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Effects of lake water level regulation on the dynamics of littoral vegetation in northern Finland

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Abstract

The effects of water level regulation on the dynamics of littoral vegetation were studied in regulated Lake Ontojärvi and unregulated Lake Lentua in northern Finland by using permanent plots. The study was carried out during 1984–1988 and the abundance of plant species was measured yearly. The annual changes were measured by comparing the mean dissimilarities (D_m) in species abundance and the diversity (mean number of species, N_{sm}) between the different research years in the same square. The mean dissimilarities in Lake Ontojärvi and Lake Lentua were 0.238 and 0.297, respectively. The difference between the lakes was not significant. The effect of the increased ecological stress was observed on the littoral zone; the number of species was lower in Lake Ontojärvi than in Lake Lentua. In Lake Ontojärvi, the area of almost permanent submersion (sublittoral) showed higher dissimilarity (D_m) and lower diversity (N_{sm}) values compared to Lake Lentua. The vegetation in both lakes was well adapted to the disturbance caused by waves and penetrating ice. The diversity and D_m values were lower on the exposed shores in both lakes compared to sheltered shores. The peaty bottoms were the most stable environment, whereas the muddy bottoms were unstable in our research lakes. Generally speaking the vegetation in Lake Ontojärvi is equally stable as in Lake Lentua. Both diversity and dissimilarity values were slightly higher in Lake Lentua. The vegetation in regulated Lake Ontojärvi is well adapted to the ecological disturbance caused by the fluctuating water level.

Introduction

About 10% (33 522 km^2) of the total area of Finland is covered by lakes. Over one third of this area (11 900 km^2) is regulated, mainly for hydroelectric purposes. The regulation is usually achieved by raising the water level during the summer (0.5–3.5 m) and lowering the winter minimum by 2–7 m. During the first few years of regulation, the littoral area is subject to considerable erosion, depending among other things on the regulation height, exposure, steepness, quality of sediment and on the rate of water level uplift (Alasaarela et al., 1989). At the same time, the changes in vegetation are obvious, including a decrease of former macrophytic vegetation, as reported in several Scandinavian lakes (Nilsson, 1981; Rørslett, 1985a). The new vegetation on eroded shores consists of disturbance-tolerant species (e.g., *Ranunculus reptans*, *Eleocharis acicularis*) adapted to the altered ecological environment (e.g., Murphy et al., 1990), which is under succession for several decades (Koskenniemi, 1987; Nilsson & Keddy, 1990). The effects of lake water level regulation has been under intensive research from the beginning of eighties (e.g., Alasaarela et al., 1989), but the reports dealing with littoral vegetation are rare and published mainly in Finnish (e.g., Granberg & Hakkari, 1980; Hellsten & Joronen, 1984; Hellsten et al., 1989). This paper concentrates on describing the dynamics of littoral vegetation during a four-year study using permanent plots, while other part of the study assesses the general ecological environment and macrophytes in regulated lakes.

Table 1. Species composition, frequency (%) and abundance (%) observed at permanent plots of research lakes.

