

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

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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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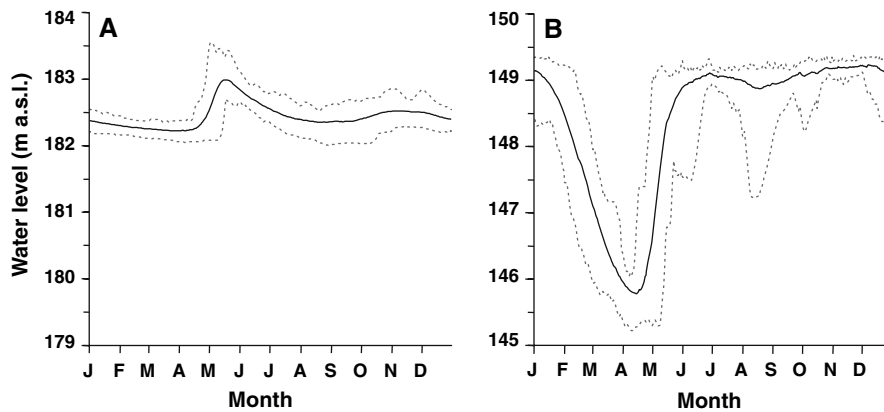


Fig. 1 Examples of annual water-level fluctuation in (a) an unregulated reference lake (Lake Änättijärvi, mean wintertime fall in water level 0.32 m) and (b) a regulated lake (Lake Iso-Pyhäntä, mean wintertime fall in water level 3.50 m). The solid

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

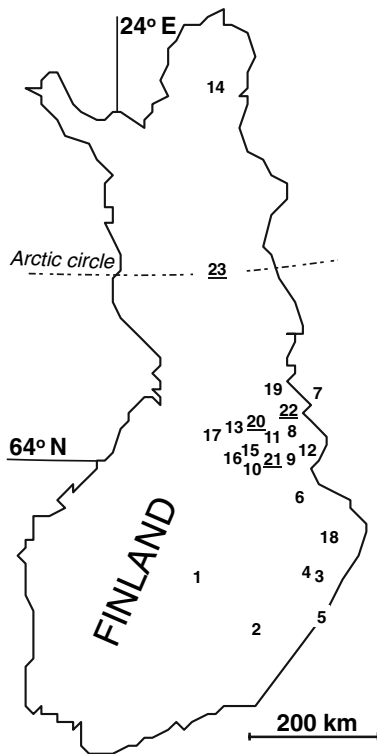


Fig. 2 Map showing location of the study lakes. For lake numbers, see Table 1. The numbers of the most heavily regulated lakes (wintertime fall in water level >3 m) are underlined

(one in Russia) between $61^{\circ}44'–68^{\circ}56'$ N and $26^{\circ}33'–30^{\circ}44'$ E (Fig. 2). The lakes represent medium to large sizes (lake surface area 11–1040 km²) 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 $\mu\text{g l}^{-1}$. 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 cm²) 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 dipteran 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.)	MDE (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	Kuitijärvi ^{2, f}	na*	198	ca 100	9.6	2.5	6.7	2.8	3.5	11	268	40
8	Änätijärvi	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, <i>n</i> = 6)	0.40	34	164	6.3	2.4	6.6	2.2	4.6	12	327	68
	Mean (lower, <i>n</i> = 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, <i>n</i> = 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 (µg l ⁻¹)	TP (µg l ⁻¹)	TN (µg l ⁻¹)	COL (mg Pt l ⁻¹)
Mean (lower, <i>n</i> = 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: ¹only from upper stony littoral, ²only from lower soft bottom littoral, ³Hynynen et al. (1997); ⁴Liljaniemi (1998); ⁵Tolonen et al. (2001), ⁶Virnes (2005) Tolonen et al. (2003); ⁷Aroviita et al. (2006), ⁸Särkkä (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:

