 days in poplar (Fig. 3c). The correspondent biomass of hyphomycetes was 18.2 mg g^{-1} DW mg in beech and 25.8 mg g^{-1} DW in poplar. The decline of ergosterol concentrations after the peak time was not significant in both leaf species. Leaf type did not have an effect on the content of ergosterol ($F_{1,35} = 2.51$, $P = 0.121$).

As leaf mass decreased in the litterbags, FPOM accumulated with progressing litter decomposition (Fig. 3d). The amount of FPOM was higher in poplar than in the beech litterbags, but differences were not significant (U-test: $Z = -0.156$, $P = 0.606$). Immediately after the storm events, the FPOM mass in the litterbags became reduced, but it increased afterwards (Fig. 3d).

At the beginning of the experiment, poplar leaves were significantly harder than beech leaves. In contrast to poplar leaves, which lost their leaf hardness rapidly after 27 days, the hardness of beech leaves did not decrease significantly during the first 42 days (Fig. 3b). Therefore, poplar leaves were significantly softer than beech at the end of the experiment. Two-way ANOVA revealed significant differences between beech and poplar leaves ($F_{1,56} = 25.38$, $P < 0.001$). Leaves of both leaf species showed an increase of leaf hardness within the first 2 weeks.

Benthic invertebrates

Benthic invertebrate communities of the litterbags were clearly dominated by Orthocladiinae, while *Caenis* spec., *Corynoneura* spec., *Chironominae* and *Dikerogammarus villosus* were less abundant (Table 1). Numbers of individuals (mean ± SD) and taxa increased quickly. After 27 days of leaf submersion, abundance (beech: 31.2 ± 7.2; poplar:

Table 1 The 10 most common taxa in all litterbags of beech and poplar, without consideration of exposure time (mean ± SD), $n = 32$ (beech) and $n = 40$ (poplar)

Beech		Poplar	
Taxon	Mean ± SD	Taxon	Mean ± SD
Orthocladiinae	41.3 ± 59.06	Orthocladiinae	45.6 ± 54.07
Caenis sp.	5.8 ± 7.97	*Caenis* sp.	4.7 ± 6.74
Corynoneura sp.	4.0 ± 8.29	*D. villosus*	1.5 ± 2.31
Chironominae	2.4 ± 4.78	Chironominae	1.5 ± 3.58
Dikerogammarus villosus	2.0 ± 3.39	*Corynoneura* sp.	1.4 ± 3.43
Gammarus sp.	1.9 ± 4.50	*Gammarus* sp.	1.1 ± 3.16
Cladocera	0.6 ± 1.03	*Gammarus roeseli*	0.2 ± 0.58
Gammarus roeseli	0.6 ± 1.30	Tanypodinae	0.2 ± 0.46
Dreissena polymorpha	0.3 ± 1.05	Cladocera	0.2 ± 0.45
Erpobdella sp.	0.3 ± 1.21	*Centroptilum* sp.	0.2 ± 0.43

42.0 ± 11.2) and number of taxa (beech: 5.6 ± 0.9; poplar: 4.5 ± 1.5) were on average values (Fig. 4). Litterbags of both tree species reached their maximum colonisation at the last sampling after 84 days (beech: 210 ± 90; poplar: 144 ± 31), i.e. a "saturation" effect could not be determined. This value (Fig. 3a, last value) is actually below the real situation, because at this date, a mass hatching of chironomid larvae, mainly Orthocladiinae, had taken place that were not quantitatively separated out of the FPOM mass as done before.

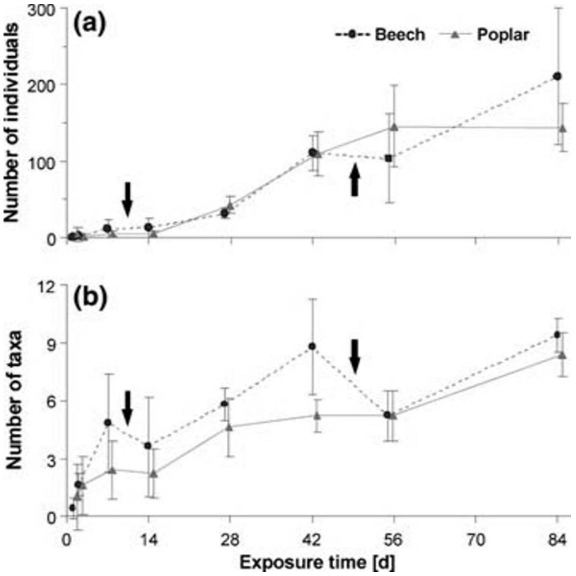

Fig. 4 Benthic invertebrate colonisation of litterbags over exposure time. (**a**) Mean abundance ± SD. (**b**) Mean number of taxa ± SD, $n = 3$–5 (beech) and $n = 5$ (poplar). Arrows mark the two extraordinary incidents of storm events from NE directions

Number of taxa (Fig. 4b) also reached its maximum after 84 days with 8.4 ± 0.4 taxa (beech, mean number per litterbag ± SD) and 7.4 ± 0.5 (poplar). The exposure time of litterbags could be determined as a significant factor considering colonisation by invertebrates (Table 2). Both invertebrate density and number of taxa showed a decrease or lower increase during the periods of storm events. Comparisons between beech and poplar in terms of invertebrate density and number of taxa did not reveal significant differences (*U*-test: invertebrate density: $Z = -0.15$, $P = 0.881$; taxa: $Z = -1.54$, $P = 0.125$). Neither could we find significant differences of species richness and eveness (*U*-test: richness: $Z = -1.92$, $P = 0.055$; eveness: $Z = -1.63$, $P = 0.103$) nor a correlation between taxon richness and exposure time (beech: $r = 0.209$, $P = 0.706$; poplar $r = 0.056$, $P = 0.760$). Nonmetric statistics underlined that the invertebrate community composition colonising the litterbags did not differ between the two leaf species, as visualised by the regular scattering of the symbols for beech and poplar samples in the nMDS plot (Fig. 5a, sampling dates pooled; ANOSIM: $R = -0.008$, $P = 0.601$). However, we could observe a clear separation between sampling dates for both leaf species (Fig. 5b, c) (ANOSIM: beech: $R = 0.67$, $P = 0.001$; poplar: $R = 0.568$, $P = 0.001$) and a reduced variability between samples with increasing exposure time. This observation is supported by a negative correlation found between Pielous's eveness and exposure time (beech: $r = -0.691$, $P < 0.001$; poplar $r = -0.534$, $P = 0.002$).

Contrary to our expectations, only few individuals of gammarids were detected in the litterbags. Most specimen occurred at the last sampling date, mainly

Table 2 Results of Kruskal–Wallis-tests on number of individuals and taxa in litterbags of beech and poplar depending on exposure time

	Beech			Poplar		
	χ^2	df	*P*	χ^2	df	*P*
Number of individuals	35.12	7	<0.001	33.16	7	<0.001
Number of taxa	29.60	7	<0.001	28.94	7	<0.001

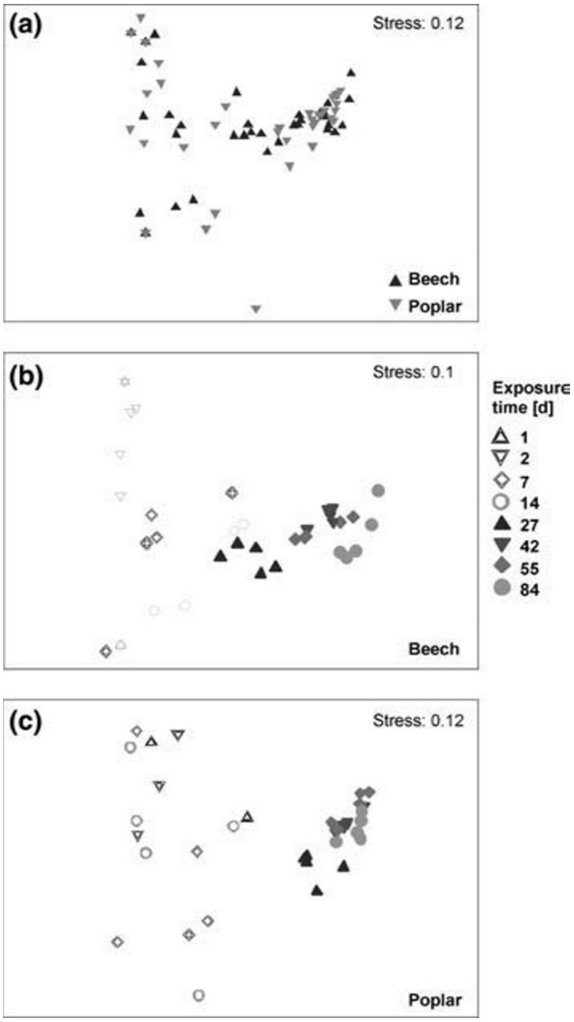

Fig. 5 nMDS plots of benthos community composition based on abundance data during the colonisation of beech and poplar litterbags grouped for all sampling dates (**a**) but differentiated between sampling dates in (**b**) for beech and (**c**) for poplar. The Bray–Curtis similarity index was applied. Overlapping symbols indicate identical benthic communities

very small *Dikerogammarus villosus* and very few individuals of *Gammarus roeseli*. Most other invertebrates were Orthocladiinae, Chironominae and *Corynoneura* spec., which are scrapers and sediment/deposit feeders. Shredders were very scarce (0–7.5% of the abundance of all individuals) and would have been even more scarce when excluding small gammarids (<3–4 mm) that are not supposed to be efficient shredders (Bohmann & Tranvik, 2001). Shredding Trichoptera (*Sericostoma* spec., *Mystacides* spec., other Leptoceridae) appeared in very low abundances after 42 days of submersion of the leaves.

Wave mesocosm experiment

Maximum wave height in the wave mesocosm measured by ADV meter was 0.14 m. The other abiotic factors were similar to that of the field experiment. The water was always saturated with oxygen. Mean water temperature in both mesocosms was 17.4°C ± 3.2 (±SD). The weight loss of the leaves was similar to the results from the field experiment; leaves of both species showed a rapid weight loss within the first 24 h. Beach leaves lost about 5% from initial dry weight in the wave mesocosm, but only 3.3% in the control; poplar lost 14 and 19%, respectively (Fig. 6). Both exposition time and treatment were significant factors in terms of mass loss for poplar and beech (Table 3).

Hardness of beech leaves declined slowly in both mesocosms (Fig. 7). Leaf hardness reduction of poplar occurred especially between days 14 and 27. In contrast to treatment, exposure time was a significant factor for hardness of both beech and poplar leaves (Table 3). During the mesocosm experiment, some of the polar leaves in both mesocosm showed increasing "window" damages (roundish hollows in the leaves) that are indicative of benthic invertebrate shredding. In the control mesocosm, more leaves were affected than in the wave mesocosm. Further investigations revealed that a considerable number of benthic animals had colonised the mesocosms during the experiment, mainly Cladocera, Copepoda, Ostracoda, Baetidae and Orthocladiinae. None of these taxa are shredders; however, we cannot exclude that the activity of these scraping and deposit-feeding activity of invertebrates in the mesocosms at least partly influenced the mass loss of the leaves. Animal densities were not quantified, but they were clearly higher in the control mesocosm than in the wave mesocosm, giving a possible explanation for the increased weight loss of poplar leaves in the control mesocosm.

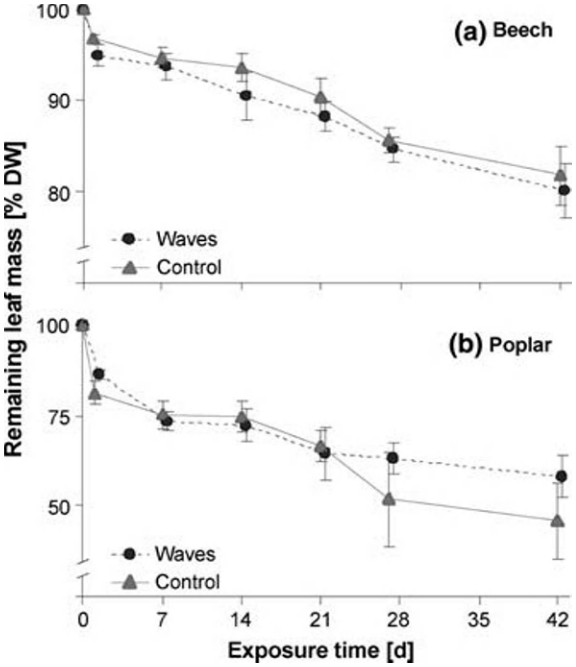

Fig. 6 Leaf degradation rate in remaining dry weight (% DW ± SD) of beech (**a**) and poplar leaves (**b**) exposed in wave and control mesocosms at 0.4-m depth, *n* = 5

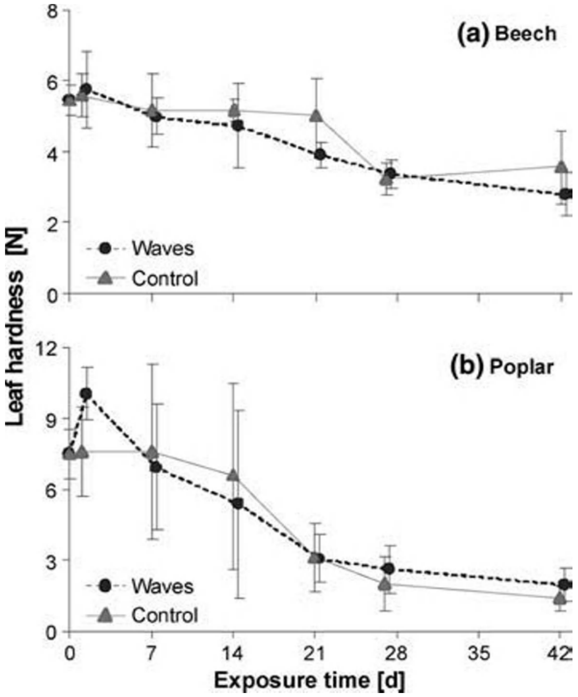

Fig. 7 Degradation rate of leaf hardness (N ± SD) of beech (**a**) and poplar leaves (**b**) over exposure time in wave and control mesocosms at 0.4-m depth, *n* = 5

Discussion

Importance of shredders

The decomposition rates of beech and poplar leaves were in the same magnitude in Lake Constance as recorded from leaf processing in streams (Gessner & Chauvet, 1994; Baldy et al., 1995; Menéndez et al., 2001). In contrast to the studies of Bjelke et al. (2005) and Bohman (2005) in mesotrophic lakes in Sweden, shredders were not abundant in the wave-impact zone of a pre-alpine lake during spring. We did not find preferences of the benthic invertebrates to one of the leaf types, as we expected from observations in

Table 3 Results of factorial ANOVA on mass loss and hardness of leaves depending on exposure time (Exp.-Time), treatment (Treat.: Wave/Control) and interaction (Exp. × Treat.)

Variable	Species	Factor	$df_{eff,\ err}$	*F*	*P*
Mass loss	Beech	Exp.-Time	5, 48	130.51	<0.001
		Treatment	1, 48	16.75	<0.001
		Exp. × Treat.	5, 48	1.40	0.243
	Poplar	Exp.-Time	5, 48	72.42	<0.001
		Treatment	1, 48	7.28	0.010
		Exp. × Treat.	5, 48	4.28	0.003
Leaf hardness	Beech	Exp.-Time	5, 48	18.10	<0.001
		Treatment	1, 48	3.60	0.064
		Exp. × Treat.	5, 48	1.10	0.371
	Poplar	Exp.-Time	5, 48	17.60	<0.001
		Treatment	1, 48	0.95	0.335
		Exp. × Treat.	5, 48	0.59	0.709

stream systems, where more recalcitrant leaf species were colonised later than leaf species with a more rapid decay (Petersen & Cummins, 1974). However, beech as well as poplar are only of low “attractiveness” compared to other leaf types e.g. alder. Apparently, shredders did not play an important role in our experiment. Rather, our results imply that invertebrates might have used the exposed leaves not as a direct food source but as habitat (Pope et al., 1999; Dudgeon & Wu, 1999).

Our observation that chironomids were the dominant species in decomposition experiments in lakes were made before by Oertli (1993) in Bois Vieux pond in western Switzerland and by Pope et al. (1999) in Scott lake (Ontario, Canada). According to the dominance of Chironomidae and to a lower extent *Caenis* spec. the most common functional feeding groups were scrapers and deposit feeders. We recognised no clear increase of shredders in the litterbags with progressing leaf decay, except for the small gammarids at the last sampling, probably originating from reproduction in spring. Further, typical biting marks of shredders were not observed on the exposed leaves of the field experiment.

Several reasons are possible to explain the low importance of shredders in our field study: (a) Phenology of the shredder species, (b) feeding preferences and alternative food sources for gammarids, (c) generally low abundance of the native gammarid species due to the recent occurrence of an invasive predator, (d) disturbance of shredder activity due to high wave impact and (e) relatively low food value and low palatability of the offered leaves.

(a) One possible reason for the unexpectedly low abundances of shredders in our litterbags is the season and low water temperatures. Many shredder species start their life cycle already in autumn during leaf fall and reach their maximum biomass during autumn and spring (Cummins et al., 1989; Bjelke, 2005). Earlier studies from the same site (Baumgärtner, 2004) documented that in Lake Constance, *Gammarus roeseli* has high biomass during winter and decreasing abundances until March. In spring, abundances increase due to reproduction, whereas biomass reaches a minimum in summer. Therefore, we expected an overlapping presence of large reproductive specimen and of small neonates during our study, which lasted from mid-February to June. Possibly, lower temperatures between mid-April and mid-May in 2005 (average 10°C) compared with the same period of the years 2000 and 2001 (15–17°) reported in the earlier study (Baumgärtner, 2004) were responsible for the lower abundance of shredders.

(b) Further, invertebrates might rather feed on the algal growth on the leaf surfaces or on accumulated FPOM than on leaf tissue (Boulton & Boon, 1991; Dangles et al., 2001). The amount of FPOM was approximately the same in litterbags of both leaf species and algae were observed on both species, giving support to this theory. At the beginning of primary production in spring, pelagic algae accumulate in the littoral near the shoreline due to wave action, and increase in importance as food source, which is also used by some shredder species (Bjelke, 2005). Shredders are rarely food specialists and may adapt their diet according to the current food offer (Friberg & Jacobsen, 1994; Bjelke, 2005; Wantzen & Wagner, 2006). This is especially true for gammarids (MacNeil et al., 1997). It is likely that during other periods of the year, for example, in autumn and early winter, when the leaves are freshly fallen and no algae are available as food source the activity of shredders might be distinctively more important than we observed.

(c) Shortly before our study began, a predatory gammarid from the pontocaspian area has invaded Lake Constance, *Dikerogammarus villosus* (Rey et al., 2005). In riverine catchments, it has already led to a dramatic decrease of the native fauna, especially other gammarid species (Dick et al., 2002). *D. villosus* causes a considerable impact on the native fauna in Lake Constance (Hesselschwerdt & Wantzen, unpublished data).

(d) The specific abiotic conditions at our experimental site might be another factor responsible for the recorded low abundances of shredders. It is an erosional site with regular wave action and therefore very low deposition of leaves. Currents and waves regularly transport the leaf litter from the littoral to the shore line and accumulate it there. Especially, after storm events, we observed accumulations of litter above the shore line and probably large amounts of leaves are broken down there out of reach of aquatic shredders. We expect more shredder activity in other parts of Lake Constance, mainly in depositional sites where wave action and currents are low and leaves can sediment on the littoral ground. Our 'unwillingly' obtained results from the wave mesocosms (more benthic invertebrates and a higher weight loss of polar in the control mesocosm than in the wave mesocosm) support this hypothesis.

(e) Based upon the ergosterol values, the fungal biomass ranged between 3.7 mg g^{-1} DW and 25.8 mg g^{-1} DW in the leaves. These values are relatively low compared to literature values from streams. Baldy et al. (1995) found 610 μg Ergosterol g^{-1} AFDM in *Populus nigra* (approximately 80–90 mg biomass g^{-1} DW). For beech Gessner & Chauvet (1994) measured 66 mg g^{-1} AFDM, (approximately 50–55 mg biomass g^{-1} DW). In a nutrient-rich stream, we found fungal biomass values as high as 55.5 mg g^{-1} DW in beech. (Wantzen, unpublished data). Possibly, these low fungal biomass values and the known low palatability of poplar and beech leaves (Webster & Benfield, 1986) reduced the attractiveness of the leaves as food for the shredders.

Importance of wave action

In the field experiment, the storm events strongly influenced the patterns of leaf weight loss, FPOM accumulation, leaf hardness (only poplar) and benthic invertebrate colonisation. In our study, the k_{day}-value for beech (−0.0065) was much higher than reported for another german lake with low wave impact, Lake Stechlin (−0.0011, Casper, 1987), indicating a high importance of wave action for litter degradation. The accelerated mass loss of both species in the litterbags during the first storm event (2nd week) was probably due to losses of leaf fragments that resulted from filling of the bags with air-dried leaves. We did not observe signs of decomposition of the leaves at either of the species at that time. However, only poplar leaves significantly lost weight during the second storm event (between days 42 and 55). At that date, poplar leaves were clearly decayed and fragmented, which was also discernable from the considerably reduced leaf hardness. We assume that shearing forces of waves were able to damage the softened leaves, remove soaked and macerated leaf tissue or to tear off whole pieces and transport them away. Even more distinctive was the effect of waves in case of FPOM, which was washed out of the litterbags during the storm events. Invertebrates were presumably washed away by the waves as well.

The mesocosm experiment revealed significant differences in leaf processing of beech leaves between treatment with and without waves. In the first 24 h, beech leaves lost about 45% more of their dry weight with wave impact than in control mesocosm. We conclude that wave action primarily modified the leaching phase of beech leaves. In the case of poplar leaves, we found no such dependence on wave impact, although poplar leaves had a significantly higher leaching loss than beech in all experiments. Beech leaves are softer than poplar; their cuticule and waxy layer probably became damaged by the mechanical stress of the waves in our experiment, so that the leaching was promoted in wave mesocosm.

In our experiment, the poplar leaves became softer and susceptible to the shear forces only after several weeks of submersion in wave mesocosm. This result is in accordance with earlier studies on the maceration effects of microorganisms and/or invertebrates (Suberkropp & Klug, 1980). Molinero et al. (1996) pointed out that hardness and robustness of leaves next to other factors can influence their proneness to abrasion and shear forces of wave action. They supposed that hydrodynamic forces especially increase the mass loss of soft leaves.

Contrary to our expectations, we observed no fragmentation of leaves in the mesocosms at all. Possibly, fragmentation only happens after a longer exposition time or when leaves are located directly in the zone of breakers as there are the most intensive turbulences. Under natural conditions, leaves in littoral are bundled off to the zone of breakers by waves and currents, and are ground there, or leaves on the beach are washed into the sublittoral zone by breakers (Merritt et al., 1984; Pieczyńska, 1986).