	ONTOJÄRVI		LENTUA	
	Freq. %.	Abun. %	Freq. %.	Abun. %
Agrostis canina L.	0.6	8.0	0.5	8.0
Agrostis capillaris L			3.0	12.0
Alisma plantago-aquatica L.	5.6	4.9	0.5	4.0
Alnus incana (L.) Moench			5.1	4.4
Alopecurus aequalis Sobol.	9.9	11.8	3.5	8.6
Andromeda polifolia L.			2.0	12.0
Aulacomnium palustre (Hedw.) Schwaegr.			0.5	8.0
Betula pubescens Ehrh.	0.6	8.0	0.5	8.0
Bryidae spp.	2.5	11.0	6.6	22.8
Bryum sp.	1.9	6.7	0.5	4.0
Calamagrostis sp.			1.0	32.0
Calliergon cordifolium (Hedw.) Kindb.	1.9	32.0	2.5	41.6
Calliergon megalophyllum Mikut.	1.9	18.7	0.5	24.0
Calliergon sp.	3.1	14.4	3.5	30.3
Callitriche palustris L.	8.1	38.6	2.5	44.4
Callitriche sp.	5.6	10.7	1.0	16.0
Calluna vulgaris (L.) Hull			4.0	62.0
Carex acuta L.			5.1	39.6
Carex lasiocarpa Ehrh.			6.6	54.5
Carex nigra subsp. *juncella* (Fries) Lemke			4.0	19.0
Carex nigra subsp. nigra (L.) Reichard			5.1	43.6
Carex panicea L.	1.9	20.0	1.0	16.0
Carex rostrata Stokes	8.7	52.0	8.6	28.5
Carex serotina Merat			1.5	25.3
Carex sp.			1.0	8.0
Climacium dendroides (Hedw.) Web. & Mohr	1.2	6.0	1.5	9.3
Drepanocladus sp.	18.6	43.3	13.1	30.6
Drosera anglica Hudson			2.5	69.6
Elatine hydropiper L.	2.5	28.0	2.5	24.0
Eleocharis acicularis (L.) Roemer & Schultes	29.8	62.3	17.7	64.0
Eleocharis palustris (L.) Roemer & Schultes	7.5	53.7	12.6	69.9
Equisetum fluviatile L.	8.7	67.4	10.1	32.6
Hieracium umbellatum L.			4.0	9.5
Hypnum lindbergii Mitt.			1.5	22.7
Isoetes echinospora Durieu	16.8	18.8	20.7	37.7
Isoetes lacustris L.			21.2	69.4
Juncus alpinoarticulatus Chaix	4.4	8.0	6.1	32.7
Juncus bulbosus L.	1.2	6.0	1.0	6.0
Juncus filiformis L.	16.8	25.6	18.7	38.0
Juncus sp.	0.6	12.0		
Lobelia dortmanna L.			14.7	43.0
Lysimachia thyrsiflora L.			1.0	6.0
Lythrum salicaria L.			1.5	26.7
Marcanthia polymorpha L.	0.6	4.0	14.7	51.0
Mentha arvensis L.			5.6	19.3
Menyanthes trifoliata L.			1.5	49.3
Molinia caerulea (L.) Moench			16.7	40.3

Table 1. Continued

	ONTOJÄRVI		LENTUA	
	Freq. %.	Abun. %	Freq. %.	Abun. %
Pedicularis palustris L.			0.5	4.0
Phragmites australis (Cav.) Trin. ex Steudel	0.6	8.0	6.1	10.7
Pinus sylvestris L.	1.2	6.0	5.6	5.5
Pohlia sp.	4.4	53.1	2.0	70.0
Pohlia nutans (Hedw.) Lindb.			2.0	38.0
Polytrichum commune Hedw.			0.5	4.0
Polytrichastrum longisetum (Brid.) G. L. Sm.	2.5	57.0	2.0	72.0
Polytrichum sp.	0.6	44.0		
Potamogeton gramineus L.	3.7	32.7	1.0	38.0
Potentilla palustris (L.) Scop.	2.5	10.0	19.7	22.4
Ranunculus reptans L.	61.5	63.7	28.8	46.4
Sagittaria natans Pallas	5.0	49.0	2.5	51.2
Salix sp.			2.0	21.0
Scorpidium scorpidioides (Hedw.) Lindb.	0.6	72.0	1.5	11.7
Selaginella selaginoides (L.) Beauv. ex Schrank & Mart	0.6	4.0	0.5	4.0
Sparganium sp.	9.3	18.4	9.6	37.2
Sphagnum sp.	2.5	18.0	10.1	25.0
Subularia aquatica L.	23.6	29.4	18.2	22.8
Trientalis europaea L.			3.0	9.3
Vaccinium uliginosum L.			3.5	13.7
Vaccinium vitis-idaea L.			2.0	36.0
Veronica scutellata L.	0.6	4.0	2.0	38.0
Warnstofia trichophylla (Warnst.) Tuom. & T. Kop	4.4	60.0	2.5	80.0

Description of sites studied

The two research lakes are situated on the Oulujoki water course (Figure 1). Lentua is a large (90 km^2) non-regulated lake with a water level fluctuation typical of Finnish lakes (Figure 2). Ontojärvi (102 km^2) has been regulated for hydroelectric purposes since 1951 with a maximum amplitude of 4.4 m and an average amplitude for 1960–88 of ca 3.4 m (Figure 2). At the beginning of the regulation, the mean summer water level was raised by one meter. The duration of the ice cover in the research lakes is usually 7–8 months. Both lakes are meso-oligotrophic, but the lake water in Ontojärvi contains slightly more phosphorous and humic substances compared to Lentua.