$$INDVAL_{ij} = A_{ij} \times B_{ij} \times 100 \quad (1)$$

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

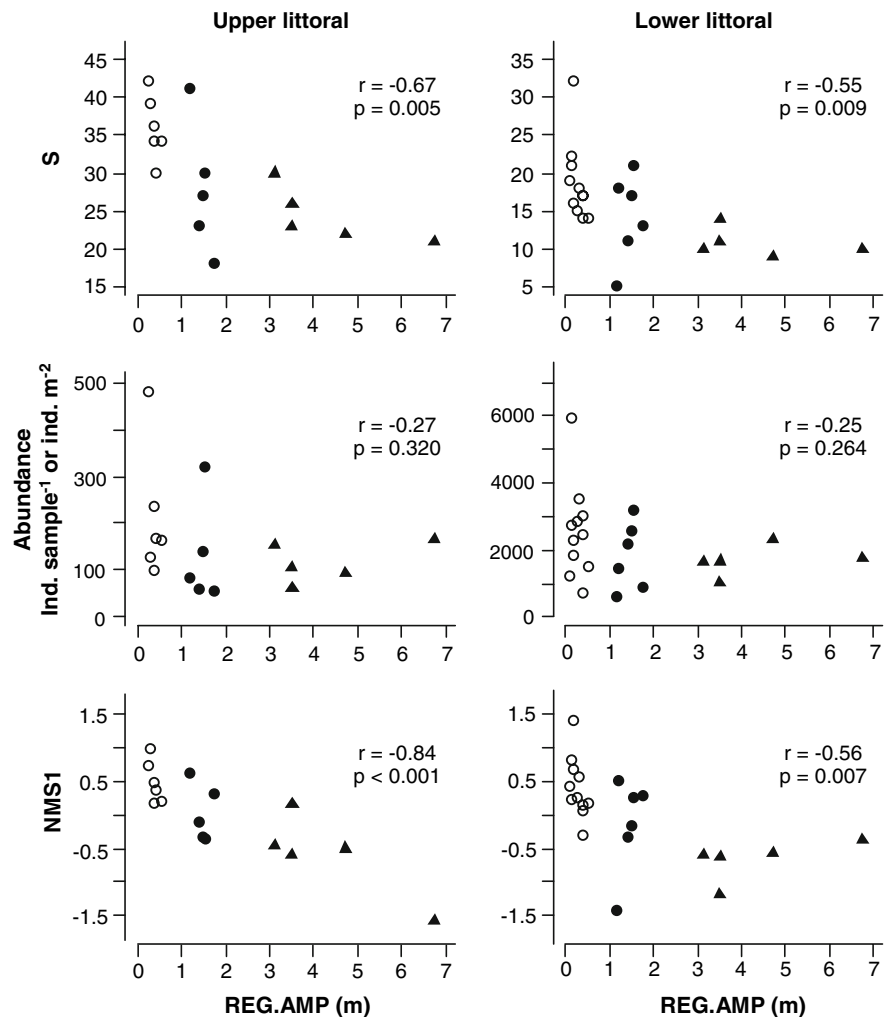


Table 2 Comparison (mean, range and ANOVA statistics) of macroinvertebrate taxon richness (S) and abundance (ABU) among the lake groups within the upper and lower littoral habitat

	Unregulated reference lakes	Regulated lakes		ANOVA	
		REG.AMP < 3 m	REG.AMP > 3 m	F	P
Upper littoral					
<i>n</i>	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					
<i>n</i>	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.

