ENVIRONMENTAL FACTORS AND AQUATIC MACROPHYTES IN THE LITTORAL ZONE OF REGULATED LAKES

Causes, consequences and possibilities to alleviate harmful effects

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Abstract

Water level regulation for purposes of hydropower production has caused notable changes in the littoral zones of regulated lakes in northern Finland. Marked geomorphological changes have taken place in the lakes with a raised water level. Lowering of the ice cover during the winter has also caused rapid changes in the littoral. Changes in the environmental conditions and aquatic macrophyte communities were studied largely by comparing the regulated Lake Ontojärvi and the unregulated Lake Lentua in the Kainuu area. The general aims of the study were to analyse environmental effects, to produce information of ecological relationships for remedial measures on the littoral and to apply the restoration methods in the management of regulated lakes.

The most obvious effect of regulation was the expanded area of extending ice, which caused an almost complete disappearance of large ice-sensitive isoetids (*Isoetes lacustris* L., *Lobelia dortmanna* L.). These species were largely replaced by small erosion resistant isoetids (*Ranunculus reptans* L., *Eleocharis acicularis* (L.) Roem. & Schult.). Another significant change was the decreased frequency of large helophytes due to increased erosion. A model based on environmental factors was able to predict roughly the main vegetation types. Permanent plot studies showed no significant differences in the stability of the vegetation between the research lakes, which means that the species pool had adapted to the harsh environment.

Restoration techniques based on mechanical protection of shorelines and revegetation were applied to Lake Ontojärvi. The hostile environmental conditions caused a rapid decline of the planted species, but tall *Salix phylicifolia* L. seedlings and *Carex rostrata* Stokes were able to survive, although in low abundance. More significant remedial measures were provided by the Ecologically-based Regulation Practices (ERP), which have been applied to several lakes under hydropower production. This procedure, which was largely based on the results of the Kainuu studies, offers a simple way to illustrate the differences between various regulation practices. Two case studies showed that an exceptional year with extremely high or low water levels can largely abolish the positive succession achieved by ERP. The huge financial losses caused by ERP for hydropower production have also promoted the use of other conventional restoration measures.

Keywords: Northern Finland, water level fluctuation, vegetation, ice, erosion

To Katariina, Päivi, Tuuli, Ilkka and Meri

List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I Hellsten S. (1997) Environmental factors related to water level regulation - a comparative study in northern Finland. Boreal Env Res 2:345-367.

II Hellsten S. Effects of lake water level regulation on aquatic macrophyte stands and options to predict these impacts under different conditions. Submitted manuscript.

III Hellsten S & Riihimäki J (1996) Effects of lake water level regulation on the dynamics of aquatic macrophytes in northern Finland. Hydrobiologia 340: 85-92.

IV Hellsten S, Riihimäki J, Alasaarela E & Keränen R (1996) Experimental revegetation of regulated lake Ontojärvi in northern Finland. Hydrobiologia 340: 339-343.

V Hellsten S, Marttunen M, Palomäki R, Riihimäki J, & Alasaarela E (1996) Towards an ecologically based regulation practice in Finnish hydroelectric lakes. Regulated Rivers: Research & Management 12: 535-545.

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1 Introduction

Finland is a land of thousands of lakes; there are more than 187, 000 lakes with an area of more than 0.05 ha (Raatikainen & Kuusisto 1988). This amounts to a total area of 32,600 km^2, which is approximately 10% of the total area of Finland. In over one-third of this lake area (11,900 km^2, including nearly 220 lakes of > 1 km^2), water levels are regulated (Alasaarela *et al.* 1989a). In northern Finland, a larger proportion of lakes are regulated than in the other parts of the country, and the main objective of lake regulation in this region is to generate hydroelectric power, with an option for flood protection. In a typical northern regulation scheme, the water level is raised by 0.5 - 3.5 m in the summer and lowered by 2 - 7 m in the winter, whereas in southern Finland the water level in the open water period remains unchanged or is lowered (Alasaarela *et al.* 1989b, Marttunen & Hellsten 1997).