Material and methods

The field data covered the species frequency and the abundance of aquatic macrophytes and bryophytes, which were sampled yearly from August till the beginning of October in 1984–88. The sampling quadrats (0.5 by 0.5 m) were marked permanently by steel rods in 16 ecologically different shore areas (Figure 1) selected according to the results of transects studies (Hellsten et al., 1989). The number of analysed quadrats varied yearly according to the following schema:

	1984	1985	1986	1987	1988
Ontojärvi	13	53	33	30	32
Lentua	9	58	53	35	43

The observations were done by setting a 0.25 m^2 steel frame divided into twenty-five 1 dm^2 wire mesh squares on the area bordered by rods. The quadrats situated under the water level were analysed by SCUBA diving with the same method. All the species growing below the highest water level were recorded. The abundance was calculated from the presence of each species at the different subsquares (0, 4, 8,...,100 %) and the frequency as a mean frequency of all observed quadrats. Only the quadrats with continuous time series were included in analysis. Bottom quality

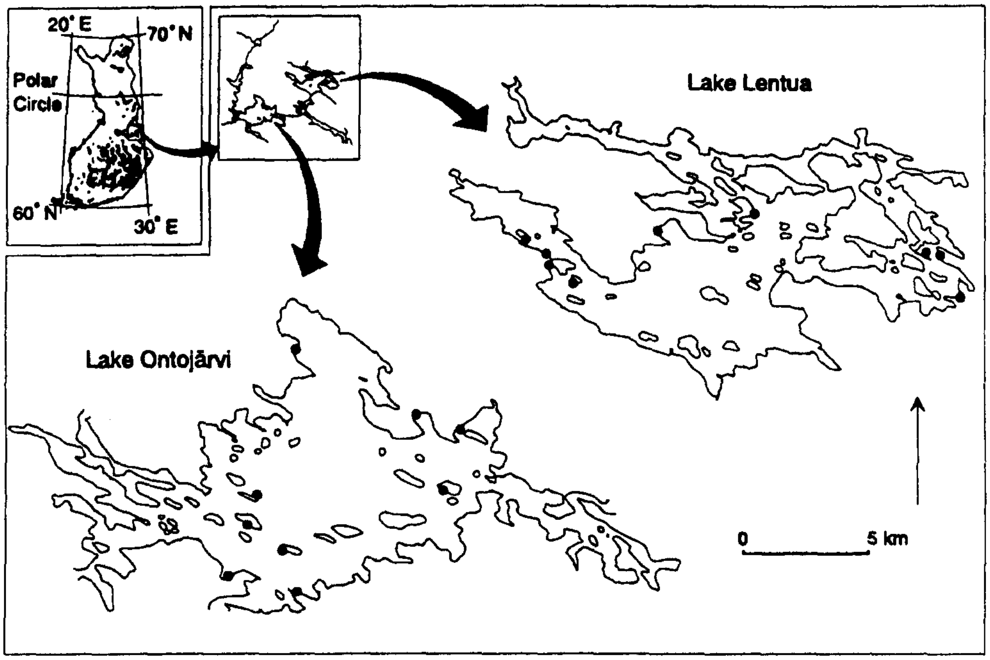

Figure 1. The location of Lake Ontojärvi and Lake Lentua in detail. Study sites indicated by filled circles.

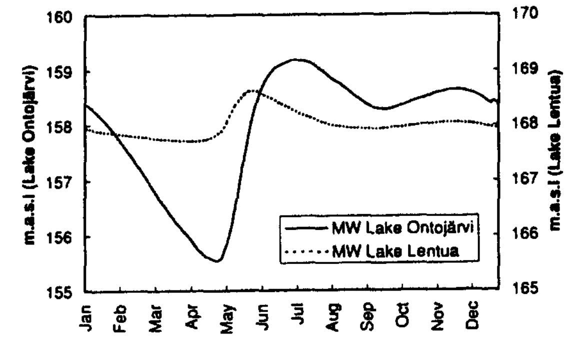

Figure 2. The mean water level (MW) calculated from the daily values during the years 1960–88.

of the quadrats was divided visually to four different classes (peat, sand, muddy sand and mud).

