

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

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**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.

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Ecological Effects of Water-Level Fluctuations in Lakes

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## 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

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 sub-continental features of the climate will get more prominent. This will cause dramatic changes in regional hydrological budgets, with associated consequences for agriculture, forestry and water management (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 draw-down 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- $\mu$ m 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  $\mu$ m). 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 <sup>2</sup> )	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- $\mu$ m 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<sup>2</sup>, 250  $\mu$ m 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, SPSS 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, Glendon 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, SPSS Inc., Chicago) using Bonferroni correction to adjust the level of significance of the pairwise comparisons.

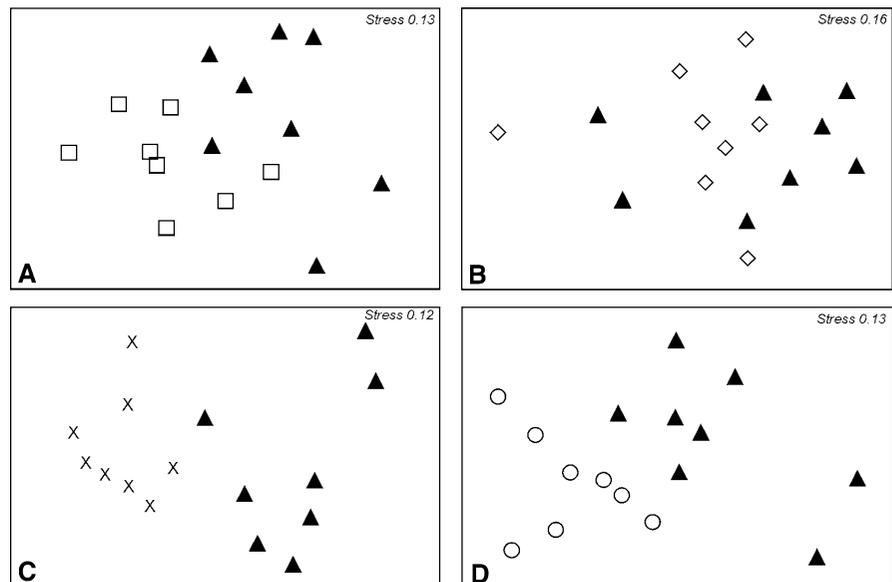
## Results

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 *Haliphus 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 draw-down 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						
<i>Gyraulus crista</i>				46*		
<i>Valvata piscinalis</i>				48*		
Bivalvia						
<i>Pisidium casertanum</i>				88***		
<i>P. henslowanum</i>				75***		
<i>P. moitessierianum</i>				38*		
<i>P. nitidum</i>				100***		
<i>P. subtruncatum</i>				50**		
<i>P. supinum</i>				50**		
<i>Unio tumidus</i>				63***		
Ephemeroptera						
<i>Caenis horaria</i>				61*		
Odonata						
<i>Ischnura elegans</i>	69***					
Heteroptera						
<i>Micronecta</i> sp.				79***		
Coleoptera						
<i>Cercyon</i> sp.	32*					
<i>Dryops</i> sp. larvae	33*					
<i>Haliplus flavicollis</i>	46*					
<i>Orectochilus villosus</i> larvae			43*			
Trichoptera						
<i>Goera pilosa</i>					46*	
<i>Lype phaeopa</i>			67**			
<i>Molanna angustata</i>				43**		
<i>Tinodes waeneri</i>					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.

## References

- ATV-DVWK (ed.), 2003. Anthropogene Einflüsse auf Niedrigwasserabflüsse. 1–85.
- Black, A. R., G. W. Barlow & A. T. Scholz, 2003. Carbon and nitrogen stable isotope assessment of the Lake Roosevelt aquatic food web. *Northwest Science* 77: 1–11.
- Czachorowski, S., 1989. Vertical distribution of Trichoptera in three Masurian lakes—Results of preliminary studies. *Polskie Archiwum Hydrobiologii* 36: 351–358.
- Czachorowski, S., 1993. Distribution of Trichoptera larvae in vertical profile of lakes. *Polskie Archiwum Hydrobiologii* 40: 139–163.
- Devin, S., C. Piscart, J. N. Beisel & J. C. Moreteau, 2003. Ecological traits of the amphipod invader *Dikerogammarus villosus* on a mesohabitat scale. *Archiv für Hydrobiologie* 158: 43–56.
- Dufrene, M. & P. Legendre, 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.
- Hill, N. M., P. A. Keddy & I. C. Wisheu, 1998. A hydrological model for predicting the effects of dams on the shoreline vegetation of lakes and reservoirs. *Environmental Management* 22: 723–736.
- Hynes, H. B. N., 1961. The effect of water-level fluctuations on littoral fauna. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 14: 652–656.
- Intergovernmental Panel on Climate Change, 2001. Climate change 2000, Summary for policy makers.
- Koskenniemi, E., 1994. Colonization, succession and environmental conditions of the macrozoobenthos in a regulated, polyhumic reservoir, Western Finland. *Internationale Revue der Gesamten Hydrobiologie* 79: 521–555.
- Lenat, D. R. & V. H. Resh, 2001. Taxonomy and stream ecology—The benefits of genus- and species-level identifications. *Journal of the North American Benthological Society* 20: 287–298.
- Ostendorp, W., C. Iseli, M. Krauss, P. Krumscheid-Plankert, J. L. Moret, M. Rollier & F. Schanz, 1995. Lake shore deterioration, reed management and bank restoration in some central-European lakes. *Ecological Engineering* 5: 51–75.
- Palomaki, R. & E. Koskenniemi, 1993. Effects of bottom freezing on macrozoobenthos in the regulated Lake Pyhäjärvi. *Archiv für Hydrobiologie* 128: 73–90.
- Palomaki, R., 1994. Response by macrozoobenthos biomass to water-level regulation in some Finnish lake littoral zones. *Hydrobiologia* 286: 17–26.
- PIC (Potsdam Institute for Climate Impact Research), 2003. Studie zur klimatischen Entwicklung im Land Brandenburg bis 2055 und deren Auswirkungen auf den Wasserhaushalt,

- die Forst- und Landwirtschaft sowie die Ableitung erster Perspektiven. 1–77.
- Schmedtje, U. & M. Colling, 1996. Ökologische Typisierung der aquatischen Makrofauna. Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft 4: 1–548.
- Smith, B. D., P. S. Maitland & S. M. Pennock, 1987. A comparative study of water level regimes and littoral benthic communities in Scottish Lochs. *Biological Conservation* 39: 291–316.
- Vadeboncoeur, Y., E. Jeppesen, M. J. Vander Zanden, H. H. Schierup, K. Christoffersen & D. M. Lodge, 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. *Limnology and Oceanography* 48: 1408–1418.
- Van den Brink, F. W. B., G. van der Velde & A. bij de Vaate, 1993. Ecological aspects, explosive range extension and impact of a mass invader, *Corophium curvispinum* Sars, 1895 (Crustacea: Amphipoda), in the Lower Rhine (The Netherlands). *Oecologia* 93: 224–232.
- Wilcox, D. A. & J. E. Meeker, 1991. Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota. *Canadian Journal of Botany* 69: 1542–1551.
- Wilcox, D. A. & J. E. Meeker, 1992. Implications for faunal habitat related to altered macrophyte structure in regulated lakes in Northern Minnesota. *Wetlands* 12: 192–203.