Conclusions and outlook

This is the first study focussing on the effects of wave action on leaf processing in lakes. The results indicate that shredders did not have an import role in leaf processing in erosional sites of Lake Constance, where waves and currents prevent deposition of leaves. However, additional constraints on the shredder activity, such as phenology and impacts by exotic species, cannot be excluded. In the field experiment, strong waves during storm events had discernable effects on the decomposition process by removing leaf fragments, FPOM and invertebrates. In contrast to our expectations, the waves in the mesocosm experiment did not cause grinding of the leaves during a 42-day period. Our results imply to study the influence of wave action and shredders over longer periods of time (particularly in case of recalcitrant leaf species like beech) and to study leaf decay during different seasons at several sites with various sediment structures and exposition to waves. The influence of aquatic microbiota (fungi, bacteria) on physical degradation of the leaves and on shredder feeding was not analysed here but certainly deserves a closer examination in future studies.

Our field observations have shown an important impact of water-level fluctuations on the accessability of leaf litter by aquatic decomposers. Dry leaf litter that becomes blown into the littoral zone often becomes accumulated in the surf zone, where it becomes physically degraded by wave action and freezing. The continuous decrease of water level in winter leads to the development of banded deposition patterns of debris. In spring, these debris dams are important sites for aquatic and semi-aquatic detritivores, e.g. tipulids were observed to oviposit into the moist debris walls above the water line. During rising water levels in spring and early summer, this POM becomes transported back into the littoral zone, and the broken leaf particles are easily retained in the coarse sediments of the erosional sites. We conclude that leaf litter decomposition should not be regarded as a homogeneously distributed process that occurs in a similar way all over the lake. In analogy to rivers, we expect process domains (Montgomery, 1999) and biotic hot spots and hot moments (Wantzen & Junk, 2006) in lakes, i.e. there are sites with different types of decomposition or storage of organic matter. Accordingly, we expect physical degradation to be high in erosional sites and low in depositional sites, while high biotic decomposition will occur in sites with intermediate hydraulic stress for invertebrate shredders and intermediate retention time for organic matter. Water-level fluctuations have a major impact on the temporal and spatial distribution of these process domains. At the same place, conditions may vary from erosional to depositional during periods of variable water levels. In pre-alpine lakes with variable sediments at different depth zones like Lake Constance, different water levels even decide over sediment composition, and thus physical and biotic elements of leaf litter decomposition.

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WATER-LEVEL FLUCTUATIONS

Use of the water-level fluctuation analysis tool (Regcel) in hydrological status assessment of Finnish lakes

Antton Keto · Anne Tarvainen · Mika Marttunen · Seppo Hellsten

Abstract Regulation of water flow constitutes the most important hydromorphological burden to Finnish lakes. The total area of regulated lakes is nearly 11,000 km^2, equalling one-third of the total area of Finnish inland waters. Extensive research projects have been carried out since the end of the 1980s to find out opportunities to mitigate harmful effects of the regulation of watercourses. A water-level fluctuation analysis tool, known as Regcel, has been developed to study water level data and to identify the most significant impacts. Results of the Regcel analysis give an overall picture of the impact of lake regulation in northern climate. The model is based on relationships between the water-level fluctuation and factors related to environmental, social and economical effects. Regcel has been used in 12 Lake Regulation Development Projects in Finland. In this article, we show how the Regcel model was applied in two cases.

Keywords Water-level fluctuation · Water-level regulation · Impact assessment · Hydrological status · Heavily modified water bodies

Introduction

Finland is a country of thousands of lakes. There are 187,888 lakes, if lakes larger than 0.05 ha are included (Raatikainen & Kuusisto, 1988). Most of the large Finnish lakes are regulated and nearly all of the large watercourses are exploited, primarily to meet the needs of hydropower production and flood protection (e.g. Marttunen et al., 2006). The total area of regulated lakes is nearly 11,000 km^2, equalling one-third of the total area of Finnish inland waters. Moreover, most of the large rivers have been harnessed for hydropower production, as all over the northern hemisphere (Dynesius & Nilsson, 1994).

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In recent decades, there has been great public pressure to modernize old regulation practices. Extensive research projects have been carried out to establish the effects of water-level regulation and to develop means of mitigating the negative impact of regulation (Hellsten et al., 1996; Marttunen et al., 2001). This has also contributed to improving assessment methods and models of the effects of lake regulation (e.g. Marttunen & Suomalainen, 2005).

The most commonly used assessment tool is called Regcel. This impact assessment model calculates more than 20 water-level parameters to give an overall picture of the ecological, social and economic effects of water-level regulation. The identification of the water-level characteristics as indicators was made in several research projects published in a review by Marttunen et al. (2001). The basic set of indicators and the use of Regcel have been demonstrated previously by Hellsten et al. (2002).

This article describes recent development of the Regcel model and two latest applications for the EU Water Framework Directive (WFD) purposes. The WFD describes hydromorphological elements as supporting the biological elements (2000/60/EC). However, unlike the biological elements, hydromorphological elements contribute to status classification only for water bodies at high ecological status. At good and moderate ecological status, hydromorphological conditions are not defined but are to be consistent with the achievement of the values specified for the biological quality elements.

On the other hand, the WFD (Art. 4(3)) allows the Member States to identify surface water bodies that have been hydromorphologically altered by human activity. If the specified uses of such water bodies (i.e. navigation, hydropower, water supply or flood defence) or the wider environment would be significantly affected by the hydromorphological changes and if the achievement of a good ecological status is not possible or no other, technically feasible and cost-effective better environmental options exist, then these water bodies can be designated as heavily modified, and good ecological potential is set as an environmental objective.

This article is structured in the following way. First, we describe the variables and basic indicators of Regcel. Second, we show the results of the 214-lake survey and hydrological status assessment with Regcel, and finally, we discuss the strengths and weaknesses of the method.

Materials and methods

Regcel is a Microsoft Excel© application performed using the Visual Basic© programming language. The Regcel model enables assessment of the major ecological and social impacts of lake regulation in Finland. It consists of 5 variables and 16 indicators inside the variables. In addition, there are seven general indicators without any specific meaning. The identification of the water-level characteristics as indicators was made in several research projects published in a review by Marttunen et al. (2001) and Hellsten et al. (2002). Indicators describe impacts of water-level regulation on aquatic macrophytes, benthic invertebrates, fishes, nesting of water fowls and recreational use (Fig. 1). Some indicators are not based on measured relationships between water-level fluctuation and ecological factor, although they have been used in many water-level regulation development projects. This article focuses on those ecological indicators where known relationship exists. All Regcel indicators and their calculation principles are described in electronic supplementary material—Appendix 1.

Regcel indicators are calculated from daily water-level observations (above sea level). Only water colour (mg Pt l^{-1}), maximum ice thickness (m) and ice-off and ice-on days are required as complementary data. Ice-off and ice-on data are not available from all Finnish lakes, but it is possible to replace them with data from a lake that has the same geographical location. In this study, the input data was taken from the databases of the Finnish Environment Institute. Table 1 shows the calculation principles of the six indicators. Altogether, 105 regulated and 109 unregulated (natural water-level fluctuation) lakes were studied with Regcel indicators. Indicators were calculated for years 1980–1999 and the average values of that period were compared to each other.

Results

Differences between regulated and unregulated lakes in Finland

The total area of the study lakes was 18,167 km^2, which accounts for 56% of the total lake area of

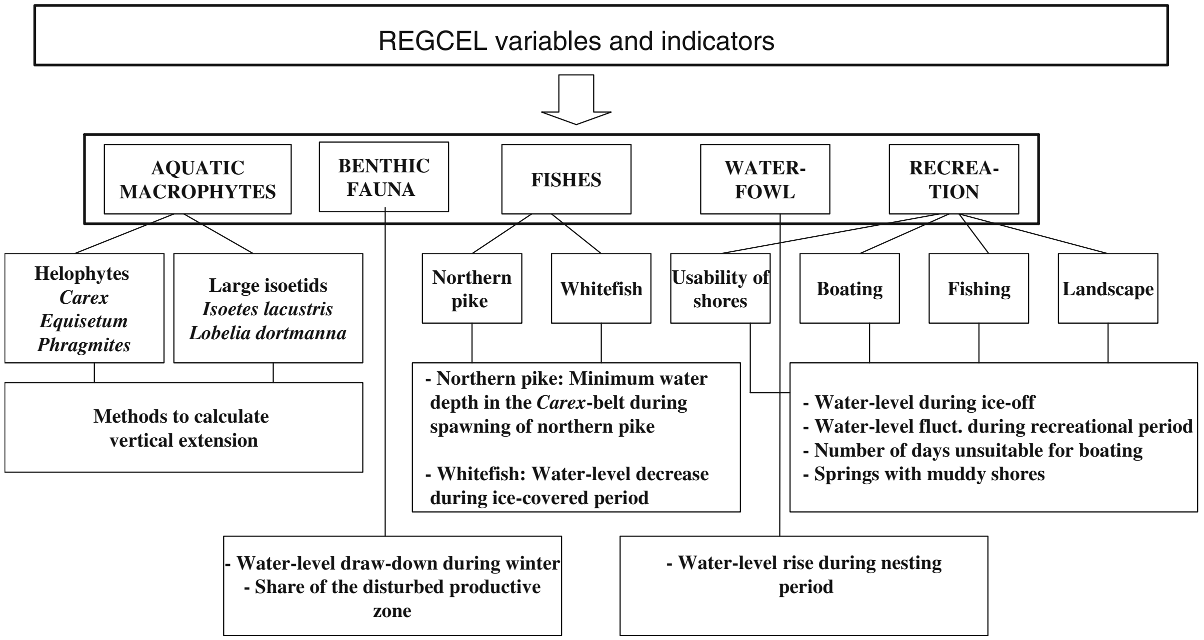

Fig. 1 Variables and basic indicators of Regcel

Table 1 Regcel indicators and their calculation principles

Variable	Indicator	Calculation principle
Aquatic macrophytes	(A) Magnitude of spring flood (m)	HW_spring period − W50_OWP
Aquatic macrophytes	(B) Maximum vertical extension of the *Carex* zone (m)	W10_OWP − W75_OWP
Benthic fauna and fish	(C) Magnitude of winter drawdown = water level decrease during the ice cover period (m)	W_IN − NW_ICP
Fish	(D) Minimum water depth in the *Carex* zone during the spawning of northern pike (m)	NW_(IO – IO + 1 month) − W75_OWP
Waterfowl	(E) Water level rise during the nesting of birds (m)	HW_nesting − W_(IO + 2 week)

Refer indicative letter (A–E) in “Materials and methods” for details

W = Observed water level (A.S.L.); HW = highest observed water level; NW = lowest observed water level; W10 = 10% fractal of water levels of calculation period; W50 = 50% fractal of water levels of calculation period; W75 = 75% fractal of water levels of calculation period; IO = ice-off date; IN = ice-on date; OWP = open water period, stretch of time from ice-off day to ice-on day; ICP = ice cover period, stretch of time from ice-on day to ice-off day; spring period = a stretch of time from 2 weeks before ice-off to 4 weeks after ice-off (altogether 6 weeks); nesting = a stretch of time from 2 weeks after ice-off to 6 weeks after ice-off (altogether 4 weeks)

32,600 km^2 in Finland. The average size of the regulated lakes was 88 km^2 (median = 25 km^2) and that of the unregulated lakes was 82 km^2 (median = 21 km^2). The area of the smallest unregulated lake was 0.4 km^2 and of the smallest regulated lake was 0.9 km^2. On the other hand, the largest unregulated lake in Finland, L. Saimaa, 4,166 km^2, and the largest regulated lake, L. Päijänne, 1,116 km^2, were also included in this survey. The mean depth of the regulated lakes was 8.4 m and that of the unregulated lakes was 7.3 m. All in all, the study covered a greater number of large lakes than small lakes in comparison with the size distribution of all lakes in Finland.

The magnitude of the spring flood (A) describes the impacts on the zonation of aquatic macrophytes and paludification of lake shores. It was calculated as a difference between highest water level of spring

Table 2 Results of 7 Regcel indicators of a national survey of 109 unregulated and 105 regulated lakes

Indicator	Regulated lakes				Unregulated lakes				Avg. difference (m)
	Avg.	Min.	Max	Std.	Avg.	Min.	Max.	Std.	
(A) Magnitude of spring flood (m)	0.24	−0.09	1.36	0.25	0.56	−0.01	1.72	0.38	0.32↓
(B) Maximum vertical extension of the *Carex* zone (m)	0.30	0.05	1.10	0.17	0.46	0.16	1.00	0.18	0.16↓
(C) Magnitude of winter drawdown = water level decrease during the ice cover period (m)	1.00	0.01	6.75	1.10	0.28	0.03	0.62	0.13	0.72↓
(D) Minimum water depth in the *Carex* zone during the spawning of northern pike (m)	−0.04	−1.63	0.56	0.30	0.27	0.02	0.61	0.13	0.31↓
(E) Water level rise during the nesting of birds (m)	0.11	0.00	0.67	0.11	0.04	0.00	0.17	0.04	0.07↓

↓ = water-level regulation has negative impact; ↑ = water-level regulation has positive impact

period and 50% fractal of water levels of open water period (Table 1). Indicator was 0.32 m lower on average in the regulated lakes (Table 2). There were seven regulated lakes where the spring flood indicator got negative values, which means that spring water levels are lower than summer water levels. The maximum vertical extension of the sedge zone (B) was calculated as a difference between 10% fractal and 75% fractal of water levels of open water period. It was 0.16 m narrower on average in the regulated lakes.

The magnitude of winter drawdown (C) demonstrates impacts on freezing sensitive macrophyte species, macrozoobenthos species and fish eggs. It is calculated as a difference between water level of ice-on date and the lowest water level of ice-cover period. Indicator was 0.72 m more extensive on average in regulated lakes. The difference is even more striking when the maximum winter drawdown value of 0.62 m in the unregulated lakes was compared with the maximum value of 6.75 m in the regulated lakes.

The minimum water depth (m) in the sedge zone during the spawning of northern pike (D) describes impacts on spring spawning fishes. It is calculated as a difference between the lowest water level during ice-off month and 75% fractal of water levels of open water period. Indicator got negative values in 49 out of the 105 regulated lakes, which means that water rises to that zone after the spawning period. In contrast, the sedge zone was inundated in all unregulated lakes. Highest values were quite the same in both lake groups.

The smallest differences between the indicators of regulated and unregulated lakes appeared in the water level rise during the nesting of water fowls (E). This indicator illustrates the impacts on those bird nests, which might drown as a result of water rise. It is calculated as a difference between the starting day water level and highest water level of the average nesting period. The nesting period lasts for 4 weeks starting 2 weeks after ice-off. Indicator was 0.07 m higher in the regulated lakes. Highest values deviated for each other 0.5 m between these two lake groups.

Determination of high hydrological status

The identification of a hydrological status includes several phases (Fig. 2). In the first phase, the most important permanent factors affecting the water-level fluctuation of a lake were determined. Correlation between the annual water-level fluctuation and basic characteristics of the lake and drainage basins showed that the lake percentage of drainage basin was best interpretive (Table 3) and can explain nearly 70% of the annual water-level fluctuation (Fig. 3).

Variation in annual water-level fluctuation between lakes is quite wide and weakens the resolution power of indicators. Therefore, lakes were divided into three types based on expert judgement: lakes with lake percentage of drainage basin less than 7%, 7–15% and more than 15%.

The second phase of the analysis included selection of ecologically most relevant water-level indicators (Fig. 2). The choice of the indicators was based on extensive studies, where representative data of aquatic macrophytes, macrozoobenthos and fishes were analysed from more than 30 regulated lakes (Aroviita & Hämäläinen, 2008; Sutela & Vehanen, 2008). Ecologically most relevant indicators were

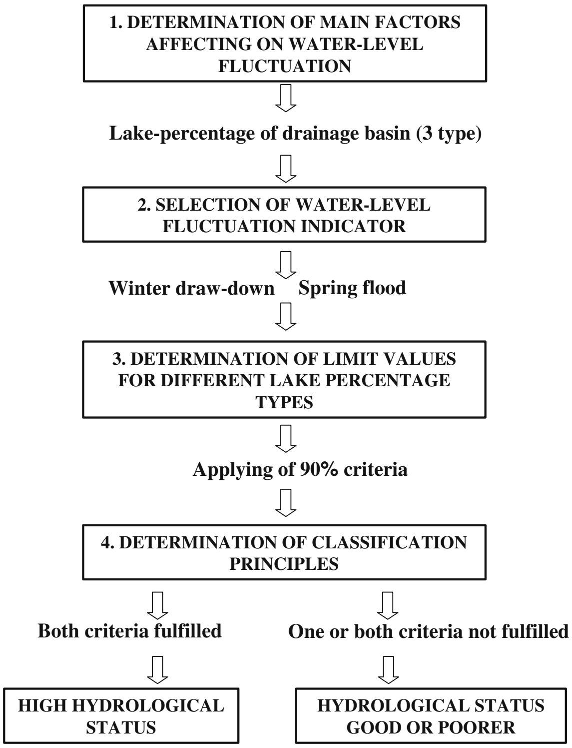

Fig. 2 Steps for determination of the hydrological status of regulated lakes

Table 3 Pearson's correlation coefficient between annual water-level fluctuation and lake characteristics based on the analysis of 105 unregulated lakes

Lake characteristics	Correlation coefficient
Lake area	−0.40
Lake volume	−0.38
Area of drainage basin	−0.10
Lake percentage of drainage basin	−0.72
Theoretical retention time of water in lake	−0.60

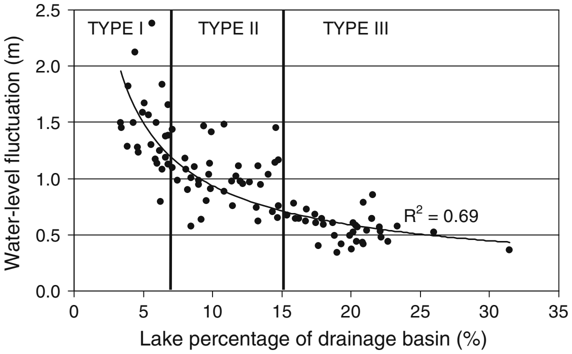

Fig. 3 The relationship between the lake percentage of a drainage basin and the annual water-level fluctuation. Division into three types is based on expert judgement

Table 4 Limit values used to identify regulated lakes with high hydrological status

	Lake percentage of drainage basin		
	Type I <7%	Type II 7–15%	Type III >15%
Magnitude of winter drawdown (m)	<0.6	<0.6	<0.3
Magnitude of spring flood (m)	>0.6	>0.25	>0.15

magnitude of winter drawdown and spring flood, which were further selected for our study.

In the third phase, the limit values for water-level indicators were determined (Fig. 2). In this case, winter drawdown and spring flood values within 90% of all observations from the unregulated lakes of the same type were accepted as high hydrological status values. Table 4 shows the values used as the limit values for the high hydrological status.

Finally, the classification principles were determined (Fig. 2). Those lakes where both winter drawdown values were lower than limit values and magnitude of spring flood values higher than limit values were classified to high hydrological status. In contrast, other lakes were given a lower hydrological status. Results of the analysis showed that 24 of 105 regulated lakes were in high hydrological status (Table 5). For example, in 15 out of the 57 regulated type-II lakes, the winter drawdown was less than the limit value (Fig. 4A). Furthermore, the spring flood values were higher than the limit value in 24 regulated lakes (Fig. 4B). Both of the classification principles were fulfilled in nine lakes (Table 5).

Table 5 Results of the identification of the regulated lakes with a high hydrological status

Lake percentage of drainage basin	Number of regulated lakes	Number of regulated lakes with a high hydrological status
Type I	17	4
Type II	57	9
Type III	31	11
Total	105	24

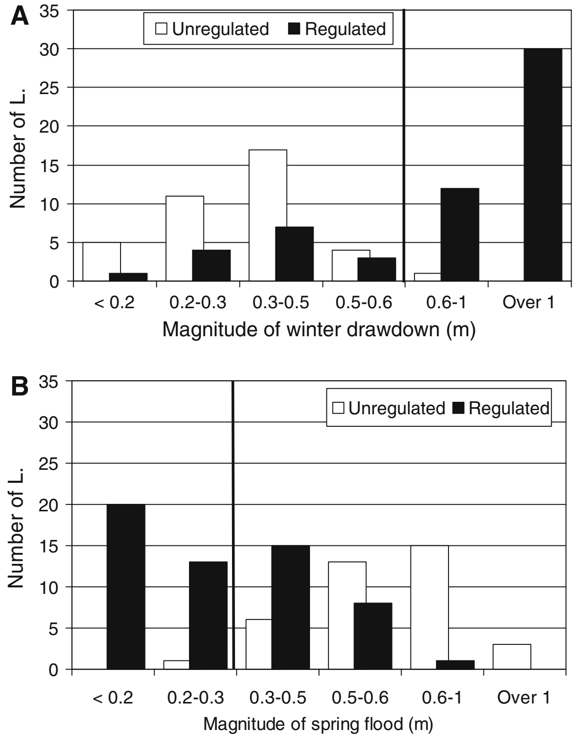

Fig. 4 Histogram of the comparison of the winter drawdown (**A**) and the spring flood (**B**) values of the regulated and unregulated lakes of type II. Vertical lines describe the limit values

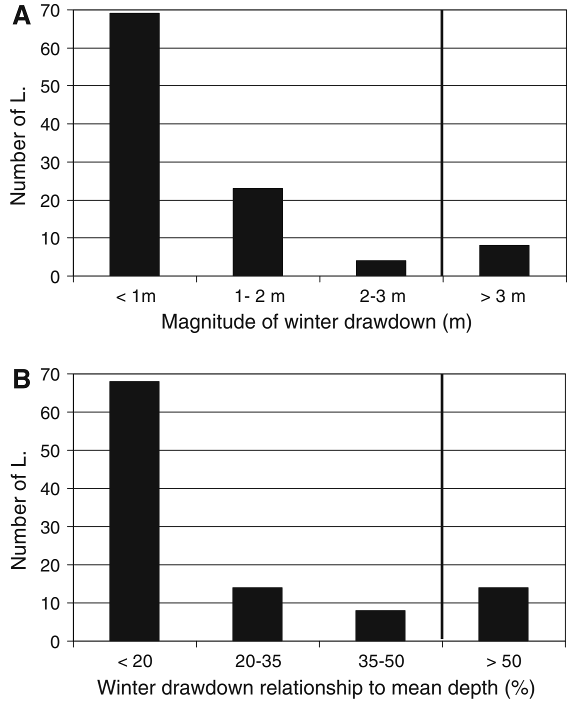

Fig. 5 Results of the provisional designation of heavily modified lakes. Lakes where winter drawdown is more than 3 m (**A**) or the winter drawdown relationship to the mean depth is more than 50% (**B**) are designated provisionally as heavily modified lakes. The vertical lines describe the limit values

Provisional designation of heavily modified lakes

In provisional designation of heavily modified lakes according to WFD, the same indicator as in the high hydrological status assessment was used, namely, the magnitude of winter drawdown. Because the previous analysis was based on a majority of large and relatively deep lakes, the winter drawdown relationship to the mean depth was selected to describe changes in small and shallow lakes. The analysis was carried out for the same 81 regulated lakes that were in a good or poorer status based on the previous high hydrological status assessment.

Nearly 70% of the regulated lakes have winter drawdown of less than 1 m or the winter drawdown relationship to the mean depth is less than 20% (Fig. 5). A total of 15 lakes of the 81 survey lakes were provisionally designated as heavily modified lakes (Table 6). A total of 14 lakes of them were designated, when the winter drawdown relationship to the mean depth was used as a criterion. One lake, where the winter drawdown was larger than 3 m, was not designated on the grounds of the winter drawdown relationship to the mean depth.