The water level data are obtained from the Hydrological Office (Figure 2). The vertical shore zonation was defined by the duration (d) of the water level during the iceless period (Hellsten et al., 1989). The eulittoral zone consisted of upper ($10\% < d \leq 25\%$), middle ($25\% < d \leq 50\%$) and lower eulittoral zones ($50\% < d \leq 75\%$). The sublittoral was divided to an upper ($75\% < d \leq 95\%$) and a lower zone ($d > \leq 95\%$). Effective fetch (L_f) was measured as proposed by Håkanson & Jansson (1983) and the shores were classified into open ($L_f > 1$ km) and sheltered (L_f 1 km) ones according to the Hellsten et al. (1989). The shores were also divided into steeply ($> 5\%$) and gently ($\leq 5\%$) sloping ones (Hellsten et al., 1989).

The annual changes in vegetation were measured by comparing the dissimilarities in species composition between the different research years at the same square. We used a calculation method modified from Nilsson & Keddy (1990):

$$D(x_1, x_2) = 1 - 1/2(W/A + W/B), \qquad (1)$$

where A is the sum of species abundances in sample x_1, B is the corresponding value for sample x_2, and W is the sum of the minimum abundance values of each species observed in sample x_1 or x_2. The values varied from 0 (no changes in species composition and abundances) to 1 (no same species between the two observations). The mean values of all the observations on a given quadrat were used as an indicator of dynamics (D_0 or D_1). Dissimilarity values were also calculated between the lakes ($D_{0/1}$). Total number (N_{sto} or N_{stl}) of observed species in same lake and mean number (N_{sm}) of observed species on a given quadrat were used as an indicator of diversity.

Results

The littoral vegetation of Ontojärvi consisted of small growing isoetids (*Subularia aquatica, Eleocharis acicularis, Ranunculus reptans*) with a few (*Juncus filiformis, Eleocharis palustris, Equisetum fluviatile*) helophyte species (Table 1). In Lentua large isoetids (*Isoetes lacustris, I. echinospora, Lobelia dortmanna*) were typical, although the small isoetids were also common (Table 1). Elodeides and nymphaeides were quite rare in both lakes. In Lentua the vegetation at the uppermost littoral was dominated by terrestrial species (e.g., *Carex* species, *Potentilla palustris*, bryophytes), while their number was low in Ontojärvi. During the research period the diversity at the littoral of Ontojärvi was lower with 27 vascular plant species and 14 bryophytes compared to Lentua with 51 vascular plants and 17 bryophytes (Table 1). The mean number of species observed per plot in Ontojärvi was 5.8 (n = 36), which was sligthly less compared to Lentua (7.1, n = 53). The difference was statistically insignificant (Mann-Whitney U-test, p = 0.051). The mean abundance of vegetation at analysed quadrats was 59% in Lentua and 58% in Ontojärvi.

There were no significant differences in the dissimilarity values (D) between the research lakes. The mean dissimilarity (D_m) between the first and last observation was 0.269 in Ontojärvi and 0.297 in Lentua, the difference was not statistically significant (t-test, p = 0.170). When the dissimilarity values were calculated as a total mean between all continuous observations, the values were 0.238 in Ontojärvi and 0.297 in Lentua, but still without statistical significance (t-test, p = 0.630). The year-to-year dissimilarities in Ontojärvi (D_o) and Lentua (D_l) fluctuated between 0.17 and 0.25 (Figure 3). The values were slighly higher in Lentua, except in the first observation period with low number of observations (Figure 3). Also the total number of species (N_{st}) was higher in Lentua (Figure 3). Different species composition is also seen as a dissimilarity value between the lakes ($D_{o/l}$), which varied from 0.4 to 0.68 during the research period (Figure 3).