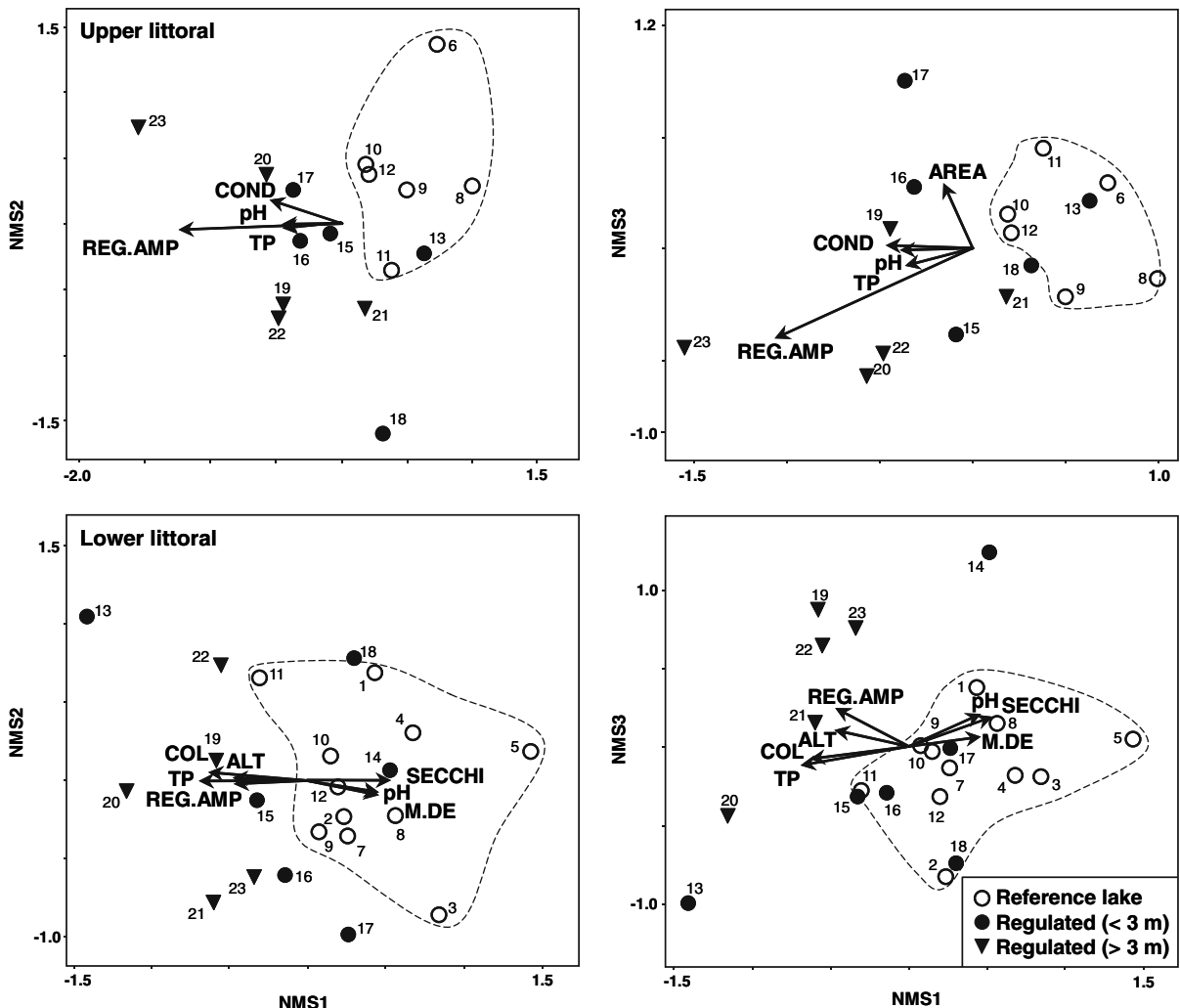


Fig. 4 Distribution of the study lakes in a three-dimensional (NMS1, NMS2 and NMS3) ordination space based on log-transformed macroinvertebrate abundance data from upper (final stress value = 7.61) and lower (final stress value = 14.47) littoral zones from unregulated reference (open symbols) and

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

drawdown limit) where organic matter tends to accumulate (Grimås, 1961; Tikkanen et al., 1989; Palomäki & Koskeniemi, 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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