Table 6 Results of the provisional designation of heavily modified lakes according to those criteria

Lake percentage of watershed	Number of regulated lakes	Number of regulated lakes designated initially as heavily modified
Type I	13	4
Type II	48	11
Type III	20	0
Total	81	15

Please note that the regulated lakes with a high hydrological status are not included in this assessment

Discussion

Differences between regulated and unregulated lakes have been studied earlier (Rørslett, 1988; Hellsten, 1997), but comprehensive hydrological status assessment models have mainly concentrated on rivers (Richter et al., 1996, 2003, 2006; Black et al., 2000; King et al., 2003). Rarity of hydrological status assessment models in lakes is based on the fact that water levels in natural lakes are not monitored, and therefore, comparative data is largely missing (Marttunen et al., 2006).

Changes in water levels due to the water course regulation may greatly affect littoral zone biota. Morphological changes are usually of minor importance or they are primarily due to water-level regulation like dams of hydropower plants (Marttunen et al., 2006). Therefore, the analysis of hydrological alterations gives, in many cases, a good picture of the overall hydromorphological status. Analysis of 105 regulated and 109 unregulated lakes showed that the ecological status was poorer in the regulated lakes based on all five ecological indicators.

The magnitude of the spring flood (A) was 0.32 m lower on average in regulated lakes. In a recent study of Partanen et al. (2006), several Regcel indicators related to helophyte species vertical extension and field measurements were compared in three Finnish lakes before and after water-level regulation. Measured vertical extension of helophytes correlated relatively well with calculated value except in eutrophic Lake Pyhäjärvi, where it was wider than calculated.

The area of emergent plant species in shallow bays and other gently sloping areas have increased due to the lowered spring water levels (Partanen & Hellsten, 2005). The paludification process is partly dependent on the availability of nutrients and partly on the availability of suitable habitats (Partanen & Luoto, 2006). Studies have shown that temporally lowered water levels by regulating the spring flood have enhanced the growth of the common reed (*Phragmites australis* Trin Ex. Steudl), which benefits from a competition-free environment during early summer (Van Den Brink et al., 1995; Keto et al., 2002; Mäemets & Freiberg, 2004; Hellsten et al., 2006). Finnish large regulated lakes are optimal growth area for reed, because wave exposure tends to keep bottom sediment saturated by oxygen, as shown in Swedish lakes by Weisner (1987).

Furthermore, in lakes with a low spring flood or raised water level, the sedge zone has been observed to be very narrow (Nilsson, 1977; Sjöberg & Danell, 1983; Hellsten, 2001). On the other hand, a high spring flood prevents competition from shrubs, grasses and mosses, since stems of sedges contain aerenchymal tissue, and therefore, can resist longer sediment with a low oxygen condition (Fagerstedt, 1992).

The magnitude of winter drawdown (C) was 0.72 m more extensive on average in regulated lakes. In earlier studies, the aquatic macrophyte and littoral macrozoobenthos data analyses suggest that in Finland, where the ice cover period normally lasts from December to May, the winter drawdown has a significant adverse impact on freezing sensitive species like large-sized isoetids (Rørslett, 1984; Palomäki & Koskenniemi, 1993; Hellsten, 1997, 2001). The reproduction success of whitefish depends on the oxygen conditions of the sediment, predation and the water level decrease during ice cover period (Gaboury & Patalas, 1984; Sutela et al., 2002). The maximum amount of whitefish eggs was found at a depth of less than 1.0 m, in seven of nine lakes (Sutela, 2003), which indicates a high sensitivity to water level decrease during the winter.

Minimum water depth in the *Carex* zone during the spawning of northern pike was 0.31 m lower on average in regulated lakes. The inundated area of sedge vegetation represents the best available area for reproduction of northern pike (*Esox lucius*), and it carries several times as many young fries as other vegetation zones, as described by Korhonen (1999).

Water level rise during the nesting of birds was 0.07 m higher in the regulated lakes on average. Especially, the Black-throated Diver (*Gavia gavia*) has been found to be very sensitive to water level rise during nesting periods, because it is mostly nesting only 0.15–0.25 m above the water level (Lammi et al., 1999). Gull species like Black-headed Gull (*Larus ridibundus*) and Lesser Black-backed Gull (*Larus fuscus fuscus*) are also sensitive to rising water levels during the nesting period. The difference in average water level rise during the nesting period doesn't indicate very well the potential negative impacts to water fowls. In all of the 109 unregulated lakes, water level rise was smaller than 0.2 m. However, there were 17 out of the 105 regulated lakes where water level rise was greater than 0.2 m, even 0.67 m.

Furthermore, the magnitude of winter drawdown was selected as the first water-level indicator in hydrological status assessment, because it explained species richness and abundance of aquatic macrophytes (Keto et al., 2006), macrozoobenthos (Aroviita & Hämäläinen, 2008) and fishes (Sutela & Vehanen, 2008). Earlier studies suggest that the magnitude of spring flood has also remarkable ecological relevance (Hellsten, 2001; Hellsten et al., 2006), and therefore, it was selected as the second water-level indicator.

Our results showed that in 20% of the regulated lakes, the hydrological regime reflects totally or nearly totally undisturbed conditions and can thus be classified with a high hydrological status. In contrast, nearly 20% of the regulated lakes can be designated provisionally as heavily modified water bodies in accordance with the EU Water Framework Directive (2000/60/EC).

Conclusion

The aim of this study was to identify those lakes in which the hydrological alterations were strong enough to cause significant adverse effects on the biology of the lakes. A method based on the use of water-level indicators was applied, because in many water bodies, there is a lack of systematically gathered biological data.

Analysis of 105 regulated and 109 unregulated lakes showed that the ecological status was poorer in the regulated lakes based on five ecological indicators. Biggest differences appeared at the magnitude of winter drawdown and the magnitude of spring flood. This means that the sedge zones are less extensive and abundance of the freezing sensitive aquatic macrophytes, benthic invertebrates and juvenile fish species have decreased. In the large lakes, the growth potential of *Phragmites* has increased due to lowered water levels and a competition-free environment during early summer (Partanen & Hellsten, 2005; Hellsten et al., 2006). Black-throated Diver and Gull-species may suffer from greater water level rise during nesting period, because the majority of nests are often situated very close to the lake shoreline. The difference in average water level rise during the nesting period doesn't indicate very well the potential negative impacts to water fowls.

Our results showed that in 20% of the regulated lakes, the hydrological regime reflects totally or nearly totally undisturbed conditions and can thus be classified with a high hydrological status. In contrast, nearly 20% of the regulated lakes can be designated provisionally as heavily modified water bodies in accordance with the EU Water Framework Directive (2000/60/EC).

The Regcel model proved its efficiency and applicability in the hydrological status assessment of lakes. A large number of lakes could be easily compared, and biologically relevant designation criteria could also be set with experts. The choice of the hydrological parameters was mainly based on many R&D-projects, which also enabled the introduction of some of these criteria into Finnish legislation (Anonymoys, 2006). The developed method is straightforward, however, it may not give reliable results in small lakes. For example, in large lakes, the changes caused by the lowering of the mean water level are not as significant as in small lakes, where the lowering can lead, e.g. to a substantial increase in aquatic macrophytes (Wallsten & Forsgren, 1989).

Though the general impact of lake regulation is quite well known, there are, however, many lake-specific factors that may alleviate or strengthen the impacts of regulation. In order to avoid misjudgements, the final choice of indicators plays a crucial role in the lake-specific analysis. Expert judgement is also needed to interpret the results and to assess the ecological significance of water-level fluctuation.

Local applications and further development of Regcel depend largely on the improvement in basic knowledge about the relationship between water-level fluctuation and environmental factors. Recent research activities are focused to connect water-level fluctuation indicators more exactly to ecological quality ratio (EQR) and furthermore to ecological status. For example, relationship between winter drawdown and aquatic macrophyte species composition and abundance was studied and preliminary threshold for good and satisfactory EQR value was fixed to the magnitude of winter drawdown of 3 m (Keto et al., 2006). Efficiency and reliability of the Regcel indicators also depend on the availability of hydrological data. In Finland, all the input data is available from the databases of Finnish environment administration. A recent study by Marttunen et al. (2006) showed that recalculated water level values and even some basic data of the ice cover period were rare in Norway and Sweden, which hampers the use of some indicators in other countries.

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WATER-LEVEL FLUCTUATIONS

Mass mortality of the invasive bivalve *Corbicula fluminea* induced by a severe low-water event and associated low water temperatures

Stefan Werner · Karl-Otto Rothhaupt

Abstract The Asian clam *Corbicula fluminea*, originating from Southeast Asia, was first recorded in Lake Constance in 2003 and developed local mass occurrences afterwards. Effects of harsh winter conditions in 2005/2006 associated with a strongly decreasing water level were studied at three different depths at and below the mean low water level (MLL, MLL −1 m and MLL −3 m). Low winter temperatures produced a massive die-off of the *C. fluminea* population. The mortality of the clams was size class and depth dependent. At the mean low water level (MLL), all clams died because of lying dry. However, at MLL −1 m and at MLL −3 m, mortality was a consequence of water temperatures around 2°C for nearly 3 months. At MLL −3 m, clams >5 mm died later than young clams <5 mm and later than clams of all sizes at MLL −1 m. But in late spring even the clams >5 mm at MLL −3 m were dead and only about 1% of the overall population of *C. fluminea* survived the winter conditions until spring 2006.

Lethal effects of low water temperatures on *C. fluminea*, which may become effective only after a time lag, were corroborated in an outdoor mesocosm experiment with constant water level and without predation.

Keywords Water-level fluctuation · Invasive · Bivalve · Winter mortality · Low water · Population

Introduction

Originating mainly from Southeast Asia, C*orbicula fluminea* was introduced to North America in the early 20th century (McMahon, 1982). Then, in the late 1960s South America was also colonized by *C. fluminea*, where it is still spreading (Ituarte, 1981; Darrigran, 2002). Europe was invaded in the 1980s (Mouthon, 1981; Bij de Vaate & Greijdanus-Klaas, 1990; den Hartog et al., 1992). Due to its meanwhile almost worldwide distribution supported by men and due to its natural dispersal characteristics, clams of the genus *Corbicula* belong to the most invasive taxa (Morton, 1979). They mainly establish in the southern parts of the temperate zone, in the subtropics, and the tropics, since its northern range is limited by cold temperatures (≤2°C; Britton & Morton, 1982; Karatayev et al., 2005).

After its invasion, *C. fluminea* became the dominant mollusc in large German rivers (Bachmann et al., 2001). The entire River Rhine from the mouth to Switzerland, the upper limit of cargo shipping

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Ecological Effects of Water-Level Fluctuations in Lakes

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(~850 river km), was colonized within 15 years (Turner et al., 1998).

In 2003, *C. fluminea* was first recorded in pre-alpine Lake Constance (Werner & Mörtl, 2004), where this clam can meanwhile constitute up to 90% of the biomass of the littoral community (Werner & Rothhaupt, unpublished data). This settlement is isolated from other occurrences of this species and may therefore be caused by men (Werner & Mörtl, 2004).

The catchment area of oligotrophic Lake Constance (Central Europe) is largely dependent on the unregulated alpine system of the Rhine River. Generally, the water level reaches a minimum by the end of February. Afterwards, the water level starts rising due to increased precipitation and snowmelt in spring, leading to a maximum in June/July. Due to this, the water level annually fluctuates within 2 m (Jöhnk et al., 2004). We wanted to observe if clam densities are affected by low temperatures combined with low water levels during winter. The specified sampling period turned out to be particularly interesting, because the winter conditions in 2005/2006 were exceptionally harsh with water levels decreasing below the usual minimum values.

Material and methods

Study area and sampling

In Lake Constance, *C. fluminea* was first recorded in a large, sandy shallow-water zone called Rohrspitz near the city of Bregenz (Werner & Mörtl, 2004), where, after 2 years, the clams occurred in high densities. Therefore, we chose this site (E 9°37′/N 47°30′) for sampling. The substrate consisted of fine sand with a grain size of 200–630 μm (90%) and coarser sand with a grain size of 630 μm–2 mm (10%).

We studied the development of the clam population at three different depths related to the mean low water level (264 cm): MLL, MLL −1 m, and MLL −3 m. Sampling dates in 2005/2006 were September 20th, December 13th, March 16th and June 27th. Daily mean water level and water temperature were continuously received from the water gauge measuring site at the harbour in Bregenz (August 1, 2005 until July 31, 2006; gauge zero is 391,89 m NN). Water temperature was measured 50 cm below the water surface (lowest water depth: 228–50 cm).

Field sampling methods and laboratory analyses

The chosen depths were located using GPS and characteristic landmarks. Asian clams were collected by Scuba divers using an infralittoral suction sampler (Mörtl, 2005) covering a sampling area of 625 cm^2. Three replicates were taken at each depth. In the laboratory, sampled mussels were fixed in 95% ethanol after each sampling day. Juvenile and adult clams were separated from sediment by the use of sieves with three mesh-sizes (250 μm, 1 mm, 2 mm). By using an electronic calliper (Preisser, Digi-Met) clams were grouped into two different size classes: (1) clams <5 mm (juveniles of the year) and (2) older clams >5 mm.

Mesocosm study

To rule out effects of water-level fluctuation and predation on survival of *C. fluminea*, we conducted a study at the Limnological Institute in Konstanz-Egg in an outdoor mesocosm with a size of $2 \times 2 \times 1$ m^3 and constant water level. We recorded the impact of natural winter temperatures on a *C. fluminea* population from the study site. We added 1331 *C. fluminea* >5 mm and, additionally, two individuals of the native unionid *Anodanta cygnea* (shell lengths: 6.3 and 6.9 cm, respectively) to the mesocosm. Water temperatures were recorded by a HOBO Pendant Temperature/Light Data Logger (Part # UA-002-XX) from December 23rd to May 3rd. Living clams were counted on December 23rd, March 15th and June 15th.

Data analyses

Clam abundance was reported as ind. m^{-2} (mean ± standard error). To achieve homogeneity of variances, all values were logarithmically transformed [ln $(x + 1)$] and checked with the Hartley, Cochran, Bartlett Test ($P = 0.05$). Data were distributed normally. Mussel density changed with time and water depth. Differences as well as interactions time × depth were tested with two-way ANOVA. Subsequently, Tukey-HSD post hoc tests were conducted. All statistical analyses were conducted with Statistica, Stat. Soft. V. 99.

Results

Field study

Abiotic factors

Water temperature and water level fluctuated strongly within the year (Fig. 1). During January 2006, the shallow water zone at Rohrspitz was covered with ice. Water temperature at Bregenz was below 4°C for nearly 4 months (Dec–Mar) and only rose slowly in spring. Water temperature reached the 10°C threshold as late as April 19th. Mean monthly water temperatures at Bregenz were on average 1.7°C lower than during the preceding six winters (Data from Wasserwirtschaftsamt Vorarlberg). In summer, water temperatures reached 25°C in late July (Fig. 1).

After a strong increase in August 2005 (55 cm within 24 h), water level continuously decreased until February 15th, when a centennial low water with a level of 228 cm above 391.89 m NN (gauge zero) was recorded. The water level was then only 2 cm above the absolute lowest water level of Lake Constance since the beginning of registration in 1850 (Internationale Gewässerschutzkomission für den Bodensee, 2006). Afterwards, the water level rose until June, when 410 cm was reached. During the whole sampling period, the water levels remained below the mean monthly water levels of the preceding years.

Development of the clam population at the field site

In each sampling month, population densities of *C. fluminea* were significantly different at the three depths (Table 1). Therefore, abundance changes over time were regarded separately for different depths.

At MLL, abundance of *C. fluminea* was the lowest of all depths. In September, 91 ± 30 older clams (>5 mm) m^{-2} and 341 ± 30 young clams (<5 mm) m^{-2} were recorded. Then all clams died when the substrate dried up. Until June, juvenile clams recolonized this site in low densities (53 ± 11 ind. m^{-2}; Fig. 1).

At MLL −1 m, clams >5 mm reached the highest mean abundance of the study area in September and December (2037 ± 829 and 1899 ± 83 ind. m^{-2}, respectively). *C. fluminea* <5 mm increased significantly during autumn ($P < 0.001$) and reached a maximum of 27,563 ± 3234 ind. m^{-2} in December. During winter, MLL −1 m did not dry up, the lowest water depth recorded at this site was at least 65 cm. Nevertheless, in this depth the clam population dropped down significantly (Fig. 1, Table 1). Abundance of both size classes of *C. fluminea* (>5 mm and <5 mm) decreased from December to March. Only ~1% of the Asian clam population remained in late spring (32 ± 16 ind. >5 mm m^{-2} and 331 ± 47 ind. <5 mm m^{-2} in June). There were no differences between abundances in March and June (Fig. 1, Table 1).

Abundance of clams >5 mm at MLL −3 m did not show significant changes from September (1052 ± 156 ind. m^{-2}) to March (965 ± 475 ind. m^{-2}; Fig. 1). However, abundance decreased afterwards (229 ± 23 ind. m^{-2}; $P = 0.014$), and in June, the soft bodies of recently died *C. fluminea* floated in the water. Abundance of small clams <5 mm significantly increased from 2228 ± 274 ind. m^{-2} in September to 26,491 ± 1589 ind. m^{-2} in December ($P < 0.001$). But then, in contrast to older clams, they significantly decreased till March (1227 ± 310 ind. m^{-2}) and abundance remained constant till June (928 ± 236 ind. m^{-2}; Fig. 1).

Mesocosm study

Abiotic factors

In the mesocosm with constant water level, water temperatures were constantly below 4°C from December to mid-March and below 2°C for nearly 2 months. An ice cover was observed between Dec 29th and mid-February. Temperature began to rise in early April and reached the 10°C-threshold on April 15th. Afterwards, water temperature quickly increased (Fig. 2).

Development of the clam population in the mesocosm

Out of 1331 clams >5 mm in mid-December only 150 ind. survived till March 15th. Although water temperatures increased afterwards, mortality of residual clams went on as in the lake: only one of the remaining 150 ind. survived till June (Fig. 2). Thus, only 0.1% of the exposed *C. fluminea* population survived. In contrast to the Asian clams, the native unionid *A. cygnea* survived these conditions.

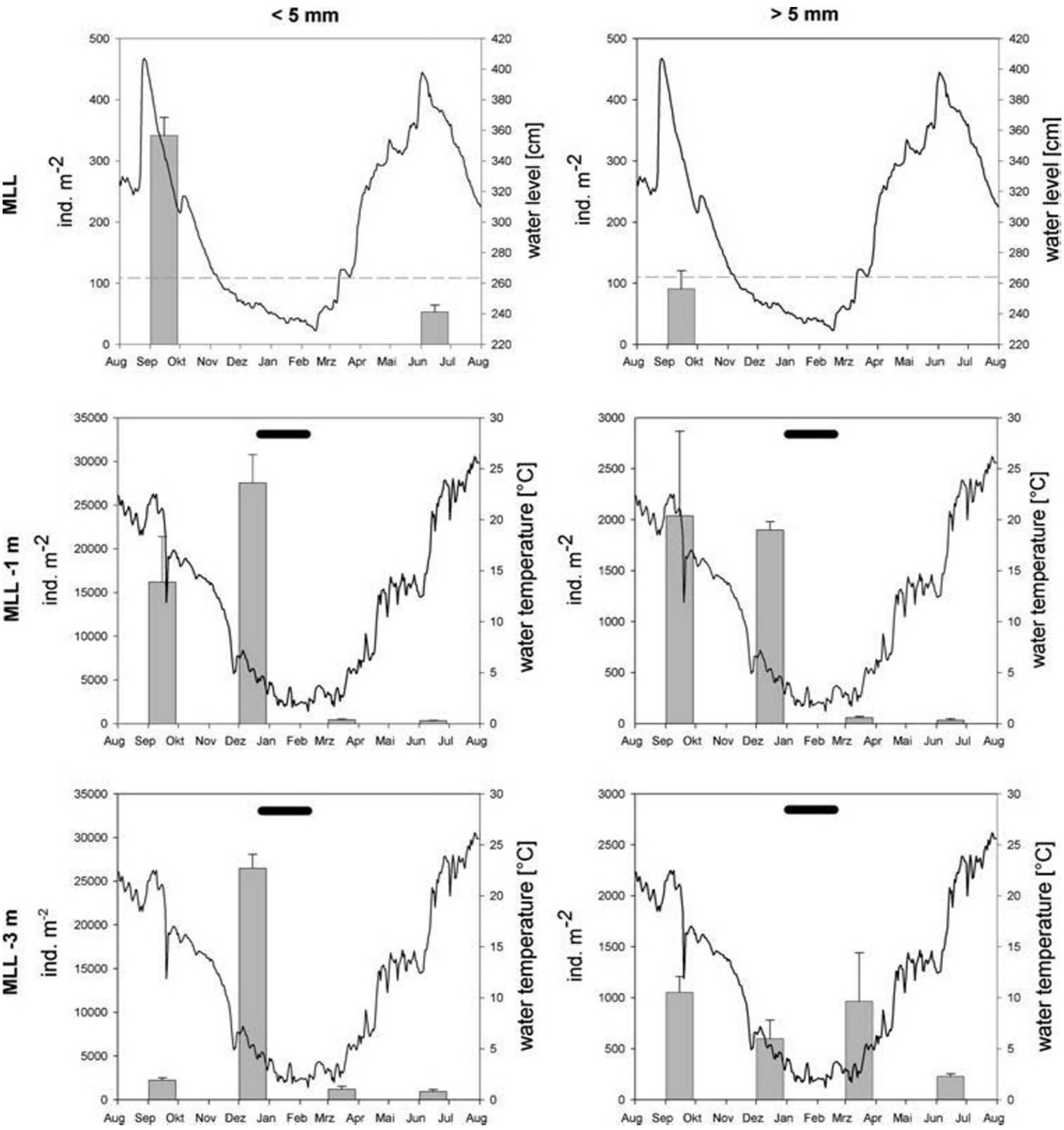

Fig. 1 Changes in *Corbicula fluminea* densities + SE for clams <5 mm and >5 mm (bars) for the three different depths MLL, MLL −1 m and MLL −3 m from Sept 2005 to June 2006. The black lines indicate the water level (upper two graphs) and the courses of water temperatures at Bregenz (lower 4 graphs). Dashed gray line marks water level when MLL fell dry. Solid black bar: ice cover at study site Rohrspitz

Discussion

During winter 2005/2006 different abiotic factors led to a mass mortality of *C. fluminea* in Lake Constance, with only ~1% of the population remaining. While in the shallowest water depth (MLL), the drying out directly led to an extinction of the population (Fig. 3), in both other depths low water temperatures for a long period affected the survival of clams. However, the date of mortality depended on clam size

Table 1 Results of two-way-ANOVA for density differences of young (<5 mm) and older (>5 mm) *Corbicula fluminea* over depth and its changes over time ($\alpha = 0.05$)