On the eulittoral zone, where most of the water level fluctuation takes place, both the dissimilarity values (D_m) and the mean number of species (N_{sm}) were higher in Lentua (Figure 4). N_{sm} was 2.5 times higher in Lentua compared to Ontojärvi on the sublittoral, whereas the differences in the dissimilarity values were small (Figure 4). The mean dissimilarities (D_m) between the different water level fluctuation zones in one lake and between the different lakes were statistically insignificant. The mean number of species (N_{sm}) decreased faster with increasing depth in Ontojärvi compared to Lentua (Figure 4).

The mean number of species (N_{sm}) and dissimilarities (D_m) varied quite slightly between the different exposure classes (Figure 5); in both cases the values were higher in Lentua without any statistical significance. The effect of the shore inclination varied; in Lentua dissimilarity values were higher at steeply sloping shores, while in Ontojärvi gently sloping shores were more unstable (Figure 5). The mean number of species was higher at gently sloping shores of both lakes, but again without statistically significant differences (Figure 5).

The D_m – and N_{sm} – values varied in different bottom quality classes with same trend observed in other ecological variables; both were higher in Lentua with the exception of D_m-value of peaty bottom (Figure 6). At peaty bottom N_{sm}-values were higher and the dissimilarity values were lower compared to other bottoms. Muddy bottom observed only in Lentua was unstable environment with low D_m-value (0.6). Statistically the differences were insignificant.

Discussion

Our results showed that during the four decades of water level regulation the vegetation of Ontojärvi has achieved a high stability. A different species composition shows, that the vegetation has obviously changed, but has now reached a stable state. The diversity of vegetation was higher in Lentua, which led also to higher dissimilarity values in species-poor littoral communities. Grime (1979) also pointed out that species richness was lower in an area of high ecological stress and disturbance (see also Rørslett, 1989). Nilsson (1981) investigated heavily regulated reservoirs in northern Sweden and found quite high dissimilarity values among the shore vegetation (see also Nilsson & Keddy, 1990). Koskenniemi (1987) pointed out that there was no notable stabilisation of vegetation on the open shores of several Finnish humic reservoirs during a six-year study. In our research lakes, the yearly fluctuation of dissimilarities was quite unpredictable, and no clear differences between the years and the lakes were observed. The high stability of the vegetation in Ontojärvi could be seen as a result of a moderate, aged water level regulation, compared to unstable heavily regulated reservoirs in northern Sweden (cf. Nilsson, 1981).

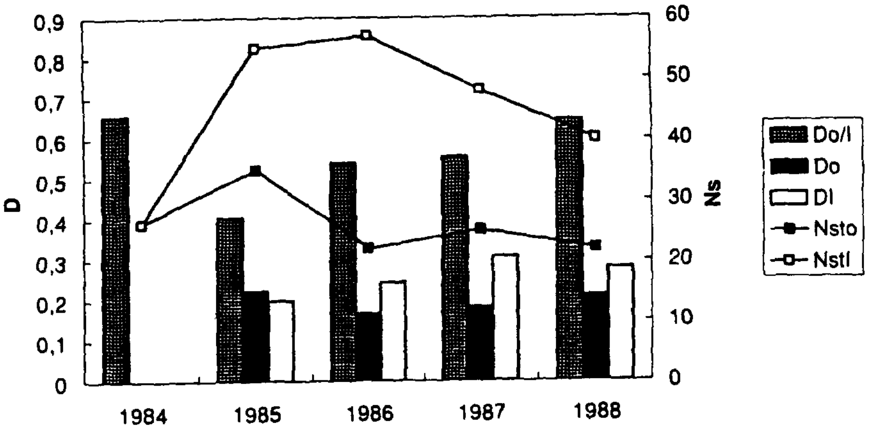

Figure 3. Dissimilarity values (D) and the number of species (Ns) during the research period. $D_{o/l}$ = yearly dissimilarity between Ontojärvi and Lentua, D_o, D_l = year-to-year dissimilarities in Ontojärvi and in Lentua, N_{sto}, N_{stl} = total number of species in Ontojärvi and Lentua.