Corbicula	Depth	Time	Effect	*F*	df	*P*
>5 mm	All	All	Time × depth	26.845	6	<0.0001
	All	All	Depth	443.593	2	<0.0001
	All	All	Time	91.469	3	<0.0001
	MLL	All	Time	100.957	3	<0.0001
	MLL −1	All	Time	54.422	3	<0.0001
	MLL −3	All	Time	5.675	3	0.0184
	All	Sep	Depth	26.891	2	0.0005
	All	Dec	Depth	615.269	2	<0.0001
	All	Mar	Depth	127.981	2	<0.0001
	All	Jun	Depth	106.841	2	<0.0001
<5 mm	All	All	Time × depth	145.279	6	<0.0001
	All	All	Depth	1143.399	2	<0.0001
	All	All	Time	189.771	3	<0.0001
	MLL	All	Time	588.838	3	<0.0001
	MLL −1	All	Time	109.735	3	<0.0001
	MLL −3	All	Time	58.820	3	<0.0001
	All	Sep	Depth	84.674	2	<0.0001
	All	Dec	Depth	6070.548	2	<0.0001
	All	Mar	Depth	298.858	2	<0.0001
	All	Jun	Depth	46.653	2	0.0002

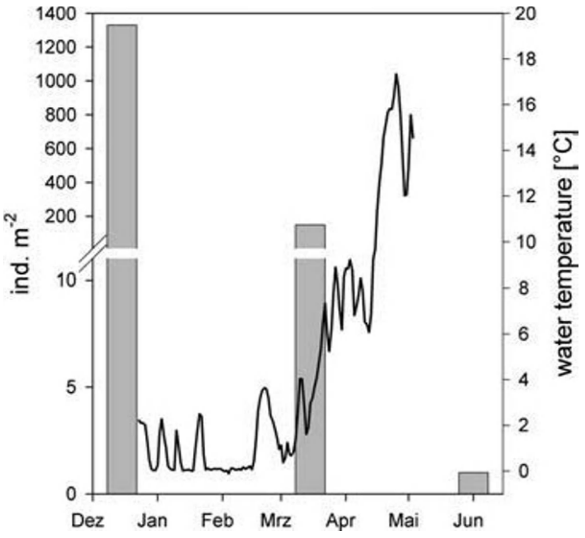

Fig. 2 Water temperatures from December 2005 to June 2006 (*black line*) and survival of *Corbicula fluminea* in mesocosm (*bars*)

and water depth. Although Corbiculidae can survive short-term extreme conditions like cold temperatures (French & Schloesser, 1996), drying outs (White & White, 1977), and hypoxia (Matthews & McMahon, 1999), these events seem to severely hurt the population when they last for weeks (French & Schloesser, 1991, 1996). Nearly all clams died at Rohrspitz between December and March, and only clams >5 mm at MLL −3 m survived this period. However, these clams still died at rising water temperatures until late spring. Impressive summer mortalities of *C. fluminea* are known from the rivers Rhine and Saône (Westermann & Wendling, 2004; Mouthon & Daufresne, 2006), which could be due to food limitation during heatwaves. Corbiculidae seem to be susceptible to food limitation under unfavourable temperatures (Vohmann & Kureck, pers. communication). However, the Chlorophyll *a*-concentration in Upper Lake Constance (upper 10 m) reaches an annual peak in May (~10 µg Chl *a*/l). Although a clear-water phase follows up in June (~3 µg Chl *a*/l), phytoplankton concentration at that time is more than three times higher than during January to March (Roßknecht, 1998). Since during preceding winters and summers, clams did not show any mortality (unpublished data) and because *C. fluminea* is additionally able to feed from the sediments by pedal-feeding (Hakenkamp & Palmer, 1999), it is unlikely that phytoplankton availability

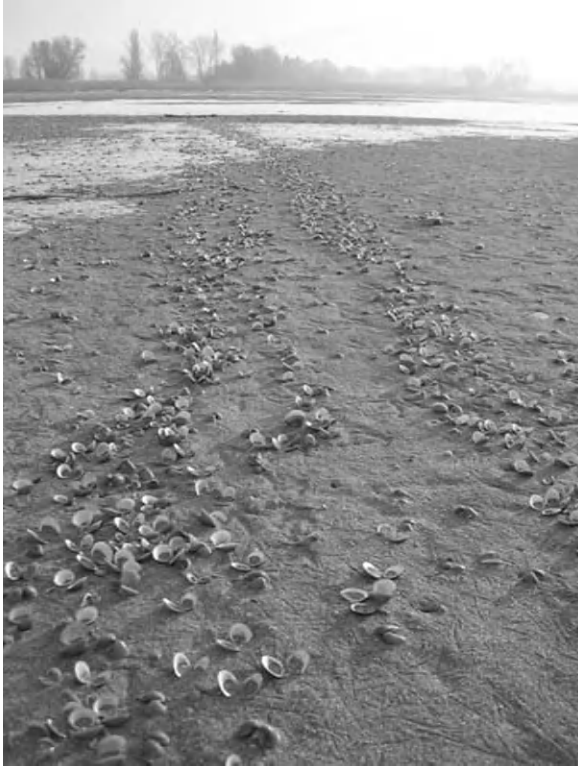

Fig. 3 Dead *Corbicula fluminea* during drought at Rohrspitz (MLL)

limited the survival of the few remaining *C. fluminea* at MLL −3 m (only 1% of former densities). Probably *C. fluminea* at MLL −3 m were too weakened and stressed to recover from the cold period in winter. Condition indices of *C. fluminea* were reported to decrease significantly after one month of temperatures around 2°C (French & Schloesser, 1996). French & Schloesser (1991) assumed that first-year clams are more susceptible to low temperatures than older clams. For perch and ruffe it is shown that bigger and older individuals have a better ability to store energy and therefore have a better resistance against different stressors than small and young (Eckmann, 2004). This might also apply for older clams (>5 mm) that survived longer at MLL −3 m than young clams (<5 mm).

Furthermore, clams >5 mm at MLL −3 m survived longer than that at MLL −1 m, maybe because water temperatures during the frost period at MLL −3 m were less extreme than that at MLL −1 m. Water temperature in shallow littoral zones respond faster to air temperature than in deeper water. Therefore, critical temperature for clam survival at MLL −3 m might have occurred later in winter or for a shorter period than at MLL −1 m, which might have delayed mortality of *C. fluminea* until late spring. Unfortunately, two temperature loggers that were exposed at Rohrspitz caused troubles: one logger fell dry after 5 weeks and the other one was stolen. Water temperatures at a mean depth of ~40 cm in the phase from Dec 15th to Jan 25th at Rohrspitz were on average 2.77 ± 0.80°C lower than water temperatures at a water depth of 50 cm in Bregenz. Furthermore, the ice cover recorded at Rohrspitz in January indicated that actual water temperatures were lower than that at the ice-free site Bregenz.

Our mesocosm study confirmed that temperatures around 2°C for 2 months or longer are lethal for *C. fluminea* (Mattice & Dye, 1976; French & Schloesser, 1991, 1996). The native unionids seem to be better adapted to low temperatures than the invasive clam. Although bivalve species differ in metabolism, the survival of both *A. cygnea* is a hint that O_2-limitation and food availability can be excluded as a reason for the observed mass mortality of *C. fluminea.* Cold winters often caused winter mortality of complete *C. fluminea* populations in the United States (French & Schloesser, 1991; Morgan et al., 2003). Due to this, the northern boundary of *C. fluminea* dispersal is limited. Beyond winter survival of single individuals, reproduction is limited by water temperature: growth as well as development of *Corbicula fluminea* begins at 10–11°C (reviewed in Karatayev et al., 2005). Schöll (2000) hypothesized that *C. fluminea* would not have established in Germany without heat pollution of rivers by power plants.

Since bivalves have very slow migration rates (some species are sessile), mass mortalities can occur, when water level sinks dramatically. Water-level decreases caused massive die-offs of Corbiculidae (White & White, 1977; Morgan et al., 2003). After 4 days of air exposure 50% mortality occurred (White & White, 1977). The study site Rohrspitz is a shallow littoral zone with a very flat ground profile and the zone with water depths of about MLL −1 m is nearly 1 km in width. Although clams tried to follow the fast sinking water level, nearly all clams dried up. Some were trapped in rest water holes that ran dry later or froze (personal observation). After this mass mortality, the substrate was littered with empty shells (Fig. 3). Physical structure of persistent and abundant shells of many bivalves is important for organization of invertebrate communities in aquatic environments (Gutiérrez et al., 2003). On soft substrates, empty *C. fluminea* shells can favour populations of benthic invertebrates that prefer hard substrates (Werner & Rothhaupt, 2007).

Until June, MLL was resettled by juvenile *C. fluminea* of the year in low densities, most probably descending from adults that survived in greater depths. Compared to this, annual re-colonization of the littoral zone by zebra mussels *Dreissena polymorpha* in Lake Constance after strong predation of wintering waterbirds with only 3% of the zebra mussels remaining is very quick (Werner et al., 2005). In comparison with zebra mussels that have planktonic veliger larvae, the ability of *C. fluminea* to re-colonize areas in lakes without strong currents seems to be limited. *C. fluminea* juveniles do not disperse as plankton, because they are released by the maternal clams in a crawling stage (Britton & Morton, 1982; Karatayev et al., 2005). However, *C. fluminea* seems to have autonomously moved upstream at least 1.2 km/year in the Savanna River, USA (Voelz et al., 1998).

Conclusion

Harsh winter conditions with water temperatures ≤2°C for weeks strongly limit survival and also dispersal of *C. fluminea,* whereas timing of mortality was dependent on size class and depth. Only few individuals remain that can reproduce and that might establish a resistance against lower winter temperatures. Natural water-level decreases can also regulate the population of this invasive clam. Consequently, quick water-level decreases in regulated reservoirs could be used as a regulation tool against mollusk invaders.

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WATER-LEVEL FLUCTUATIONS

An extension of the floodpulse concept (FPC) for lakes

**Karl M. Wantzen · Wolfgang J. Junk ·
Karl-Otto Rothhaupt**

Abstract This paper delivers a conceptual framework for the ecological functioning and biodiversity patterns of lakes that is based on the floodpulse concept (FPC). The specific characteristics of rivers and lakes considering water-level fluctuations are compared, with respect to catchment linkages, temporal patterns, and hydraulic forces of flooding and drawdown. The influences of floodpulses on element cycles, biodiversity, and adaptations of lake biota are analyzed, and the importance of multi-annual flooding cycles is highlighted. The degree by which these water-level fluctuations influence lake ecosystems strongly depends on lake morphology, where shallow lakes or those with large shallow margins are the most sensitive. Although floodpulses play a major role for ecosystem services such as lake management and climate change mitigation schemes, this issue is only scarcely dealt with. Tenets of the extended FPC for lakes are formulated in order to overcome this problem.

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Ecological Effects of Water-Level Fluctuations in Lakes

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Introduction

In rivers, the patterns of water-level fluctuations (the floodpulse) have been recognized both for ecological and biodiversity concepts (Junk et al., 1989; Tockner et al., 2000; Junk & Wantzen, 2004) and for management and restoration schemes (Sparks et al., 1998; Schiemer et al., 1999). In lakes, however, these pulses have yet to receive attention (Keddy & Fraser, 2000; Coops et al., 2003; Mooij et al., 2005). However, this lack of knowledge stands diametrically opposed to recent developments. Both climate and human impacts tend to impair water-level fluctuations in lakes. Current climate models affirm that the frequency of irregular climate events (extreme rainfall, extended drought) is increasing, while predictable hydrological events, such as long lasting springfloods caused by snowmelt in the mid-elevation mountains of the temperate zones are decreasing (IPCC, 2001). Moreover, many direct man-made manipulations of lake levels change timing, frequency and fluctuations of water levels in lakes. For example, Scandinavian lakes dammed for hydropower suffer untimely drawdown in the winter caused by large energy demands. Many lakes of the world, such as Lake Kinnereth (Israel), witness a continuous drawdown due to drinking water demand.

These current trends cause an additional need to formulate an overarching concept for the effects of water-level fluctuations such as floodpulses in lakes. This paper summarizes the current studied effects of water-level fluctuations in lakes, compares them with similar processes in rivers, and formulates an extension of the floodpulse concept (Junk et al., 1989; Junk & Wantzen, 2004) for lakes.

There are many open questions about effects of water-level fluctuations in lakes:

- What are the differences in lake flooding compared with river flooding?
- Is it possible to define “flooding-types” of lakes according to their climatic and morphological conditions?
- How is the biota of the lake littoral adapted to the influences of floodpulses?
- How do human activities influence floodpulses in lakes and how can they be managed better?

This paper attempts to answer these questions based on four case studies which delineate the extremes in climatic gradient (temperate to tropical) and morphological gradient (deep to shallow).

Case study lakes

Lake Constance (Bodensee): temperate-deep

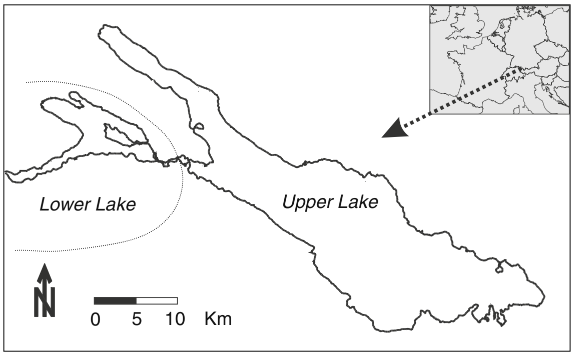


Fig. 1 Map of Lake Constance. Graph provided by Martin Mörtl

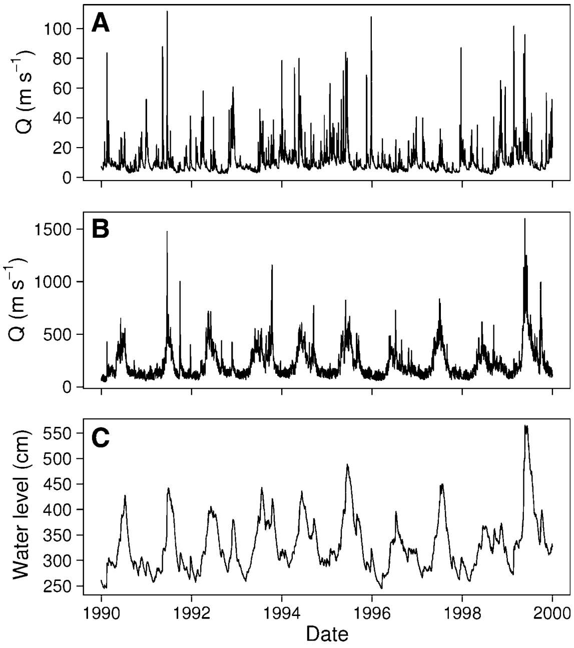


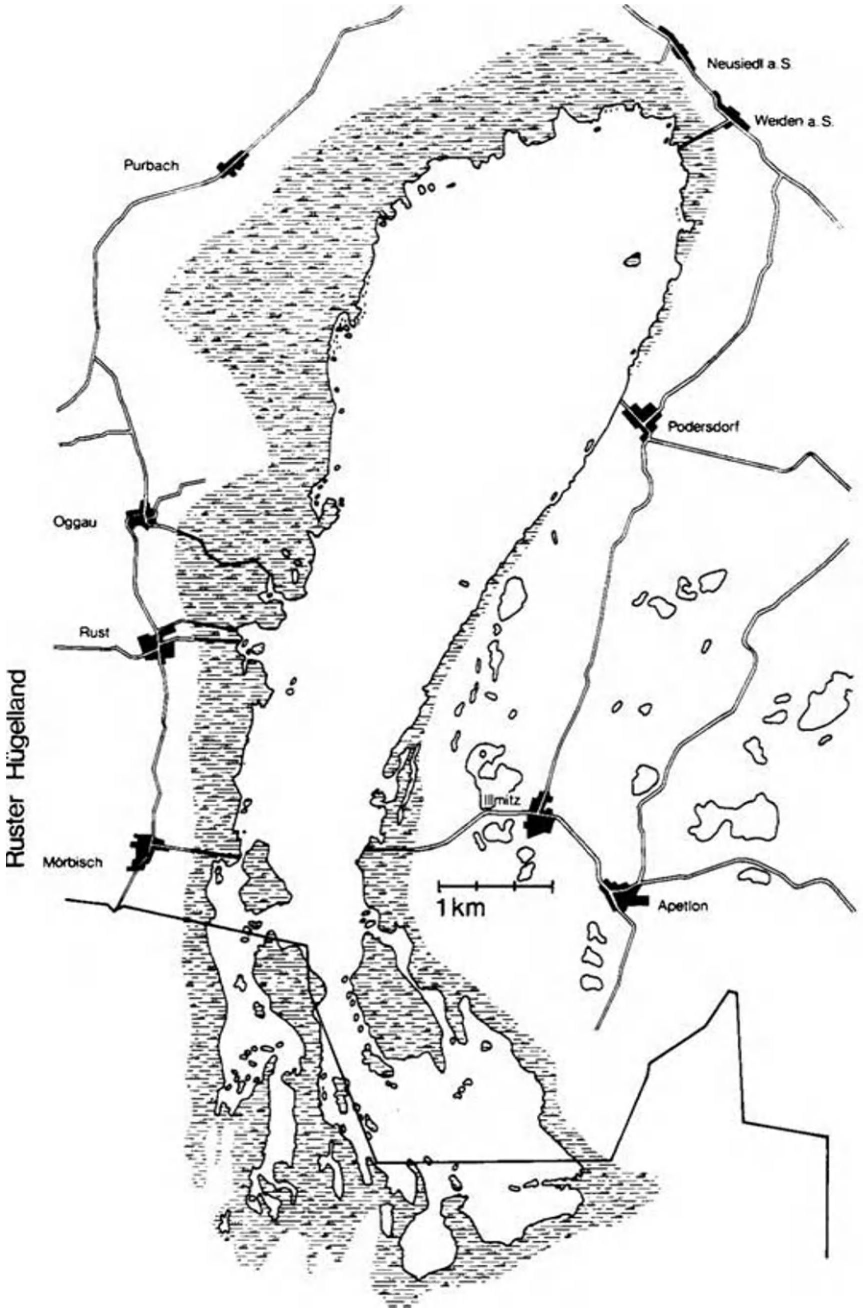
Fig. 2 Discharge of tributaries to Lake Constance (**A**) Schussen (catchment size 791 km^2) at Gerbertshaus, (**B**) Alpine Rhine (catchment size 6,119 km^2), and (**C**) of Lake Constance (catchment size of the Upper Lake 10,410 km^2) at Konstanz harbor. Note the “smoothening” of the discharge/gage patterns with increasing catchment size. Daily data by LUBW Baden-Württemberg and BAFU, Switzerland. Graph provided by Karsten Rinke

Today, only few lakes such as Lake Constance are left unregulated in Central Europe (Fig. 1). Lake Constance consists of subbasins, the deep “Obersee” (473 km^2, maximum depth 254 m) with steeply sloped banks, and the shallow “Untersee” (63 km^2, maximum depth 20 m). The lake has been subject to intensive studies (e.g., Bäuerle & Gaedke, 1999; Straile et al., 2007, and several papers in this issue). Its annual water-level fluctuations average 1.3 m. The littoral zone is affected by strong seasonal dynamics in water level and water-level-driven environmental factors caused by storage of precipitation in the alpine parts of the catchment during winter, and a superposition of rainfall and snowmelt in early summer (Fig. 2). High-water phases lead to a dislocation of gravel and the formation of gravel bars which represent new habitats. Water levels drop from summer to winter, and large littoral zones become exposed. During the heart of winter (December to March), the superficial sediments in the dry-fallen zone often freeze, while the lower-lying substrate layers—which are often oxygen-poor to anoxic—remain unfrozen. Subsurfaces in smaller streams remain in this zone and represent ice-free refuges. From March through mid-July, water levels rise and the epilittoral zone becomes flooded. There is a large seasonal variation in this type of flooding. In 1999, the water level (measured at the Port of Konstanz) was 560 cm, exceeding the long-term average maximum of 420 cm by far, and flooding large areas (Schmieder et al., 2004).

Neusiedler See: temperate-shallow

Neusiedler See (Lake Fertõ, Fig. 3) is a steppe or plain lake, situated on the Hungarian-Austrian border, with a surface area of 309 km^2. It is an extremely shallow lake with an average depth of 1.1 m. Outside of two small permanent tributaries, the lake mainly receives influxes of groundwater and direct rainfall. Neusiedler See's outflow is regulated (Löffler, 1997; Dinka et al., 2004). Seasonal water-level fluctuations in Neusiedler See show a relatively regular pattern with annual amplitude of about 0.4 m (Fig. 4). These fluctuations are governed by the seasonal interplay of

Fig. 3 Map of Lake Neusiedler See (from Dinka et al., 2004)



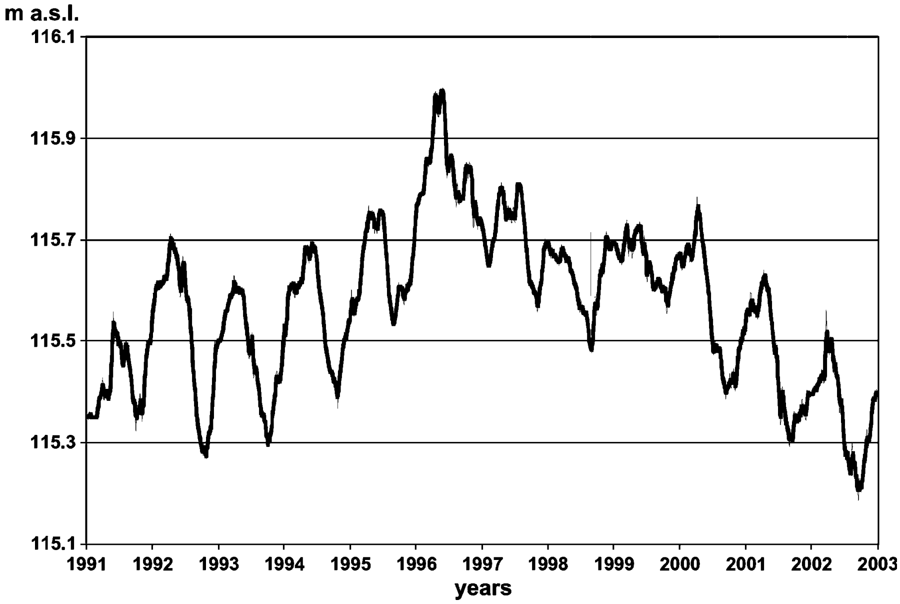


Fig. 4 Hydrograph of Lake Neusiedler See 1991–2003 (from Dinka et al., 2004)

evaporation and inflow (Dinka et al., 2004). Evaporation from the lake surface is low early in the year, when the air is moist and the lake water is relatively cold. Hence, water levels rise in late winter and spring. Maximum water levels occur in late spring to early summer (May/June). Evaporation from the lake surface and evapotranspiration from the extensive reed belts are highest in the second half of the vegetation period. Consequently, the water level decreases during summer and autumn and reaches its minimum in late autumn (October/November). The overall seasonal patterns of water-level fluctuations in Neusiedler See is comparable to the pattern observed in Lake Constance; however, the seasonal events occur about two months earlier in Neusiedler See.

Superimposing the typical seasonal patterns the long-term fluctuations in the water level of Neusiedler See are important drivers of ecological processes (Löffler, 1997). Consecutive wet and cold years cause an increase in water levels, whereas a sequence of warm and dry years can cause a decrease. When the water levels are high, reed stands and open water areas are connected. However, at low water levels, the water surface is discontinuous and some areas with water become disconnected. Moreover, the water levels have a great influence on the chemical composition of the lake water. Conductivity and ion concentrations increase in low water years (Dinka et al., 2004).

Lake Titicaca: tropical-deep

Lake Titicaca is a high-mountain (3809 m altitude) endorheic lake in the Andes of Bolivia and Peru (Fig. 5, Roche et al., 1992). Its climate is cold and semiarid with mean annual temperatures of 8°C and precipitation between 790 mm and 950 mm a year. The surface water temperature ranges from 10°C to 16°C. The lake catchment covers an area of 49,010 km^2. The lake itself has an approximate size of 8,490 km^2. The mean depth of the main basin is more than 100 m, its maximum depth 280 m, the mean volume 930×10^9 m^3. It has pronounced annual and multi-annual water-level fluctuations (Fig. 6). The annual minimum occurs in December, just before the start of the rains. The increase of water occurs more quickly, as all inputs are concentrated during a 5-month period, whereas losses due to evaporation are spread more evenly over the year. From a time series of daily records from 1914 to 1989, Roche et al. (1992) identified an annual range of 0.4–1.8 m and a total interannual range of 6.27 m. The lake shows pronounced phases of higher and lower water levels. Fluctuations in water levels are decisive in determining the separation and re-establishment of communication (flow) between the two subbasins. They have a direct impact on the zonation of the aquatic macrophytes in the lake. A palynological reproduction of the lake environments revealed

Fig. 5 Map of Lake Titicaca (modified after Villwock, 1993)

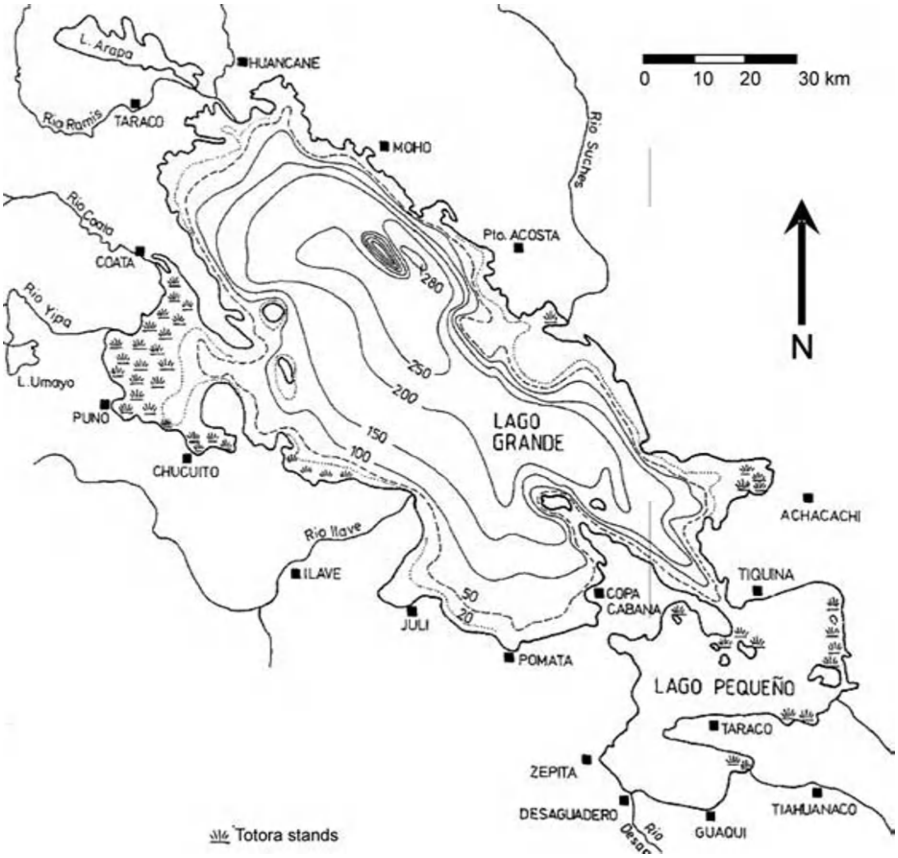


Fig. 6 Water-level fluctuations of Lake Titicaca, measured at Puno (modified after Pawley et al., 2001)

that the quillwort *Isoetes* occurred during the pleistocenic low-water periods; however today, it occurs only in lakes in higher regions of the Titicaca catchment (Ybert, 1992). The recent macrophyte vegetation is characterized by submerged *Myriophyllum* and extensive "totora" bulrush belts *(Schoenoplectus californicus* ssp. *tatora)* stands, which form the basis for traditional management practices (Villwock, 1993).

Lake Chad: subtropical-shallow

Lake Chad is a shallow lake in an endorheic basin in the semiarid Sahel Zone of northern Africa (Fig. 7). The lakeshores and shallow water areas are covered by aquatic macrophytes. Its climate is characterized by a pronounced annual dry and wet season that results in annual water-level fluctuations of about 1 m (Fig. 8A). Because of the shallow landscape gradient, large areas fall dry during low-water periods, consequentially favoring terrestrial herbivores and insectivores. With the onset of the rains water levels rise, and macrophyte growth in the mud flats is accelerated due to the release of nutrients that were recycled during the low-water period. The new habitats are quickly occupied by aquatic fauna. Lake Chad receives water both from direct precipitation and from the southern Logone-Chari Rivers. The adults of many fish species of the lake perform extensive reproduction migrations to the rivers and their floodplains (Carmouze et al., 1983). In the 1960s Lake Chad had an area of more than 26,000 km^2, making it the fourth largest lake in Africa.

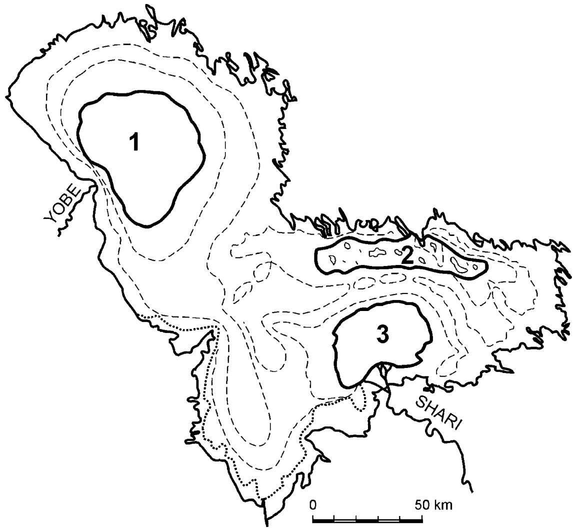


Fig. 7 Recession of Lake Chad after 1972, and development, as of 1975, of different facies in the surviving parts of the lake, based upon aquatic plants and phytoplankton. (1) Evolution towards a natron pond; (2) Towards a swamp; (3) Towards a river delta (modified from Carmouze et al., 1983)

In the 1970s, a drop in water level had caused a separation of the lake into two subbasins (Fig. 8B). By 2000, its size had decreased to less than 1,500 km^2. This is due to reduced rainfall combined with a greatly increased demand for irrigation water which was being drawn from the lake and the rivers which feed it. The largest of these is the Logone-Chari River system. The probability exists that Lake Chad may shrink further and perhaps even disappear altogether in the course of the 21st century.

Water-level fluctuations (WLF) and floodpulsing in lake systems compared to rivers

Some definitions

In a graphical plot, a fluctuating water level in a natural water body appears more or less like a sinoidal curve (Fig. 9). All properties of the curve can be used to define the qualities of the changes: the steepness of rise

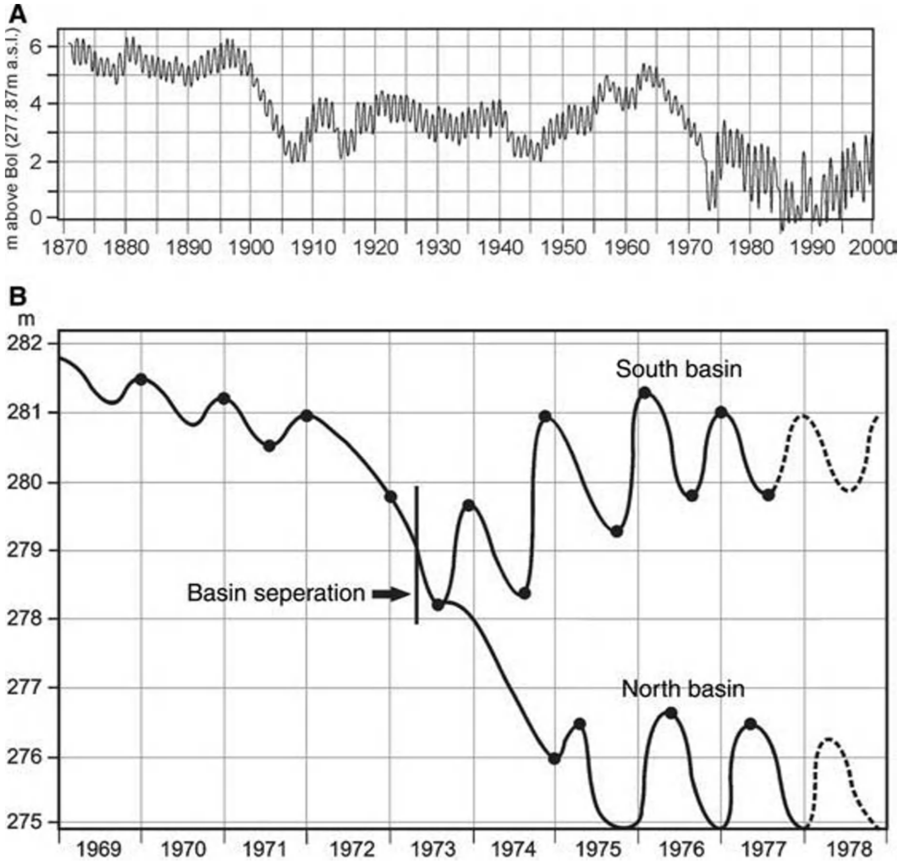


Fig. 8 (**A**) Long-term trend of annual minimum and maximum water levels in Lake Chad (Evans & Mohieldeen, 2002). (**B**) Effects of Lake Chad's recession during the 1970s. At first, the two basins separate, later, the north basin temporarily dries up, while the south basin almost regains its original depth (modified from Carmouze et al., 1983)

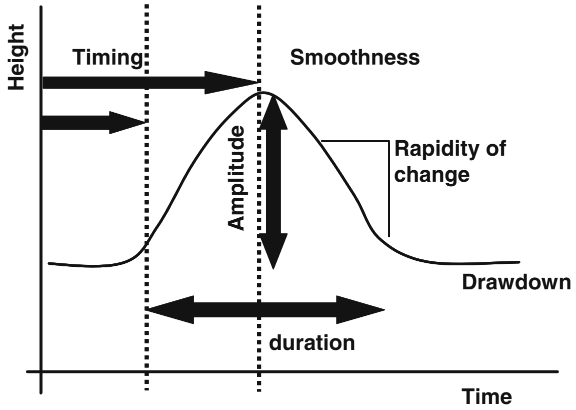


Fig. 9 Characteristics of a floodpulse (strongly modified after Welcomme & Halls, 2001)

and drawdown, the total duration, the amplitude, and the frequency by which it recurs (Puckridge et al., 1998). To be able to define interferences to the life cycle of the biota by flood/drought events, it is important to analyze the resilience of organisms to such changes ("phenological window of susceptibility") and/or their ability to use floodborne resources at that time ("window of opportunity," Gafny & Gasith, 1999; Junk & Wantzen, 2004).

Water level fluctuation (WLF) is a neutral term that is not limited by any of these dimensions. As shown elsewhere (Hofmann et al., this issue), in extreme cases a WLF can be as short as seconds (in the case of waves) or last centuries (in the case of lake drawdown). An analogy: the spatial dimension can range from millimeters to hundreds of meters. In our paper, we want to limit the scope of water-level fluctuations to those events that are within the temporal and spatial scale of most living organisms, i.e., limit the temporal dimension to a range from hours to several years, and the spatial (vertical) dimension from several centimeters to meters of water level. In the transverse dimension, the same flood size can translate into a small or large extension of flooded area (Aquatic-Terrestrial Transition Zone, ATTZ), depending on the slope of the landscape. Because the term "flood pulse" has gained wide acceptance in international ecological literature for similar phenomena in rivers, we will adopt this term here; however, we will stress the differences between river and lake flooding. Moreover, there may be recurrent patterns that are responsible for interannual variation which we term "multi-annual patterns."

Water-level fluctuations in rivers and lakes

Do floods and droughts affect rivers and lakes in the same way? There are distinct properties in each system type, such as the unidirectional flow and the higher kinetic energy of river water, which has consequences for transport and turnover of sediments and solutes. Aquatic-terrestrial interactions tend to be more intensive in rivers than in lakes as they are more tightly intertwined with their catchments. The oblong shape of rivers makes them perfect corridors in the landscape to favor gene flow between remote areas, compared with the generally more or less rounded shape of lakes.

On the other hand, there are some general patterns concerning processes and effects during the cyclical rise and fall of water that occur in the Aquatic-Terrestrial-Transition Zone (ATTZ) of any freshwater body. During *rising water levels*, habitat conditions worsen for terrestrial animals and plants. If the pattern of flooding is predictable (i.e., occurring during a predictable time of the year), terrestrial organisms of floodplains may have adapted their lifecycles to cope with these adverse conditions, either by producing water-proof propagules and resting stages, or by migrating into non-flooded areas (see reviews on plants by Bornette & Amoros, 1996; Gurnell et al., 2003 and for invertebrates by Adis & Junk, 2002). Aquatic organisms can then occupy these habitats, many of which make use of floodborne resources such as drowned terrestrial organisms, fruits from floodplain trees, and primary production in floodplain water bodies (Junk, 1985; Bayley, 1991; Wantzen et al., 2002). Such flooding triggers the development of a highly complex habitat mosaic with sites of variable stages of succession and with steep gradients in ecological factors (e.g., oxygen saturation, salinity, temperature, flooding period, current) in the floodable areas (Amoros & Bornette, 2002; Poole, 2002; Ward et al., 2002; Wantzen et al., 2005a); however, floods may also homogenize the characteristics of otherwise uncoupled water bodies (Thomaz et al., 2007). Generally, biodiversity is higher in the ATTZ than in a permanent water body (Tockner & Ward, 1999; Ward et al., 1999; Junk et al., 2005; Marchese et al., 2005). Organic and inorganic matter that becomes dissolved or suspended during rising water levels causes increased turbidity and release of nutrients from the rewetted floodplain. Moreover, waters conveyed by floods often contain dissolved and particulate-bound nutrients from catchments that additionally enhance the productivity of floodplains. These floodborne nutrient inputs may cause an increased growth of algae and macrophytes. During later stages of succession in floodplains, algae may be outcompeted by aquatic macrophytes due to their more efficient shadowing, release of allelochemical substances, and nutrient uptake by macrophytes. This causes “alternating stable states” also found in shallow lacustrine environments (Scheffer & Jeppesen, 1998). Large proportions of organic carbon may become accumulated during the aquatic phase in the ATTZ due to mostly anoxic conditions in the sediments (Nogueira et al., 2002). In rivers, feeding on terrestrial resources and floodborne primary production by floodplain species compared to permanent river channel dwellers causes a better growth rate known as “floodpulse advantage”(Bayley, 1991).

During *decreasing water levels*, these processes become partly inverted, i.e., aquatic organisms migrate back into permanent water-bodies, and the stranded aquatic substances become used by terrestrial organisms (Adis et al., 2001; Junk & Wantzen, 2004) or mineralized by microbes. It is remarkable how fast flooding and drawdown may mobilize a large part of the available carbon and nutrients in the ATTZ (Nogueira et al., 2002). This “system-reset” mechanism is especially effective in shallow floodplains that oscillate between flooded and arid conditions, e.g., in tropical and subtropical zones (Wantzen & Junk, 2006). The steep redox gradients of the floodplain sediments that support a vivid microbial activity are triggered as well by the regular changes between wet and dry conditions (Boon et al., 1996).

While these processes are increasingly well understood in pulsing river-floodplain-systems, there is a large demand for information on pulsing lakes. This is largely due to the fact that most lakes (e.g., in Central Europe) have been regulated for centuries, and therefore, reference conditions of natural flooding and drawdown are hardly known. On the other hand, many classical studies of lakes have considered these ecosystems as closed systems that hardly interfere with their terrestrial environment (“The lake as a microcosm,” Forbes, 1887), or the open water column has been studied isolated from its benthic and littoral zones. Indeed, the water volume stored in the littoral zone is often negligibly small compared to the open water zones, but current research indicates that the contribution of the littoral zone to the whole organic matter turnover is disproportionally high compared to the central part of the lake (Sala & Güde, 2006). Most lakes, if not all, are heterotrophic, i.e., dependent on the organic inputs from their catchments (Sobek et al., 2007), and it is especially so for their floodplains.

Landscape gradient

The degree by which floodpulses interfere in ecosystem processes of flooding systems compared to regulated systems (see discussion in Junk & Wantzen, 2004) depends very much on landscape morphology. For example, in steep rocky valleys, such as alpine lakes and reservoirs, the ATTZ is only scarcely developed and the number of biota affected by WLF is small even during larger fluctuations (Fig. 10A). Conversely, shallow littoral zones of low-gradient landscapes provide much more space for aquatic-terrestrial interactions, as larger areas become flooded. This is the case, e.g., in the Untersee of Lake Constance, and in shallow lakes, e.g., Lake Chad or the Neusiedler See (Fig. 10B). Most of these lakes have large reedbelts (see Scheffer, 2004 for further case studies). Many lakes have elements of both deep and shallow lakes, e.g., Lake Titicaca or the Obersee part of Lake Constance (Fig. 10C). These lakes have a deep lake basin with steep sublittoral slopes, but the eulittoral zone includes shallow slopes that bear extensive floodplain areas. In this situation, extreme fluctuations may trigger a die-back of the floodplain vegetation by drought or unusually high floods (Schmieder et al., 2004). Most lake types, however, have a slope that is intermediate between these extremes, that is, the water-level fluctuations cover a moderately steep gradient so that the biota may migrate along the ATTZ (Fig. 10D). These patterns are basically the same for rivers and lakes.

Catchment linkages

Apart from the landscape gradient, there are several other morphological metrics that describe the morphological linkages between the lake main water body and its ATTZ. Due to the limited length of lakes, several of these metrics ranges are of lower

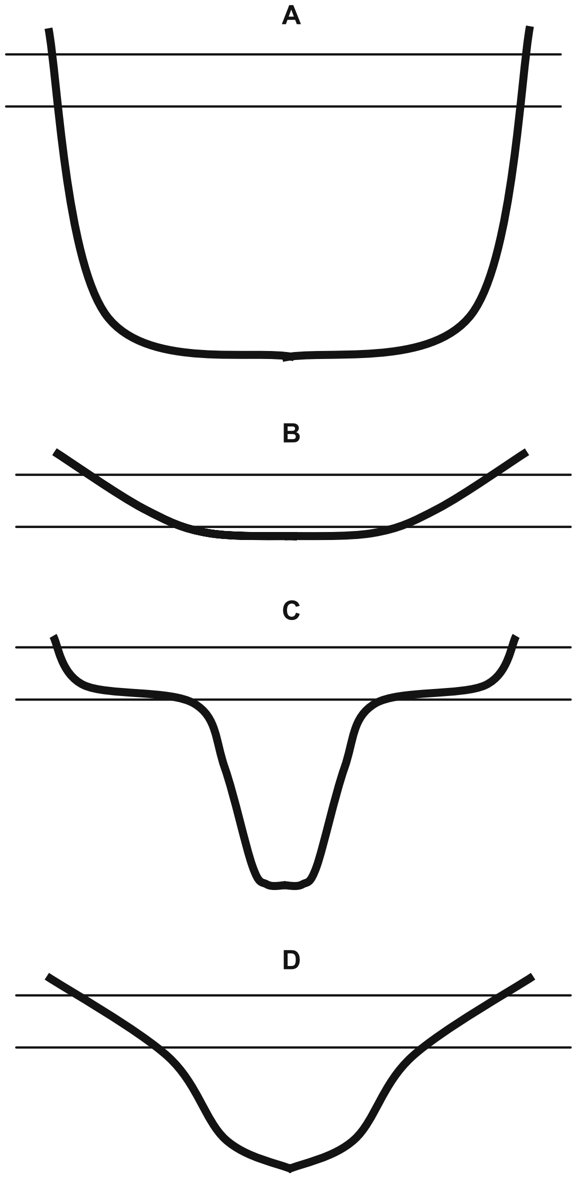


Fig. 10 Morphological lake types with different importance of water-level fluctuations (minimum and maximum water levels indicated by horizontal lines): (**A**) Large, deep lake with steep banks, (**B**) Shallow lake, entirely influenced by the floodpulse, (**C**) Combined type of A and B with deep central trough and extensive shallow floodplains, (**D**) "Average" lake with moderate floodplain area and permanent central trough

dimensions in lakes compared to rivers (e.g., basin diameter, basin perimeter, basin shape, compactness ratio, shoreline development; see Wetzel, 2001, for a comprehensive comparison of lake and river systems). The catchment aspect is especially important for the lake-river comparison. Lakes rarely integrate over such a large range of areas with heterogenous geochemistry (reflecting in water quality), rainfall patterns (floodpulse patterns), and biogeographical units (species exchange) as rivers do. Consequently, lakes receive much less heterogenous sources of water, dissolved and suspended solids, and allochthonous organic matter than rivers. On the other hand, lakes may reflect regional rainfall patterns better than rivers, although real-world conditions may vary strongly from these hypothetical considerations due to regional climatic patterns, and the way water accesses the lake. Large shallow lakes with a high amount of on-site rainfall and lakes with a strong riverine influence will have more pointed hydrographs than those fed mainly by diffuse inflow from groundwater and riparian wetlands (Fig. 2).

Temporal patterns of the floodpulses

Like in rivers, flood pulses in lakes may be multimodal (i.e., many flood events per year) or monomodal. They may be predictable (i.e., occurring at a given time, e.g., snowmelt events in spring) or unpredictable (e.g., effects of a strong summer rain). Regional climatic patterns affect riverine and lacustrine floodplains in similar ways, notwithstanding the general differences in their linkages to the catchments described above.

Lakes have a much higher residence time than rivers. Therefore, multi-annual patterns have a much stronger influence on the habitat structures of the ATTZ of lakes compared to rivers. In deep lakes with shallow floodplains (Fig. 10C), long-term low-flood-years may cause a disconnection of the floodplain from the main water body and a die-back of the aquatic flora and fauna (see case study of Lake Titicaca). Longer periods of high-flood-years (including higher water levels during the "low-water period") in turn may raise the organic matter belts in floodplain zones of lakes and create a "floating littoral" including riparian vegetation. This phenomenon has frequently been observed, e.g., in lakes that were artificially impounded or in floodplain lakes of naturally oscillating areas (Wantzen et al., 2005a).

Hydraulic forces

The main difference between flooding riverine and lacustrine systems is the (mostly) unidirectional flow in rivers compared to the multidirectional and weaker currents in lakes. This difference reduces the predictability of the occurrence of hydraulically shaped habitats in lakes.

Both rivers and lakes have erosional and depositional sites; however, their arrangement is different. In rivers, the low-order sections are generally erosional, the mid-river sections have a balanced ratio of erosional and depositional sites, and the lowermost sections and deltas are mostly depositional. Floodpulses shape the "riverscape" (Ward, 1998; Allan, 2004) by creating and abandoning meanders and their substructures (e.g., Wantzen et al. 2005a). There are no analogous structures in lakes, apart from those that are created by riverine activities (oxbow-lakes). In lakes, the position of erosional and depositional sites is defined by the main wind direction and internal currents (which may be influenced by tributary rivers). Due to this difference, the habitat dynamics and the attainable diversity of floodplain habitats are higher in rivers than in lakes.