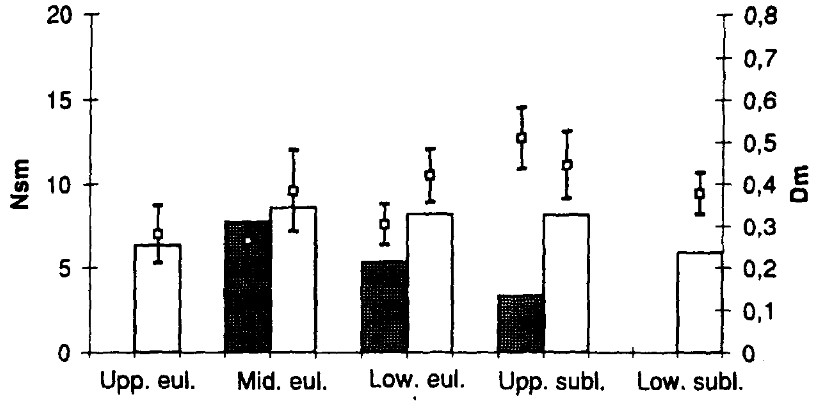

Figure 4. Mean number of species (N_{sm}) and mean dissimilarity (D_m) between the different water-level fluctuation zones. Symbols used: filled bars = N_{sm} in Lake Ontojärvi; white bars = N_{sm} in Lake Lentua; hi-low-lines = mean dissimilarity (D_m) with ±SE.

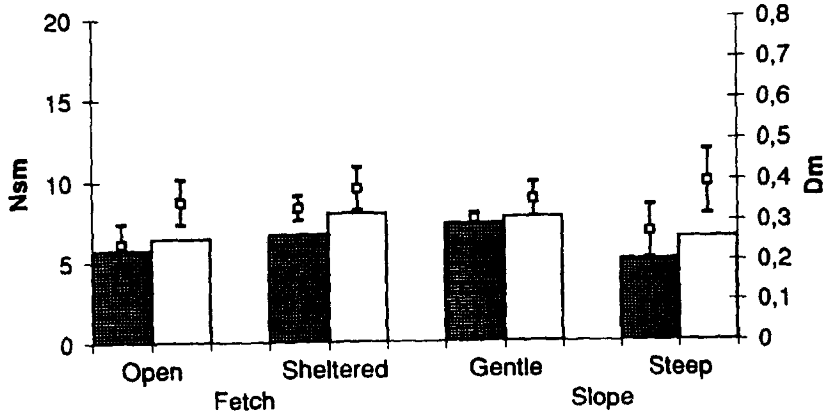

Figure 5. Mean number of species (N_{sm}) and mean dissimilarity (D_m) between the different exposure and inclination classes. Refer to Figure 4 for details.

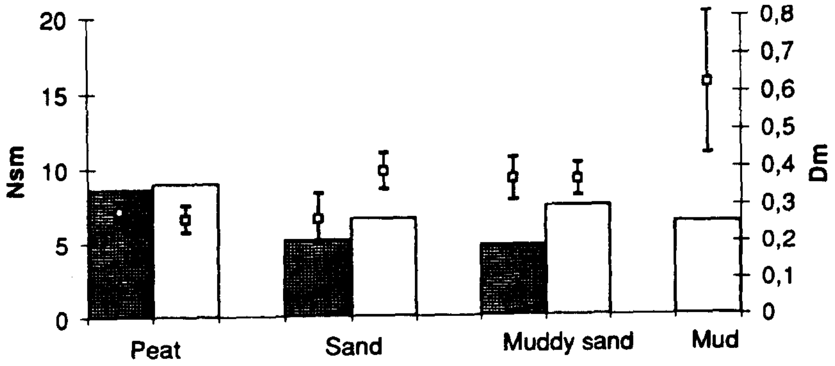

Figure 6. Mean number of species (N_{sm}) and mean dissimilarity (D_m) between the different bottom quality classes. Refer to Figure 4 for details.