In rivers, particulate organic matter and suspended inorganic sediments either become accumulated in the lentic zones of the main channel, in the floodplain, or they become transported downriver. The analogous sites in the lake littoral are depositional lake ends that receive large amounts of sediments from tributaries, and bights that accumulate wind-driven particles. Hydrological events that mobilize these sediments in rivers are generally flood events known as "system reset flooding" (see Wantzen et al., 2005a), while in lakes additional wind forces are needed to develop sufficient water movement. Due to tighter aquatic-terrestrial linkages, the overall inputs of inorganic and organic substances are much higher in rivers than in lakes; therefore, the development of floodplains (and the process of terrestrialization with inorganic sediments in floodplain water bodies) is much faster in rivers. For example, the deposition of drifting large woody debris often acts as condensation nuclei for sediment accumulation in rivers (Gurnell et al., 2001). However, backflooding in river mouths of tributaries often creates organic matter-rich depositional sites (that can become part of the ATTZ) in a similar fashion for both rivers and lakes.

Due to the reduced current in lakes compared to rivers, the sediment structure of the ATTZ may differ tremendously between both system types. The current in rivers permanently mobilizes the fine particles, creating an upstream-downstream sorting of grain sizes. In lakes, the zone that is exposed to waves for the longest time of the year has the coarsest sediments, while the average grain size decreases with wave exposure (i.e., downwards on the floodplain gradient). During drawdown in lakes, the moving surf-zone touches very different types of sediments than those that result from a zonation during the high-water phase. For deep lakes with an extensive eulittoral zone, this phenomenon has important consequences for littoral currents and for deposition patterns. In the Upper Part of Lake Constance, fine-grained sediments become suspended in the surf-zone during the low-water period and are locally transported to the edge of the steep sublittoral zone. Because the sediment-loaded water has a very high density, it plunges down into the profundal zone thereby co-precipitating organic matter particles and bacterial "lake snow" (Grossart & Simon, 1998). Sediments of different depth zones may also be chemically different so that the surf zone mobilizes variable qualities and quantities of dissolved substances during changing water levels.

Influences of floodpulses on the ecology of lakes

Element cycles and productivity

Floodpulses represent biochemical hot moments (McClain et al., 2003) for the ecosystem. The timing of the flood cycle during the activity period of the biota is crucial for the biologically mediated matter turnover (Wantzen & Junk, 2006).

During the flood phase, several processes facilitate the deposition and temporal storage of organic matter in the ATTZ of lakes. Apart from drowned terrestrial biomass, rising water collects the organic matter that has become deposited during a drought and carries it to the surf zone. This terrestrial leaf litter becomes degraded by waves and is then contributed to the littoral zone as FPOM (see contribution by Pabst et al. in this issue). In the shallow and light-penetrated littoral zones, benthic algae and aquatic macrophytes are fertilized by nutrients from terrestrial mineralization thus producing additional ("floodplain-autochthonous") biomass. Large amounts of organic matter derived from pelagial phytoplankton become deposited or reused in the flooded sediments. The retention of seston in the littoral is fostered by adhesion of particles on sticky biofilm surfaces and by the current-reducing effect of the macrophytes. In carbonate-rich lakes, macrophytes, especially characean algae, precipitate calcium carbonates which create a matrix of fine organic and inorganic particles (Kufel & Kufel, 2002). Below the oxidized surfaces of these sediments, there are anoxic layers that temporarily store or release large amounts of reduced carbon compounds. Studies in Finnish lakes have shown that there is a close interplay between vegetation type in the littoral and the changes of net productivity due to flooding of the ATTZ: high water levels may decrease productivity due to reduced production of biomass; however, net productivity may increase at other sites where decomposition of litter is reduced due to high water levels (Larmola et al., 2004).

During drawdown, large areas of organic sediment deposits become exposed to light and air. In northern temperate lakes, such as Lake Constance, the drawdown occurs in autumn when most of the allochthonous leaf litter inputs take place. Frost and wave action break down this organic matter into small particles that are either carried into deeper zones of the littoral or remain in the dry zone. In other systems, e.g., in Mediterranean climates, the drawdown occurs during the vegetation period. Here, macrophytes become stranded and consumed by the terrestrial biota or are mineralized. The drawdown also lowers the pressure of the surface water body on the surface-near groundwater layers. Consequently, groundwater seepage into the littoral zone becomes strongly enhanced. The dissolved (mostly reduced) organic and inorganic substances of these outflows locally enrich the remaining lake water and may cause considerable algal and bacterial growth. These seepage sites can be easily visualized by the mass occurrence of algae or iron-oxidizing bacteria, especially in the area below extensive reed belts. Rainfall on exposed sediments can mobilize large amount of nutrients and increase the already-high nutrient concentrations in the remaining water bodies, especially in reservoirs (Geraldes & Boavida, 2004).

Biodiversity patterns

The permanent change between dry and wet conditions affects the biodiversity patterns of biota in the ATTZ of lakes in several ways. First, the alternating of habitat characteristics allows a sequential use of a given habitat by different species. This means that although the diversity of a biotic assemblage at a given time may be low, the chronological sequence of different assemblages during an entire flood cycle may yield a very high biodiversity (Junk & Wantzen, 2006). Flooding creates a spatiotemporal mosaic of connected and unconnected water bodies that are beneficial for the co-occurrence of organisms, e.g., shallow-water refuges for small animals that are otherwise heavily predated by fish. Especially in lakes, the size of sediment particles varies with depth along the ATTZ and variable water levels precede over variable physical habitat structures (Beauchamp et al., 1994; Gasith & Gafny, 1998). Gasith et al. (2000) showed that fish in Lake Kinnereth vary their habitat preference according to water-level fluctuations, as their risk of predation depends on sediment size.

Secondly, the pulse shape changes between years (Fig. 9). This allows a meta-effect on diversity. In different years, different groups of organisms may be successful, considering their windows of opportunity (Gafny & Gasith, 1999) and phenological windows of susceptibility (Junk & Wantzen, 2004). In Lake Constance, different flood situations have been shown to trigger the occurrence of various plant strategies (Peintinger et al., 2007). For example, the endemic forget-me-not *(Myosotis rehsteineri)* flowers only during the low-water phase and focuses on survival during sediment shifts of the flood phase (Schulz, 2007). In years with intensive water-level fluctuations, this species is very successful; however, in consecutive years of low water level, it is nearly outcompeted by purely terrestrial plants.

Another potential reason for a high biodiversity in the ATTZ compared to other habitats is that the ATTZ represents a switchboard of aquatic and terrestrial conditions that can be colonized by both aquatic and terrestrial “visitors” and by an autochthonous fauna and flora (Junk & Wantzen, 2006). This theoretically high number, however, may be reduced in the case of severe stress which acts differently for different biotic groups. Wisheu & Keddy, (1992) have developed a centrifugal model for the distribution of shoreline wetland plants that includes both the gradients of distribution and the competitive processes between the species. Several authors have highlighted the importance of the intermediate disturbance hypothesis (Connell, 1978) for the assessment of the effects of floods in freshwater systems (e.g., White, this issue, Witthöft-Mühlmann et al., 2002). The hump-shaped biodiversity curve indicates that the highest co-occurrence of species is possible at a moderate level of disturbance which results in a reduction of competition, but that does not exercise a severe physical stress on organisms (Ward & Tockner, 2001).

Floodpulse adaptations of lake littoral species

Adaptation of species traits to floodpulses requires that either the species encounters a somehow predictable floodpulse (e.g., a monomodal floodpulse, or a set of polymodal pulses occurring at the same time of the year) or the floodpulse pattern occurs over a sufficiently long enough time to evolve adaptations (Junk et al., 1989). We argue that adaptation to floodpulses represents a selection advantage for riverine species colonizing the littoral zones of lakes and vice versa. Mass mortality of the clam *Corbicula fluminea* in Lake Constance during winter drought is an example of how an invasive species can become hampered by water fluctuations (see Werner et al., this issue). On the other hand, the invasive amphipod *Dikerogammarus villosus* migrates into greater depths of the lake during winter drought that affects the upper littoral zone and has been shown to be a successful invader of Lake Constance (Hesselschwerdt & Wantzen, unpublished manuscript).

The occurrence of macrophytes is strongly controlled by water-level fluctuations, especially in shallow lakes (Beklioglu et al., 2006). Many floodpulse-adapted species have survival strategies that include production of drought-resistant seeds, escape from drought via apical meristems that are released during autumnal storms (e.g., the water weed *Ceratophyllum demersum*), or a sequestration of nutrients into drought-resistant tubers before water levels drop. Sensitive phases during life cycles are still not fully understood. For example, a long-term study on the vegetation of the ATTZ of Lake Constance revealed that of two specialist species, *Ranunculus reptans* showed a positive effect during flooding but not *Littorella uniflora* (Peintinger et al., 2007). Reed *(Phragmites australis)* is generally adapted to flooding; however, reed belts were severely damaged by an extraordinary flood in 1999 (Dienst et al., 2004). Apart from direct impacts (e.g., water stress, oxygen stress), WLF may indirectly affect even floodpulse-adapted species. In reed belts, high water levels and high water temperatures during summer floods foster the development of pathogenic fungi, which may kill the reed plants (see paper by Nechwatal et al., this issue).

Flooding is a strong selector for woody plant species in the ATTZ (Keogh et al., 1999; Nunes da Cunha & Junk, 2001; Wittmann et al., 2004); therefore, only species equipped with a number of adaptations to flooding are found in these systems (Waldhoff & Junk, 1998; Waldhoff et al., 2002; Parolin et al., 2004). Once the root systems are flooded and become anoxic, trees switch from respiration to alcoholic fermentation, which reduces the energetic yield (Kreuzwieser et al., 2004). Apart from direct oxygen stress, anaerobic soil conditions also foster denitrification, which favors the existence of tree species with nitrogen-fixing symbionts, e.g., *Alnus glutinosa* in Central European lakes (Nickel et al., 1999). These physiological constraints limit the occurrence of trees in flood zone; therefore, Keddy and Fraser (2000) use the tree line to delineate the ATTZ of lakes.

Terrestrial invertebrates can escape flooding by vertical or horizontal migrations, or they remain in the flooded habitat in a flood-resistant life stage. Flood drives many terrestrial species out of their refuges making them an easy prey for predators and scavengers just above the surf zone (e.g., hunting spiders, carabid, and cicincelid beetles). While these phenomena are relatively well understood in river floodplains, especially in the tropics (see Zerm & Adis, 2000; Adis et al., 2001; Adis & Junk, 2002; Paetzold et al., 2005), studies from lakes are scarce (Strand, 2005). We expect that due to the smoother shape of the floodpulses in lakes compared with those in rivers, flood-adapted terrestrial migrators (that evade the flooded area) suffer less from floodpulse-caused mortality in lakes than in rivers. Consequently, the number of scavengers specialized in feeding on carcasses that accumulate at the surf zone should be lower in lakes.

Several studies have shown that aquatic invertebrates clearly react to floodpulses in lakes (see contributions by White et al., Baumgärtner et al., and Brauns et al., this issue). Many benthic invertebrate species are able to survive in the upper part of the flood gradient during droughts and may profit by the warm and predator-free conditions during early flooding. For example, eggs of the mayfly larvae of the genus *Ecdyonurus* survive winter droughts above the water level and use the small ponds in the upper zone of the ATTZ in Lake Constance for the development of early larval instars (Wantzen et al., 2005b). The same occurs with the most common mosquito of Lake Constance, *Aedes vexans*. This species oviposits on moist soils just above the surf zone. Consecutive years of decreasing flood maxima may then cause the accumulation of large egg banks, as eggs may survive several years. If these years are followed by a high flood that activates these egg deposits, catastrophic mass emergences of mosquitoes may occur (Kless, 2003). Adults of other aquatic insect groups were regularly observed ovipositing directly on the already dry-fallen parts of the ATTZ of Lake Constance, e.g., several species of the dragonfly genus *Sympetrum* and of the dipteran genus *Tipula* (KMW, pers. obs.).

When water levels rise, many fish species quickly colonize the flooded ATTZ either to find food resources for themselves or their offspring (Welcomme, 1979; Bayley, 1991; Wantzen et al., 2002) or adequate spawning sites (Humphries & Lake, 2003). In Lake Kinnereth, Gafny et al. (1992) could show a direct dependence of the fish species *Mirogrex terraesanctae* on the water-level fluctuations that provide algae-free, clean stone surfaces for their adhesive eggs.

High trophic-level organisms such as birds and mammals have received much less consideration in recent WLF-related studies (see review paper by Leira & Cantonati, this issue); however, there is a large database on wading bird species that depend on the floodpulse for foraging in shallow waters and exposed sediments, and for breeding on the dessicated ground (e.g., Erwin, 1985; David, 1994).

The impact of multi-annual flood pulses on lakes: a comparison between Lakes Chad and Titicaca

Multi-annual patterns of several (2–100) consecutive years of higher or lower WLF ranges are crucial for the establishment or local extinction of species in the ATTZ. Drivers for this multi-annual climate variability vary regionally, e.g., ENSO phenomena in South America, the Sahelian Precipitation Anomaly in North Africa, and the North Atlantic Oscillation (NAO) in Europe (Blenckner et al., 2007). Large rivers and large deep lakes recover relatively quickly from these events, because water masses are large and subpopulations of plants and animals can find refuges for surviving such a critical period, but shallow lakes or lakes with extensive shallow margins (Type B and C, Fig. 10) may become seriously affected, as shown by a comparison between Lake Chad and Lake Titicaca.

Lake Chad is affected by Sahelian precipitation anomalies (Thompson, 1996). Every couple of decades, multi-annual extreme droughts hit the Sahel Zone (Fig. 8A). During these periods, the lake area shrinks dramatically as shown in the drought that started in 1972, (Dumont, 1992). In 1965–1968, during a multi-annual wet period, the lake covered an area of 18,000 km^2 with a mean depth of 4 m and a maximum depth of 12 m. In 1972 an exceptionally strong drought period began. When a certain water level was reached, the lake basin split into a northern and a southern basin (Fig. 8A, B). In the northern basin that has only insignificant tributaries, the water level resided about 3 m. Transparency decreased from 90 cm to 10 cm and electric conductivity increased. Because of high evapotranspiration rates, the water accumulated mineral salts, and during the dry season the lake reduced further to a series of temporary natron pools. The southern basin continued as a comparatively small lake because it received water from the southern Lagone-Shari Rivers, but its water level fluctuated annually by about 2 m (Fig. 8B). At the beginning of the next wet cycle in 1976, the southern basin covered an area of about 6,000 km^2, but the northern basin remained dry.

During the following 4 years the aquatic macrophyte covering the lake basin expanded about fivefold and algal biomass increased but the diversity decreased. Salt-intolerant species such as *Cyperus papyrus* were reduced. In the saline northern basin a species-poor algal community established itself that was dominated by very resistant and toxic Cyanobacteria. As a result, zooplankton diversity decreased. Increased silt loading led to a reduction of bivalves. Mass mortalities of fish occurred, and several species became locally extinct. Within one year (1974) species richness in the fish community dropped from 34 to 5–8; only those species showing high tolerance to low oxygen concentrations and high feeding plasticity survived. After 1976, Lake Chad seemed to stabilize at a new level, but in the 1980s a new extended drought started that lasted about 10 years. In 1984, the southern pool shrunk to a size of only 2,000 km^2. From the mid-1990s increasing rainfall led to a rise in water level (Fig. 7) and late 1999 saw the heaviest rains in central Africa in the last 30 years. Since 1973, the annual flood amplitude is about twice as high as it was before (Dumont, 1992).

This example shows that multi-annual large changes in hydrology can represent a heavy stress factor in shallow lakes, especially when the water level is decreasing. If this stress situation occurs over a period of a few years only, abundance patterns shift towards species that can survive in refuges or resting stages in the sediment. The other species return once the lake regains its original setting. Such environmental changes may even increase habitat diversity and species diversity in comparison with stable systems through the control of populations of highly competitive species. However, if the stress increases towards desiccation and surpasses the thresholds of the system, local extinction of species may occur in a very short period of time, as shown in the northern basin of Lake Chad.

The capacity of recovery of those lakes depends on the available refuges, for instance, in permanent swamps in their surroundings and especially on feeder rivers where relict populations of the lake fauna can survive. Recovery will require years or decades depending on the complexity of the communities and the level of specialization and may even lead to a new biocoenosis. For Lake Chad, Dumont (1992) postulates a simplification of the biocoenosis because of an increasing number of multi-annual droughts. The fact that shallow lakes have almost no endemic species points to the relative frequency of such heavy disturbance events. A similar reaction to multi-annual dry and wet periods can be observed in large tropical and subtropical wetlands, e.g., the Okawango Delta in Botswana (Ramberg et al., 2006), the Central Delta of the Niger River in Nigeria, (Lae, 1994), and the Pantanal in Brazil (Junk et al., 2006). Diversity of aquatic species is maintained by the connection with large river systems that act as refuges for wetland subpopulations.

Even in deep lakes annual and multi-annual fluctuations may affect at least parts of the system as shown for Lake Titicaca. There are two major shallow areas in the lake: the subbasin Lago Pequeno and the Puno bay. The annual water level oscillations of 1 m have little impact on the lake and the ATTZ, but there are also multi-annual water level changes related to El Nino phenomena (Fig. 6, Pawley et al., 2001). In the first half of the 20th century, the difference between the highest water level in 1933 and the lowest water level in 1943 reached about 4 m. This difference had a strong impact on the shallow water areas. During the high-water period, the harbor of Puno, the rail road, and the adjacent plains were inundated and the harvest destroyed. During extreme low-water levels large shallow areas along the shores fell dry and nearly all stands of the bulrush totora (*Schoenoplectus californicus* ssp. *totora*) dried out. In the Puno subbasin alone, 23,000 ha of totora swamps were destroyed with negative economic consequences for the local population that uses the plants for boat and roof construction and as food item. There were dramatic effects on the Uru people who lived in the totora swamps and whose social structure became disintegrated when they had to leave the drying swamps (Monheim, 1956). In 1986, during the peak of the multi-annual high-water period, the *Chara* stands and the deep water *Potamogeton* stands in Lago Pequeno died because of reduced light conditions. The decomposition of large amounts of organic matter led to anoxia and the death of benthic animals. When the lake level decreased, *Chara* stands quickly re-established but not the deep water *Potamogeton* stands. In Lago Grande, lake level rise had little effect on the macrophyte stands, because of higher water transparency.

The ecological consequences on the lake have not been studied in detail, but the following hypotheses can be established. Lake Titicaca is an oligotrophic lake with very low algal production as indicated by a secchi depth of up to 10 m. A considerable part of aquatic primary production takes place in shallow water areas that are colonized by dense stands of emergent and submersed aquatic macrophytes. These stands are important habitats and spawning grounds not only for the endemic fish subfamily Orestinae, but also for birds and amphibians (Pawley et al., 2001). Fast changes in water level of several meters considerably reduce the productive area and the habitats for the aquatic fauna because the plants cannot adjust their distribution quick enough to offset the changing hydrological conditions.

Floodpulses in lakes and man

Ecosystem services of an intact ATTZ and a natural floodpulse regime in lakes

The floodplain zones of lakes generally fulfill the same ecological functions and ecosystem services as the riverine ones do (Manring, 2005; Bohensky et al., 2006). The most prominent ecosystem services of lake floodplains are:

- climate buffering
- flood control
- buffering of allochthonous nutrient inputs
- storage and release of carbon compounds
- self-purification of water
- sites of increased plant and bacterial productivity
- sites of reproduction, feeding and growth of invertebrates, fish, amphibia and birds
- sites of high biodiversity, including endemic and rare species
- tourism/recreation/aesthetic value

In lakes that are aligned with river courses, the function as hydrological buffers is especially important. The ATTZ of these lakes acts as a reservoir that dampens the discharge of the rivers. For example, Lake Constance buffers a considerable part of the floods that affect the cities along the Rhine river.

The positive effects of enhanced primary production and fish productivity in floodplain zones of lakes has been shown mostly for tropical lakes (e.g., Lim et al., 1999; Welcomme & Halls, 2001). The case studies of the Chad and Titicaca lakes have shown how entire human social groups depend on the functioning of the ATTZ of lakes. In temperate lakes it can be assumed that flooding is equally or even more important than in the tropics, as the shallow floodplain waters heat up disproportionally compared to their deeper water bodies (Güde et al., 2004).

The importance of lake floodplain zones as temporary carbon storage sites is still severely underestimated in global climate models. Although it is evident from the occurrence of deep black sediment layers (consisting largely of organic carbon) in the ATTZ, they are rarely mentioned in climate models. A recent study on small water bodies in the US has shown how important these aquatic habitats are for the storage and release of carbon (Euliss et al., 2006).

Lake management

Human activities interfere with natural hydrological regime of lakes in several ways. On a local scale, the natural fluctuations of lakes have been reduced by regulation of the lake in- and outflow. Many lake floodplains in the "developed" countries have been isolated from their main water bodies. Moreover, damming has created a number of new lakes with management schemes that often differ strongly from natural WLF. On a regional scale, sealing of the surfaces by urbanization and systematic regulation of all tributaries has led to an increased flashiness of lake hydrographs, as the buffer function of the ATTZ has been cut off, and all regional precipitation immediately arrives in the main water bodies. On a global scale, climate change effects interfere strongly with the water regime, due to extended drought periods and increased probability of storm flow events (IPCC, 2001).

The management of water levels in lakes follows several principles: (i) to keep the water level high until an increased demand for water (drinking water, hydroenergy) occurs, (ii) to keep the water level permanently low in order to gain land from the ATTZ, (iii) to keep the water level stable on an average level in order to guarantee flood-protection and permanent navigability due to stabilized water levels in river channels that connect lakes. Principle I is valid for many Mediterranean lakes and for dams. In the Mediterranean region, however, lakes have suffered a permanent drawdown in the past years due to lacking rainfall and an increased demand on drinking water for a growing population (e.g., Lake Kinnereth, Gasith, pers. comm. and see Beklioglu et al., 2007). As an example for Principle II, many lake levels have been lowered in the medieval period in order to gain fertile land in Central Europe (e.g., "Federsee" in Southern Germany) or to create permanent access to islands (e.g., Greater Plöner See, Northern Germany).

Many examples for Principle III are known from prealpine lakes which were stabilized to protect the cities at the lake margins. The old sluices in the cities of Luzerne and Zurich (Switzerland) give impressive proof of the tradition of water level regulation. Considering the current climate change effects, principle III is likely to become increasingly important because many more lakes than before will be included in flood and drought management schemes. Now that climate models have gained sufficient predictive power, efforts are strongly needed to improve our knowledge about these effects and to develop scenarios of how to deal with it on the landscape planning level. It follows clearly from the arguments delivered above that the preservation of still-existing floodpulse regimes and of the ATTZ in lakes should become first priority in lake management schemes. Moreover, already-existing regulated lakes (e.g., dam lakes) may either be deregulated or regulated in a management scheme that reduces environmental impacts. The REGCEL project from Finland (see contributions by Aarovita et al., this issue) is a positive example of how winter drawdown can be limited or regulated according to requirements of natural populations.

Climate change

Climate models predict an increase of stochastic events (unpredictable floods and droughts) and a reduction of so-far predictable elements of the hydrologic regime (snowmelt and summer drought). Moreover, a general trend towards drier conditions can be anticipated for many regions worldwide, thus creating multi-year low water phases as discussed above. Current trends within long-term series, e.g., for Lake Constance, indicate an increase in exceptional hydrological events (Joehnk et al., 2004). The effects to the whole lake ecosystem are manifold: Like many other prealpine lakes, the upper section of Lake Constance is largely characterized by a steep trough shape, and a shallow "rim" for the littoral (Type "C," Fig. 10). Extreme droughts would cut of the shallow margins of the lake and strongly affect the biota. In winter, larger areas of exposed sediments freeze, leading to increased mortality of surface-dwellers (e.g., *Dreissena* mussels), and in summer when water levels are supposed to be highly important habitats for aquatic organisms that depend on the littoral are lost. Considering that large populations of wintering waterbirds depend on these mussels (Werner et al., 2005), and that a large part of the fish community depends on the shallow lake areas (Fischer & Oehl, 2005), multi-annual low-water phases should lead to tremendous losses in biodiversity and productivity of the whole ecosystem. As a result of the extraordinarily hot summer temperatures at Lake Constance in summer 2003, carp *(Cyprinus carpio)* yields have skyrocketed. Along with the spread of warm-water adapted organisms, a range of parasites and pathogens that did not previously appear deleterious to the fauna and flora, e.g., fungal diseases in reed, have increased (see contribution by Nechwatal et al., this issue) as well as a large number of fish diseases. The heating-up of the dry part of the ATTZ attracts migrating birds from southern regions and the number of northern migrators is declining (H. G. Bauer, pers. comm.) showing a shift in migrators. Shallow lakes (Type "B", Fig. 10) would periodically cease completely during multi-annual droughts (Mooij et al., 2005; Beklioglu et al., 2007).

Untimely floods, on the other hand, are unlikely to be met by resource-use traits of floodplain species. For example, aquatic invertebrates only slowly colonized the recently flooded ATTZ after a rapid flood in summer 2005 (Wantzen et al., unpublished data). In contrast, terrestrial species that rely on continuous dry conditions are supposed to suffer high mortalities. Notwithstanding, not only the habitat structures become severely altered by irregular floodpulses but also human constructions. For example, recent changes in the hydrological regime have led to an increased erosion of archaeological sites in the littoral of Lake Constance.

Moreover, shallow lakes in central Europe were predicted to suffer a range of negative alterations due to climatic changes, including increased disturbance, reduction of biodiversity, especially of birds and other biota depending on a clear water stage, an increase of cyanobacterial dominance in phytoplankton communities, increased botulism and waterborne diseases, and a benefit invasive species (Mooij et al., 2005). In summary, the functions and importance of the ATTZ and of flood events deserve more attention in conceptual models of climate-related effects on lake ecosystems (Blenckner, 2005; Blenckner et al., 2007).

Based on long-term studies and transplant experiments with macrophytes, Keddy & Fraser (2000) have established management guidelines for wetlands in large lakes, which recognize the maintenance of the floodpulse as the most important factor in shoreline wetlands.

Conclusions: an extension of the FPC for lakes

Our analysis has shown that the floodpulse concept applies to lakes, however with some adaptations that consider the specific characteristics of lake ecosystems. Due to structural differences between rivers and lakes, floods tend to develop less erosive forces; therefore, less inorganic and organic sediments are mobilized and repositioned in lakes than in rivers. Consequently, flood-mediated landscape patterns such as meandering etc. as found in rivers (e.g., Schumm, 1977) do not occur in lakes; however, their bank structures (erosional/depositional sites) are more strongly influenced by wind forces. Therefore, the habitat diversity in the ATTZ of lakes is supposed to be generally lower than in rivers. Due to the increased residence time in lakes, their floodpulse pattern tends to be less spiky and the drawdown tends to be slower than in rivers. The more depositional characteristics of lake ecosystems facilitates the storage of organic matter in the ATTZ compared to the more dynamic floodplain structure of rivers. The oblong shape of rivers results in their more intensive aquatic-terrestrial interactions than lakes; however, in lakes with a large ATTZ this general pattern can vary. In terms of biodiversity, the corridor shape of river systems increases their resilience to catastrophic flood events and multi-annual drought periods compared with lakes. Hence, the ATTZ acts as a reservoir of resilient species that may recolonize the permanent water body after catastrophic events in both rivers and lakes.

Reformulating the tenets of the Floodpulse Concept (Junk et al., 1989; Junk & Wantzen, 2004) for lakes, it can be stated that:

- natural floodpulse patterns vary between years and show multi-year phases of drier and wetter years
- the cross-sectional morphology of the basin and the hydrological regime of the catchment are decisive for the spatiotemporal pattern of the flooding and drying
- the floodpulse acts as a strong filter that selects flood-adapted species to colonize the ATTZ, thereby fostering evolutionary processes
- species occurring in the ATTZ are adapted to maximize the use of floodborne resources during their lifecycles (“windows of opportunity”) and to minimize losses due to negative effects of floods and droughts on specific lifecycle stages (“phenological windows of susceptibility”)
- the timing of the occurrence of a given water level and the period by which an organism can use the floodborne resources or cope with adverse conditions caused by the floodpulse is crucial for the survival of the species in the ATTZ
- the higher the predictability of the floodpulse pattern (including a long-term temporal pattern that allows evolutionary processes) the better the biota are adapted
- due to the increased decomposition and remineralization of nutrients and additional inputs from the catchment or the main water body during the wet-dry cycle, aquatic systems with a pulsing floodplain are more productive than those with a stable water level (floodpulse advantage)
- the interannual variation of the water level allows a sequential use of the ATTZ by different species and thus fosters biodiversity
- the natural intra-annual variation of floodpulses interferes with the species-specific adaptations of the biota and therefore fosters the variable dominances of different species between years
- management schemes for floodplain systems should take advantage from the natural processes triggered by the floodpulse (including increased productivity)

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WATER-LEVEL FLUCTUATIONS

Effects of water-level fluctuations on lakes: an annotated bibliography

Manel Leira · Marco Cantonati

Abstract Water-level fluctuations (WLF) in lakes and rivers, especially their extent, frequency and duration, are dominant forces controlling the functioning of these ecosystems. In particular, WLF play an important role in the lake's littoral and aquatic–terrestrial interface processes. WLF may take place on different spatial and temporal scales under natural conditions but water levels have been artificially modified in regulated lakes, and their impacts are expected to be enhanced within the actual global change scenarios with forthcoming management problems. This article presents an overview on the literature published on this important topic since 1991 by using journals indexed in the ISI Web of Knowledge. The overall objective was to examine temporal and spatial trends in publications on WLF, the specific aspect of WLF concerned and their main effects. Throughout the article we have used case studies to illustrate different effects of WLF on the variety of lake habitats and indicators that have been studied. Overall, the number of papers published on the subject since the 1990s has risen steadily, when less than ten papers were published each year; until 2006 and peaking in 2005. The greatest number of papers on WLF has been carried out in Europe and North America (c. 73%). These data also showed that the effects of WLF have not been studied equally for different groups of organisms. There is a greater interest on macrophytes, which are the most studied group of organisms (18.4% of the papers). Nearly 7% of the papers deal with algae, and zooplankton and invertebrates account for a 7% followed by fish. WLF effects on ecosystems are very complex, and the biological effects in lakes are greatest in shallow water and littoral areas, where even small changes in water levels can result in the conversion of large areas of a standing-water environment in air exposed habitats. Finally, these data might serve to highlight knowledge gaps still existing on this topic and, in particular, some of the approaches that can potentially contribute to solve several of these lacunae are explored.

Keywords Water-level fluctuations (WLF) · Literature · Spatial trends · Temporal trends · Effects · Indicators · Lake management · Lake habitats · Littoral

Introduction

Lake ecosystems are subject to a number of natural and anthropogenic stressors. Typical man-made stressors

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Ecological Effects of Water-Level Fluctuations in Lakes

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include pollution of water and sediments with toxic substances or excessive nutrient inputs, invasion by non-native species, and changes in the physical characteristics of a local environment by fixation of the riparian zone. Changing water levels are another stressor on lakes and littoral communities. Water-level fluctuations (WLF) in lakes are dominant forces controlling the functioning of lacustrine ecosystems (Wilcox & Meeker, 1992; Poff et al., 1997). WLF, especially their extent, frequency and duration, play an important role in the lake's physical processes (e.g. the geomorphologic processes of erosion and sedimentation). Biota, in particular those living in vegetated riparian areas, respond differentially to water-level dynamics, either directly or indirectly. Direct effects on the biological communities include physical disturbance by wave activity. Indirect effects include the reworking of substrates (which can enhance or restrict colonization by vegetation, and which in turn depends on silt accumulation to establish roots), and alteration of habitats suitable for aquatic flora and fauna. Any significant change to the water level of a lake will affect not only the physical processes, but also the biological productivity. Therefore, WLF might have an overriding effect on lake ecosystem health and integrity.

Under this framework, the growing anthropogenic effects on regional hydrology, including lake-level regulation and the anticipated climatic change, has consequently raised the plea for more data on the relationships between water-level changes and ecosystem responses (Coops et al., 2003; Coops & Havens, 2005). Since then, the study of water-level regimes in lakes has gained relevance enough so that there are more papers on WLF effects than ever, and they are published in a wide array of journals.

In this article, we address the following questions about WLF studies: (1) How many papers have been written about WLF since 1991? (2) What were the specific subjects of these studies? (3) What geographical area(s) were considered? and (4) Which taxa were involved?

The potential effects of lake-level changes have been judged by impacts at the physical level, i.e. transparency, sedimentation patterns, erosion; at the species level, i.e. target species, and by indicators at the ecosystem level, i.e. carrying capacity and biodiversity.

First, we describe the general characteristics and trends of papers published on WLF. Next, we review the available literature dealing with the effects of WLF and how indicators of the functioning of lakes are affected. Throughout the article, case studies are used to illustrate different effects on the variety of lake habitats and indicators that have been studied. We have grouped the references in four broad categories to narrow down possible areas of interest: (1) Effects on the physical environment; (2) Effects on lake biota; (3) Ecosystem effects and (4) Modelling studies. Finally, we have included a section exploring the future research opportunities in WLF studies.

The data presented in this article were compiled from journals indexed in the ISI Web of Knowledge. The searches used the following keywords individually or in combination: lake-levels, water levels, change, variation, fluctuation, impacts, effects, ecological and thresholds. On average ca. 1700 papers were browsed for a total of 243 WLF papers. We defined a paper as a WLF study when one or more of the selected keywords appeared in the title, abstract or keywords (see above). The searches were extended to cover the complete table of contents of all titles appearing in journals within all subject categories likely to publish any work on the topic, such as e.g. *Hydrobiologia*, *Hydrological Processes*, *Lake and Reservoir Management* and *Freshwater Biology*. This approach yields a number of 130 journals (those including more than two of the papers considered are listed in Table 2) and probably covered most of the published scientific literature on this subject. Freshwater, inland brackish and saline lakes, either regulated or not, were considered, but not lotic habitats. Short communications/notes of a journal or reports were not considered either. These selected papers were then read and classified according to several classification systems according to the descriptors used by the authors (Table 1). The data were then categorized into each of the areas of interest (physical environment, biota, ecosystem and modelling). Initially, the terms used by each author were considered (Table 2), which results in some overlap, that is, many of the papers dealing with the effects of WLF on organisms were also concerned with aspects at the habitat and ecosystem level. For example, if a paper dealt with physical environment and biota, this paper would be classified in both categories. That is, a paper might say it was examining WLF effects on macrophytes, but it might

Table 1 Keyword list by major topic

Topics	Keywords
Physical habitat	Aquatic, Area, Basin, Bay, Beach, Bogs, Catchment, Circulation, Climate, Coast, Coastal, Currents, Depth, Drawdown, Energy, Eolian, Erosion, Estuaries, Euphotic, Evaporation, Everglades, Floodplain, Flow, Fluctuations, Habitat, Hazards, Headwater, Inshore, Interface, Lacustrine, Lagoon, Lake, Lake Level, Light, Littoral, Meadow, Morphology, Morphometry, Offshore, Pelagic, Pond, Pools, Residence, Ridge, Sediment, Seiche, Stratification, Swamps, Temperature, Volume, Water budget, Waves, Wetland, Width, Wind, Zonation
Biota	Algae, *Anguilla australis*, aquatic plant, aquatic pollen, aquatic vegetation, *Barbatula*, Biological indicators, Birds, Bivalves, *Chara*, Cladocerans, Coleoptera, Common-Loons, *Coreopsis rosea*, Cyanobacteria, Cyanoprokaryotes, *Daphnia*, diatoms, *Dreissena*, *Elliptio complanata*, Emergent, Floating, Flora, Floristic, Forest, *Gavia immer*, *Hippuris vulgaris*, Hydrophytes, *Hygrophila*, Ichtyoplankton, Invertebrates, *Isoetes lacustris*, Largemouth bass, Larvae, *Littorella uniflora*, macrophyte, Mosses, Mussels, nannoplankton, Northern pike, *Nymphaea*, *Oncorhynchus*, Ostracods, Panktivores, Perch, *Phragmites*, Phytoplankton, Picoplankton, Piscivorous, Plants, Pollen, Rotifers, *Salvelinus alpinus*, *Sphagnum*, Submergent, Tree, Trout, *Typha*, Unionids, vegetation, Zebra, Zooplankton
Ecosystem	Abundance, Acidification, Adaptive radiation, Alkalinity, Alternative states, Anaerobiosis, Assemblage, Autotrophy, Behavior, Biodiversity, Biogeochemistry, Biomanipulation, Biomass, Carbon, Carrying capacity, Chlorophyll, Colonization, Community, Competition, Conservation, Decomposition, Disturbance, Diversity, Ecological status, Ecosystem, Environmental change, Eutrophic, Eutrophication, Eutrophy, Food web, Function, Gradients, Growth, Impacts, Loadings, Management, Migration, Mortality, Nutrients, Organic matter, Phosphorus, Physiology, Productivity, Recruitment, Reproduction, Species composition, Structure, Succession, Survivorship, Tolerance, Top-down, Toxicity, Trophic, Water quality
Modelling	Artificial Neural Networks, Databases, Generalized logistic model, Geographic information systems, GIS, Model, Model coupling, Modelling, Prediction, Regression, Remote sensing, Response surface, Satellite
General study	Limnology, climatology, ecology, hydrology, paleoecology, paleolimnology, paleoclimate

also have involved measuring physical parameters as light and sedimentation (i.e. physical environment descriptors).

The objective was not to compile information on all papers dealing with the effects of WLF in the vast literature but to compile enough papers to provide an overview of the current state of the art. These data can form the basis to direct attention and research towards underrepresented subjects. It will also provide a comparative base for scientists already

Table 2 Number of papers on the Journals consulted in the present study and their impact factors (IFs) in 2006 (Journal Citation Reports, 2007)

Source title	Record count	Percentage	IF
HYDROBIOLOGIA	30	12.3	1.049
JOURNAL OF GREAT LAKES RESEARCH	11	4.5	1.000
JOURNAL OF PALEOLIMNOLOGY	9	3.7	3.016
JOURNAL OF HYDROLOGY	7	2.9	2.117
WETLANDS	6	2.5	1.109
AQUATIC BOTANY	6	2.5	1.338
CAN. J. OF FISH. AND AQUATIC SCI.	5	2.1	1.882
FRESHWATER BIOLOGY	5	2.1	2.502
ARCHIV FÜR HYDROBIOLOGIE	4	1.7	1.362
LIMNOLOGY	4	1.7	0.682
LIMNOLOGICA	4	1.6	0.722
GROUND WATER	3	1.3	1.117
QUATERNARY SCIENCE REVIEWS	3	1.2	4.113
BIODIVERSITY AND CONSERVATION	3	1.2	1.423
COMPTES RENDUS DE L ACADEMIE DES SCIENCES	3	1.2	1.484
WATER RESOURCES	3	1.2	1.894

Only journals with more than two articles published on the subject are shown working on the topic and place them into an international perspective. All statements relative to studies on the effects of WLF refer to the database from the ISI journals only, and conclusions are based on this dataset.

For the sake of brevity, only those papers that are not published in this volume appear in the reference list following this text.

Temporal trends

Issues published in leading journals (Table 2) from 1991 to 2007 (till September) were consulted. During most of the 1990s, less than ten papers were published each year, which used any of the descriptors adopted in this bibliography review, and describe the effect of WLF on habitat, biota, and ecosystems or their modelling (Fig. 1). Thereafter, the number has risen until 2006 and peaking in 2005, when 27 papers on the subject have been published (the papers included in the present volume which derive from the WLF Workshop organized in Konstanz in the same year were not considered for this compilation). As an average, circa 18 papers have been published every year during the 2000s which self-identified as WLF studies.

Geographical patterns

Country or territory of origin may influence the distributional pattern of WLF works produced (Fig. 2). Most of the studies on WLF in the last 25 years have been carried out in Europe and North America (c. 73%). Although the reason might be geographical (lakes are not evenly distributed on the earth's surface; most are located in high latitudes and mountainous regions, e.g. Canada alone contains nearly 50% of the world's lakes), in most of the developing countries limnological works are still likely to be limited by economic constraints preventing the possibility to carry out projects on contemporary issues, like global change or modelling of ecological processes.

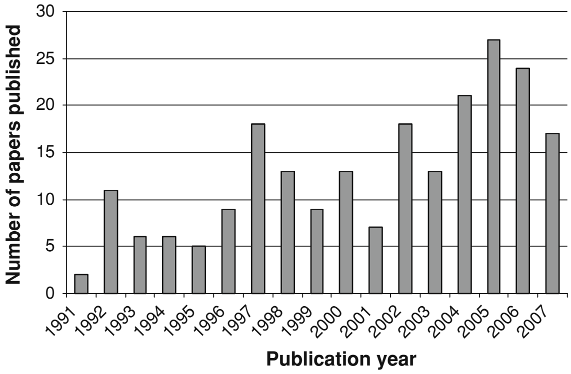

Fig. 1 Number of articles published on WLF effects in journals indexed in the ISI Web of Science since 1991

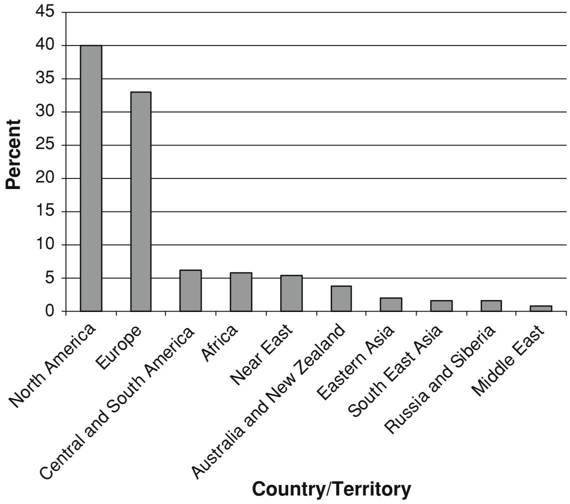

Fig. 2 Broad geographical areas where the effects of WLF have been studied

Subject category

The papers on WLF had a broad ecological scope and dealt with topics ranging from ecosystem functioning and conservation to water resource management and geosciences (Fig. 3). Most of the papers were classified under the broad denomination of *Marine and Freshwater Biology*. Human-dominated subjects, such as *Civil* and *Environmental Engineering* accounted for only c. 9% of the papers, and pollution accounted for only 12% of the papers.

Descriptor of type of WLF environmental effect

All authors identified the aspect of the environmental quality affected by the WLF that their study was focused on (Fig. 4). There are far more papers that

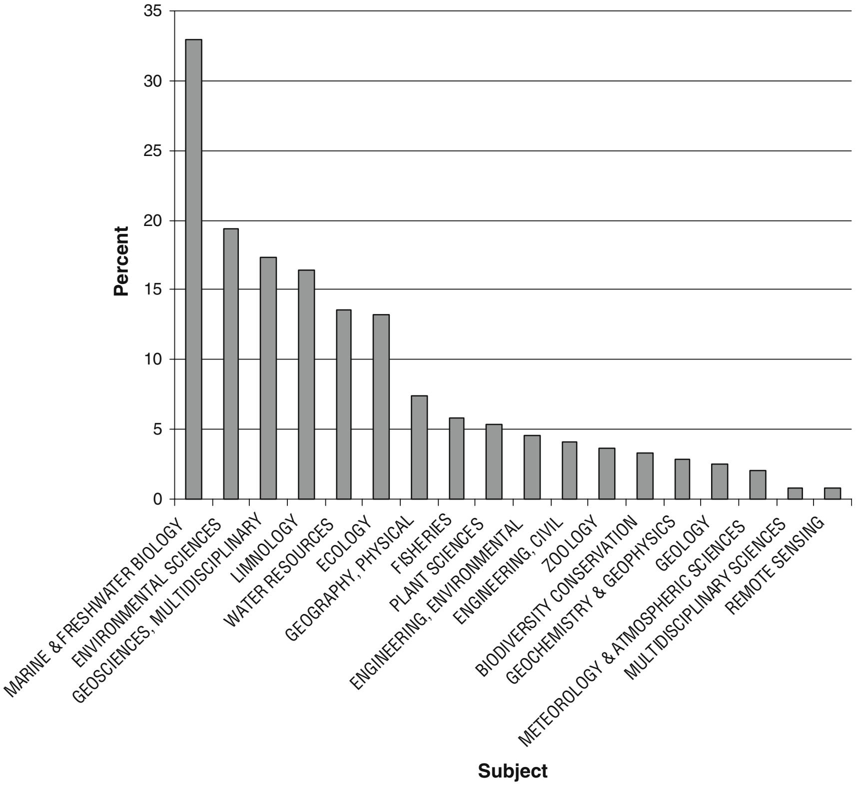

Fig. 3 Percent of articles on WLF that fall into each subject category

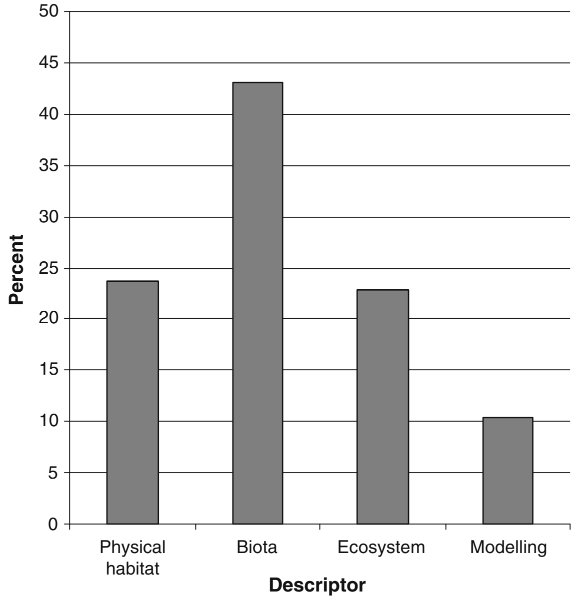

Fig. 4 Percent of papers on WLF effects for different type of object of study

address the impacts of WLF on aquatic plants (e.g. macrophytes) than any other group of organisms and many authors discuss WLF effects on lakes ecosystem and physical habitat based on distribution and dynamics of aquatic vegetation (although often vaguely).