The zonation of vegetation is mainly due to depth, but the range of water level fluctuation has an influence on width of the different zones (e.g., Hutchinson, 1975; Rørslett, 1985b). The dissimilarity values were higher on the eulittoral zone of Lentua compared to Ontojärvi; this Carex- dominated vegetation was rather stable in the driest part of the littoral and could probably be regarded as the most stable vegetation in Ontojärvi. In our research lakes, the water level is stable during the open water period, which tends to increase the stability of the vegetation. In the Swedish reservoirs the fluctuating water level during the summer affects negatively the abundance of vegetation (Nilsson & Keddy, 1990; Nilsson, 1981). Peat bottoms are also quite common on the eulittoral of sheltered shores, which increases the diversity and stability of vegetation as observed also by Nilsson (1981) and Koskenniemi (1987).

The littoral is also subject to penetrating ice during the winter. The vegetation in both lakes was well adapted to the disturbance of ice. In Ontojärvi the whole littoral was affected by ice, while in Lentua it affects only on the eulittoral (Hellsten et al., 1989). The effect of ice was also obvious on the sublittoral of Ontojärvi and caused slightly higher dissimilarity (D_m) and lower number of species (N_{sm}) compared to Lentua. The effects of ice on species composition and distribution of aquatic macrophytes are described in several studies (e.g., Erixon, 1981; Renman, 1986; Rørslett, 1985a) and they are clear also in our research lakes (Hellsten et al., 1989). The amphibious, short lived isoetids such as *Eleocharis acicularis*, *Subularia aquatica*, *Ranunculus reptans* and *Isoetes echinospora* have increased their distribution, whilst the long-lived isoetids *Isoetes lacustris* and *Lobelia dortmanna* have disappeared.

The sublittoral is usually quite a suitable environment for aquatic macrophytes. The positive relationship between macrophytes and sediment organic matter is also widely known (Duarte & Kalff, 1986; Wisheu & Keddy, 1989), but too soft sediments also limit the vegetation (Spence, 1982; Barko & Smart, 1983). In Lentua, the dissimilarity of vegetation is high at the area of muddy sediments. On the other hand, Rørslett (1985b) showed that the mortality of aquatic macrophytes was highest near the lowest limit of the macrophytes due to the reduced light intensity. In Ontojärvi, organic rich bottoms were situated in deeper areas due to the high rate of erosion, but the lower sublittoral was almost without vegetation due to reduced light penetration measured in studies of Hellsten et al., (1989).

Exposure affects the vegetation both directly through physical disturbance by waves and currents and indirectly by changes in sedimentation (e.g., Keddy, 1982). The diversity and D_m values on open shores were lower in both lakes compared to sheltered shores. It is generally believed that both the diversity and the abundance peak of vegetation occur on sheltered shores (Nilsson, 1981; Keddy, 1983). On the other hand, Rørslett (1987) pointed out in Lake Thyrifjord that exposure had no effect on floristic diversity, though its effects on the performance of the vegetation are clear. Nilsson & Keddy (1990) did not find any marked changes in the similarity values between weakly and moderately exposed shores. In our research lakes fewer species found on open shores are well adapted to the strong erosion.

Slope affects the organic matter content of the sediment (Håkanson & Jansson, 1983), and steep slopes are physically difficult places to be colonised by macrophytes. The effect of littoral slope was partly difficult to estimate. The diversity values were higher on gently sloping shores in both lakes as shown also by Duarte

& Kalff (1986), who found higher biomass and cover of macrophytes at gently sloping shores.

Conclusion

Littoral vegetation was relatively stable in both Ontojärvi and Lentua. The species observed in Ontojärvi were well adapted to the hostile ecological environment with several stress-tolerant and ruderal species, although the diversity was clearly lower. Surprisingly the dissimilarity was higher in Lentua, which could be related on higher diversity. The only remarkable exceptions were found at the sublittoral of Ontojärvi, where the effect of wave and ice-erosion caused higher dissimilarity with low number of species compared to Lentua.

From the viewpoint of lake management, the dissimilarity values observed at permanent plots do not alone give a true picture of the state of regulated lakes. Because vegetation is well adapted in a hard ecological environment, the often quite minimal yearly changes in species composition and abundance are rather difficult to analyse. On the other hand, research based on species composition and further to strategy analysis (e.g., Murphy et al., 1990) provides a better view of the state and succession of the lake ecosystem.

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