Over 40% of the WLF papers were about the effects on the biota, followed by physical habitat and ecosystem level studies (which could include habitat as well as other organisms) (Fig. 4). Modelling made up only a small percentage of papers even though there is a relatively major effort to understand the risks from WLF on human structures.

An examination of species group studied provides insights into common targets (Fig. 5). There are far more papers that focus on the effects of WLF on aquatic plants than any other group of organisms (18.4%). Nearly 7% of the papers deal with algae (either phytoplankton or phytobenthos), while zooplankton and invertebrates account for a 7% and another 7% deal with fish. Birds and mammals are far less in the main scope of papers. Several conclusions can be drawn from this figure: (1) Aquatic plants feature prominently as the subject of WLF papers far more than any other organism; (2) many papers deal with the effects of WLF on lake wetlands and littoral habitats; (3) plants are the primary indicator of

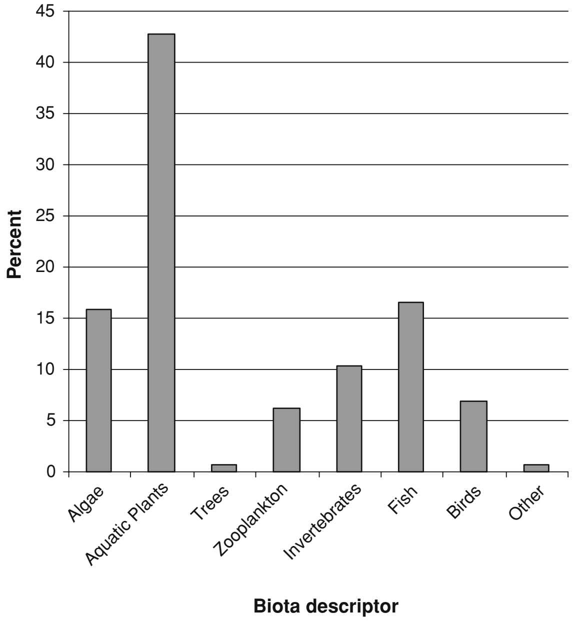

Fig. 5 Percent of papers examining the effects of WLF on biota for the major species group

physical habitat and ecosystem level studies and (4) there have been relatively a few papers on high trophic-level organisms.

In general, the studies explore the ecological consequences of biophysical alterations caused by WLF. A number of the papers describe the impacts of water-level changes on biota, environmental flows, geomorphologic processes, and landscape, but regarding the effects of regulation, withdrawal and dam construction. Other articles make comparisons between regulated and non-regulated systems (e.g. Wilcox & Meeker, 1992), and some describe physical characteristics and ecological aspects of littoral habitats, while others provide conceptual frameworks for proposed impact assessment methods (e.g. Wilcox & Whillans, 1999; Wantzen et al., this volume). Only a few studies highlight the major scientific challenges and opportunities involved in effectively addressing this kind of research (e.g. Meyer et al., 1999). On the other hand, most of the studies focused on a single species, although the diversity of ecological subjects targeted in the various publications covers a wide range of living organisms. Albeit this kind of approach can have an important social impact in environmental policy and decision making, it might make it difficult to develop an integrative ecosystem approach.

Effects on physical environment

The fluctuations of water level alter the lake morphometry and transform the characteristics of the sedimentation zones (erosion, transportation, accumulation; Håkanson, 1977), thereby water-level drawdown enhances sediment erosion and focusing and has the potential to fundamentally change littoral sediment and biogeochemical characteristics (Furey et al., 2004). Bedford (1992) explored the physical effects of the Great Lakes on tributaries and wetlands, particularly through the effects of short and long-term WLF and accompanying transport disruptions, including flow and transport reversals. Rhodes & Wiley (1993) report that declining water levels may cause contaminated sediments to be resuspended and this will represent a potentially long-term environmental remediation problem (compare Skoulikidis et al., this volume).

One of the main alterations of water levels in lakes is that it affects light penetration (Loiselle et al., 2005), thereby causing a change in the littoral area available for benthic algae and macrophyte growth, which in turn might cause a shift in the distribution of primary production between pelagic and littoral habitats. In addition, exposure of new substrate during periods of extreme low water levels may facilitate the expansion of emergent plants. Hudon (1997) shows a strong negative relationship between seasonal water level and the percentage of emergent plant cover in Lake Saint-Pierre on the lower St. Lawrence River. Moreover, spatial and temporal differences in the water chemistry due to the WLF have been shown to exert a strong influence on habitat conditions at different sites of the lakes (Dinka et al., 2004). The magnitude and frequency of WLF in lakes are also evident in wetlands, where small changes in water levels can have important effects on their size and distribution (Morin & Leclerc, 1998).

However, one of the major impacts of a decrease in average water levels might be the effect on the temperature regime of lakes, which can be reflected in a deepening of the thermocline, and a longer stratification period. Results indicate that physical processes are sensitive to short-term changes in hydrology, and that the combined impacts of short-term climate variation and anthropogenic manipulation of hydrology may be greater in shallow reservoir ecosystems, but the magnitude of these differences is mediated by basin morphometry (Nowlin et al., 2004). Another significant effect of this change in the temperature regime of the lakes is its potentially significant impact on the movement, feeding and spawning habits of fish in the lakes.

Although climate change was not in itself a focus of this literature review, studies of the impacts of climate have great relevance to the assessment of potential effects of WLF on lakes (Noges, 2004). For example, climate change research has addressed changes in lake circulation, water levels and the ecological impact of these changes on wetland functions and values (Mortsch, 1998). Magnuson et al., (1997) examine the physical changes that might come from climate change and would in turn affect phytoplankton, zooplankton, benthos and fishes. Aquatic ecosystems and organisms do not necessarily exhibit coherent responses to climate changes and variability, even if they are in close proximity, and many complex reactions are expected to altered temperatures, thermocline depths, light penetration and nutrient availability. Furthermore, climate change effects interact strongly with the effects of other human-caused stresses such as altered patterns of land use, eutrophication, acid precipitation, water withdrawal, toxic chemicals and the spread of alien organisms. All these factors combined may reduce or enhance climate-induced changes, which, in turn, can have an important effect on the goods and services provided by freshwater ecosystems (Meyer et al., 1999).

WLF are also of concern for a number of social and economical reasons. Human actions (dredge-fill, damming and water-level regulations) can alter the water-level regime impacting the aquatic resources and resulting in dramatic alterations to the entire ecosystem, because of complex feedback responses among the various components of the system (Busch & Lary, 1996; Crowder et al., 1996). WLF can also have potential effects on coastal developments and human activities (e.g. Lake Van, Turkey; Kilincaslan, 2000). For example, rising lake levels will allow large waves to affect broader shoreline reaches (Brown et al., 2005) increasing shore erosion and posing engineering problems to protect community interests (Hamilton, 1987). In addition, the effects of physical disturbance by wave action in terms of WLF also have an impact on the presence, species richness, cover and depth limits of the low-growing, shallow water macrophyte community (Riis & Hawes, 2003).

Effects on biota

This category includes literature describing the effects of changes in water levels on biological populations and communities. The studies could be divided into those that focused on impacts on flora versus those that focused on fauna. The effects on flora include literature that describes impacts on phytoplankton, aquatic macrophytes and tree species, while the effects on fauna describe mostly disturbance on fish populations and invertebrates.

Studies on the impacts of water-level changes on flora were generally restricted to littoral areas, shallow lakes and wetlands. For example, Hellsten et al., (1996) investigates the environmental effects of water-level regulation for purposes of hydropower production in the littoral zones of regulated lakes (northern Finland). In addition to the obvious changes in the distribution of aquatic macrophytes, Hellsten et al., (1996) notes that the response of the littoral is slow, and the effects may appear gradually over several decades. Similarly, Jean & Bouchard (1991) showed that the time lag between a reduction in WLF and the relative stabilization of species distribution could be a reason for the importance of spatio-temporal variables, and account for the undetermined portion of species variation.

Lacustrine wetlands normally have a variety of plant communities arranged along an environmental gradient that are influenced by interannual water-level fluctuation. Depth, duration and frequency of inundation influence plant community composition, but depth has been considered less important, while the duration of individual flooding events is important in segregating the plant communities (Casanova & Brock, 2000). In prairie potholes in North America, the magnitude of interannual WLF determines the kind of vegetation change observed (van der Valk, 2005). High water levels can eliminate most emergent species while low water allows emergent species to become re-established from seed and terrestrial annuals to dominate the vegetation invoking water depth tolerance as the primary determinant of distribution of emergent species. These changes in vegetation are always accompanied by changes in vertebrates, amphibians and birds (Euliss et al., 2004).

The functioning of shallow lakes is also supposedly very sensitive to WLF. The characteristic ecology of floodplain lakes is in part due to their relatively strong WLF (Van Geest et al., 2005a, b). Moreover, littoral plant communities in shallow lakes located in semi-arid to arid regions appear to be particularly susceptible to water-level fluctuations (Beklioglu et al., 2006). Expansion of submerged vegetation is not only related to high water levels during winter and reduced amplitude of WLF, but also to the lake morphometry. Submerged plant development would be coincident with either an increased morphometry index or a flatter bottom profile.

Macrophytes were by far the most studied group. Though most of the efforts are focused on the changes of macrophyte area as controlled by WLF (e.g. Wallsten & Forsgren, 1989; Dienst et al., 2004; Hudon et al., 2005), studies have addressed many different aspects of macrophyte biology and ecology (Wagner & Falter, 2002; Urbanc-Bercic & Gaberscik, 2004; Nishihiro et al., 2004a, b; Paillisson & Marion, 2006; Imamoto et al., 2007). The strong response of wetland vegetation to hydrological conditions underlines their vulnerability to water-level variations resulting from regulation and climate variability (Murphy, 2002). It was also found in a number of studies that unregulated lakes support structurally more diverse plant communities at all depths, while lakes with reduced fluctuations in water levels host less diverse plant communities (e.g. Wilcox & Meeker, 1991). Similarly, in natural non-regulated systems the species richness was much lower in lakes with inter-annual level variations than in lakes with intra-annual fluctuations (Riis & Hawes, 2002).

Much less attention has been paid to terrestrial plant communities, although terrestrial species are also very sensitive to water-level changes as they are only able to establish during dry phases between short floods (Ferreira, 1997; Casanova & Brock, 2000). In particular, forest structure, floristic composition, species richness and diversity index, in tropical floodplain forests have been related to variation of the flooding duration (Ferreira, 1997). Areas inundated for longer periods of time show a lower number of species and less diversity due to selective pressure of adaptation to a flooded habitat.

WLF also have an effect on the algae biota within the lake. Periphyton communities are generally very resistant and resilient to changes in lake level (Hawes & Smith, 1993). Composition and structure of epilithic and surface sediment diatom assemblages show a rather specific depth zonation. As regards the epilithic diatoms of a carbonate mountain lake affected by marked natural WLF (Cantonati & Angeli, 2003), Cantonati et al. (2008) could identify three depth-distribution zones by means of quantification, physiological, functional and community structure parameters. The shallow depth-distribution zone was characterized mainly by the disturbance due to WLF. As regards the surface sediment diatom assemblages (Angeli & Cantonati, 2005), diversity was found to be higher in the upper part of the depth gradient where WLF have the strongest influence. Among the periphyton community the most likely assemblage to be affected by low lake levels are the epiphytic forms attached to plants. In addition, in freshwater lakes, fluctuations of the water level could be a steering factor determining the habitats of diatom assemblages in the lake (Punning & Puusepp, 2007). WLF also affect phytoplankton development (abundance, biomass, size structure, taxonomic composition, species diversity and rate of community compositional change) (de Emiliani, 1997; Noges & Laugaste, 1998; Coops & Hosper, 2002; de Domitrovic, 2003; Kangur et al., 2003; Stockner et al., 2005).

Studies on fauna included both aquatic fauna and terrestrial species. In general, these impacts were very subtle, and not connected directly with the level change, but rather indirectly. Direct effects on invertebrates (Aroviita & Hämäläinen, Baumgärtner et al., Muskó et al., Werner & Rothhaupt, this volume) and zooplankton (Mageed & Heikal, 2006) include changes in the structure and dynamics of taxa that cannot withstand dry periods which subsequently lead to a limiting of their distribution by low water levels (Rossa & Bonecker, 2003; Bowers & De Szalay, 2004, 2005). Indirect effects are generally through alteration of habitats (e.g. substrate composition, periphyton growth, resuspension versus sedimentation). Particularly important are those habitats with cobbles and macrophytes (Brauns et al., this volume) that provide an extensive suitable habitat for periphytic algae which are their major food source, egg-laying and tube building, and also provide a refuge from predation (Scheifhacken et al., 2007). However, different zooplankton groups seem to show different sensibility to WLF and are distinctly affected by floods (Ortega-Mayagoitia et al., 2000). Fortunately, most macroinvertebrate species can survive complete desiccation for periods of at least 1 month (Leslie et al., 1997).

The mobility of fish might lead to the conclusion that WLF are likely to have only minimal direct effects in most cases. However, fish uses littoral habitats temporarily and this use may be impeded by untimely drought events. Changes in the water level can have potentially important direct environmental effects for eulittoral benthic fish communities (Sutela & Vehanen, this volume) which include loss of suitable spawning habitat (Auer et al. 1982; Gafny et al., 1992) and shelter availability around the lake edge (Fischer & Ohl, 2005) by low lake levels. Large lake-level variations can determine the depth distribution of macrophytes, and hence having indirect effect on fish communities (Rowe et al., 2003), and even may have a significant influence on substance levels in fishes (Sorensen et al., 2005). Mean mercury concentrations in young-of-the-year (YOY) yellow perch at different sampling location varied significantly from year-to-year showing a strong positive correlation with WLF and providing strong evidence that some variable or process affecting mercury bioaccumulation is influenced by water-level dynamics (Sorensen et al., 2005).

The impact of WLF on bird life is generally mediated through impacts on macrophytes and shallow habitats, which provide feeding and nesting grounds, and refuge from predators. Magnitude and frequency of water-level change during the nesting season can adversely impact reproductive success of many wetland bird species (Hake et al., 2005; Desgranges et al., 2006). High levels during the breeding season could lower reproductive success as nests and feeding areas are flooded.

Ecosystem effects

This category includes papers that describe ecosystem effects from changes in water levels. The biological effects of WLF in lakes are greatest in shallow water and littoral areas, where even small changes in water levels can result in the conversion of a standing-water environment to an environment in which sediments are exposed to the air, or vice versa. The patterns of water-level change are the driving force that determine the overall diversity and condition of wetland plant communities and the habitats they provide for a multitude of invertebrates, amphibians, reptiles, fish, birds and mammals. The role of WLF has been studied in diverse habitats, but central to most of these studies are the relationships among nutrients, trophic web and variations of the water level at very different timescales (daily, seasonal and multi-annual, compare Hofmann et al. and Wantzen et al., this volume).

Long-term water-level studies in wetlands in the prairie pothole region of North America and proxy data (e.g. tree rings) for water levels in this region indicate that oscillatory WLF around a long-term mean have occurred for thousands of years (van der Valk, 2005). Field studies indicate that two kinds of vegetation change are common during wet–dry cycles: fluctuations and successions. Fluctuations are changes in the relative abundance of species between the wet and dry phases of the cycles. Successions are changes in species composition. Experimental studies at the ecosystem- and species-level have confirmed observations made during field studies of semi-permanent wetlands, e.g. that water depth tolerance is the primary determinant of distribution of emergent species. Repeated drying and rewetting events in wetlands can, in addition, cause substantial release of phosphate by chemical changes and activation of P-mineralizing enzyme, which may last even when the water table is returned to the original level (Song et al., 2007). Under these circumstances, a general understanding of how aquatic vegetation responds to WLF is needed to guide restoration of wetlands because inter-annual and seasonal variations often confound effects of costly remedial actions (Chow-Fraser, 2005).

WLF are among the major driving forces for shallow lake ecosystems and play an important role on the structure and function of these ecosystems (Coops et al., 2003). In the low-lying parts of the Netherlands, the water-level regime of lakes is strictly regulated. This is needed for reducing risks of flooding and economic purposes, including maximum agricultural benefit, but fixation of water levels has had a severe impact on the functioning of (semi-)aquatic ecosystems. Coops & Hosper (2002) reviewed the benefits of natural WLF, considering the impacts on nutrient inputs, nutrient concentrations, phytoplankton development and turbidity. Into the context of multiple use of lakes, the need for ecologically based water-level regimes is stressed, which are likely to lead to enhancement of water quality and biodiversity (compare Keto et al., this volume).

Shallow lakes have become the archetypical example of ecosystems with alternative stable states (Scheffer & van Ness, 2007). Fluctuation of environmental conditions may affect the stability of lakes and extreme water levels may cause shifts between the turbid and the clear, macrophyte-dominated state (Beklioglu et al., 2007). High water levels may lead to loss of submerged macrophytes, causing a shift to a turbid state (Engel & Nichols, 1994). Low water levels may invoke desiccation and freezing of the lake bottom and, in some cases, damage the vegetation sufficiently to push a lake to a turbid state (Blindow et al., 1993). An opposite effect of low-water extremes can also take place because of the higher risk of fish kills due to anoxic conditions in summer or winter, leading to clear water conditions that promote subsequent vegetation dominance (Van Geest et al., 2003). However, lakes of the northern Great Plains may be resilient to severe winter conditions, possibly because of the recruitment of fish from regional metapopulations during summer (McGowan et al., 2005). Lake-level fluctuations are common in the North American Great Plains region, where large-scale climate systems (El Nino, the Pacific Decadal Oscillation) and periodic droughts cause substantial hydrologic variability in both summer and winter. Lower water levels during winter are likely to promote the buffer mechanisms that reinforce a macrophyte-rich, clear-water state in shallow prairie lakes. Predicting how WLF will impact trophic state variables among a population of lakes will be difficult, if not impossible, and any accurate predictions will have to be made after first examining several mechanisms within individual lake systems, as there might not be an overall relation between trophic state variables and lake-level fluctuation (Hoyer et al., 2005). However, individual lakes show direct, inverse, or no significant relations between lake trophic state variables and water-level fluctuation, regardless of the magnitude of WLF.

Current paradigms of reservoir ontogeny suggest that WLF may increase sedimentary nutrient release, causing long-term eutrophication of water bodies formed by dryland flooding. Less is known of the changes in nutrient status following conversion of natural lakes into reservoirs. Hambright et al. (2004) used historical hydrological and limnological data, and paleolimnological records of sedimentary P accumulation to evaluate changes in nutrient storage in Lake Kinneret, Israel since 1860. Impoundment in 1932 increased WLF and altered seasonal hydrologic patterns in the lake. Geochemical analysis of sediment deposits indicated that hydrologic management of natural lakes have increased sedimentary nutrient flux under circumstances where lake volume and water levels become more variable. Water level appears to be a significant factor affecting the content of dissolved inorganic nutrients. Large inter-annual WLF will decrease stability of the ecosystem (Kangur et al., 2003). Although man-made changes and natural environmental changes were significant, it has been suggested that the Lake Kinneret ecosystem did not deviate from the level of resilient fluctuations (Gophen, 2000).

Research opportunities

Studies on WLF are to awake a considerable interest in Europe, or at least they should, as the EU Water Framework Directive (WFD, 2000/60/EC) is a major issue. In Europe, with a lake population of c. 500,000 natural lakes, lakeshore habitats and the associated wetlands are of great importance to the total biodiversity of European landscapes (Schmieder, 2004). For the first time, on a European scale, the WFD provides the frame for the assessment and monitoring of the ecological status of lakes. The WFD focuses on entire surface water bodies, including their associated wetlands under influence of their natural WLF. However, for a successful application of such integrated assessment, the provided set of quality elements has to be adapted for an approach specific to lake shores.

Strong effects of anthropogenic changes in the fluctuation of water levels have been shown for Mediterranean (e.g. Greece, Turkey, Israel) and north temperate and Nordic (The Netherlands, Finland) regions. In addition, climate change will most likely affect lakes hydrology through its effect on water-levels and ground-water systems. According to model predictions, hydrological extreme events due to climate change will be more frequent and different regional scenarios are anticipated. While global climate models predict more winter rainfall in temperate regions, the opposite is predicted for Mediterranean regions due to a scarcity of rain precipitation and higher temperatures. In either case the effects of global climatic changes on lake levels would be ecologically significant. Altogether, global climate change and increasing human demands for water may alter normal hydrological cycles, with implications for water quality and ecosystem services. Deep knowledge of lakes hydrological regimes and scientifically based predictions of possible changes in its level, taking into account variability in climate and future climate change, are, therefore, required (Coops et al., 2003).

Moreover, lakes are complex ecosystems composed of distinct habitats coupled by biological, physical and chemical processes. While the ecological and evolutionary characteristics of aquatic organisms reflect habitat coupling in lakes, studies on WLF have largely focused on pelagic, benthic and littoral habitats in isolation from each other. Habitat coupling has important consequences for nutrient cycling, predator–prey interactions, and food web structure and stability (Schindler & Scheuerell, 2002).

Since many WLF impacts will take years to manifest, the assessment of such impacts should cover a long enough period of time. Lake monitoring at a series of adequately representative scales, is essential for an objective assessment of the environmental impacts associated with the fluctuation of lake levels. However, long-term monitoring data series are valuable resources but rarely extend back for a period long enough, and even where they do exist there is often a problem of data comparability due to these changing methodologies and analysts. In the case of lake ecosystems, one of the best ways to obtain long-term data is the paleolimnological method (Battarbee, 1999). Paleolimnological methods for defining baselines and restoration targets and identifying causes of change are already well established, and have been extensively illustrated in different reviews (e.g. Smol, 2002). Several studies have been successful in investigating water-level variations in small temperate lakes (Yang & Duthie, 1995; Dearing, 1997; Hannon & Gaillard, 1997), and recent studies in paleolimnology (e.g. Punning & Leeben, 2003) successfully compared long-term limnological monitoring data (from 1971 to 2001) with sediment core record showing that the quantitative and qualitative analyses enable to describe sedimentological processes and distinguish the water-level changes on the recent sediment. However, also the results of the present bibliography work show that the potential of paleolimnology for the study of the long-term effects of WLF and to determine pre-disturbance conditions in systems affected by anthropogenically enhanced WLF is still largely underexploited. A before-after, control-impact paleolimnological study is being carried out (Serieyssol C.A., personal commun.) in dammed lakes in the Voyageurs National Park, Minnesota, USA. A paleolimnological approach has also been adopted to assess the effect of human-induced WLF on high altitude lakes in the Adamello-Brenta Natural Park (Northern Italy). The natural water levels of a number of lakes have been altered and artificially manipulated for almost half a century by a series of dams built to serve the water supply and hydro-electric industry. However, using lakes in these ways has altered lakeshores through artificially manipulating lake levels and recent deregulation has prompted the feasibility of restoring these lakes to their original shore-line status. A recent study of the subfossil diatom content in the sediments of two of these Alpine lakes (Garzonè and Serodoli) has revealed the historical effects of man-induced changes on the lake levels during the last decades. Variations in sediment composition and downcore diatom communities in the lakes could be explained by changes in the lakes water-level (Leira, unpublished). Nevertheless, these techniques might still require refinement and tailoring in order to be fit specifically for this kind of studies and undisturbed paleolimnological time series are scarce in shallow lakes and wetlands.

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