The littoral undergoes considerable geomorphologic changes during the initial stages of lake level regulation, especially if the water level is raised to increase the storage capacity of the lake (Sundborg 1977, Nilsson 1981a, Newbury & McCullough 1984, Mark 1987, Mark & Kirk 1987, Rørslett 1988a, Hellsten & Alasaarela 1984, Alasaarela *et al.* 1989b, Wilcox & Meeker 1991). This leads to major geomorphologic changes, including breakdown of the organic surface layer and erosion of minerogenic matter. The water level is usually lowered during the winter, when the need for electricity is greatest and the enhanced storage capacity for the spring flood is important. As a consequence, the ice layer may extend down to the bottom, causing the sediment to freeze and to be partly eroded by scouring (Nilsson 1981a, Erixon 1981, Rørslett 1985a, Palomäki & Koskenniemi 1993, I). As the water level is kept relatively low during the early spring, the spring flood is much lower than before and tends to shift towards the midsummer (Alasaarela *et al.* 1989a, Wilcox & Meeker 1992).

Aquatic macrophytes are an essential part of the productive zone in northern lakes (Pearsall 1920, Hutchinson 1975, Spence 1982). The littoral vegetation provides a living habitat for benthic fauna and zooplankton and a feeding area for fish (e.g. Tikkanen *et al.* 1988, 1989, Wilcox & Meeker 1992). Moreover, it serves a spawning ground for several fish species and is also a favourable habitat for fish fry (e.g. Huusko *et al.* 1988, 1989, Wilcox & Meeker 1992). Alterations in the structure of the vegetation tend to bring about dramatic changes in their living conditions, leading to a decrease in the production of zooplankton (e.g. Lindström 1973, Selin & Hakkari 1982, Huusko *et al.* 1988), benthic fauna (e.g. Grimås 1961, 1962, Palomäki 1994) and spring spawning fishes (e.g. Gaboury & Patalas 1984, Huusko *et al.* 1989, Wilcox & Meeker 1992). The littoral vegetation, especially emergent plants, is also a main component of the shore landscape. If it disappears due to water level regulation, the lake becomes less attractive for recreation. On the other hand, the excessively dense vegetation often stimulated by the lowered summertime water level hinders the use of the shoreline, which can be considered a negative impact (e.g. Pieterse & Murphy 1990). In this context, it should also be taken into consideration that the littoral vegetation protects the shoreline against erosion by waves and currents (Foote & Kadlec 1988, Raspopov *et al.* 1988, Coops *et al.* 1991, 1994, Keränen *et al.* 1992, Juntura *et al.* 1999).

A majority of the changes in the littoral zone of regulated lakes result from changes in water level fluctuation. These erosional processes affect directly the littoral zone, causing destruction of vegetation and affecting the successional status of vegetation, as reported in several Scandinavian lakes (Nilsson 1981a, 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 1988). On the other hand, the disappearance of large isoetids due to the increased effect of ice has been reported in several cases (Quennerstedt 1958, Rørslett 1984, 1985a,b, 1987b,c, 1988b, 1989, Renman 1989, Rintanen 1996). The effects of water level regulation are also related to water quality. When the water is transparent, the negative effects of a fluctuating water level are less severe, due to the wider productive zone, than in the case of turbid water (Rørslett 1988a, Alasaarela *et al.* 1989a, Palomäki 1994). The effects of water level regulation on lakes have been under intensive research in Finland since the early 1980s (Alasaarela 1988, Alasaarela *et al.*1989a). However, reports dealing with littoral vegetation are rare, and most of them have been published in Finnish (Granberg & Hakkari 1980, Granberg & Ruohonen 1985, Hellsten & Joronen 1986, Hellsten *et al.* 1989).

The main objectives of the present study were:

1. to identify and describe the relationships between aquatic macrophytes and the environmental factors affecting the littoral zone of a lake following regulation (I, II),
2. to develop a preliminary model in order to estimate the effects of water level regulation practices on aquatic macrophytes (II, V),
3. to compare the stability of aquatic vegetation by means of permanent plots (III),
4. to estimate the possibilities to regenerate the shore vegetation by means of planting (IV) and
5. to develop and apply an ecological regulation practice (ERP) to northern regulated lakes (V).

2 Material and methods

2.1 Study area

Lake Lentua (90 km^2) is the largest non-regulated lake in the Oulujoki watercourse (Fig. 1). Lake Ontojärvi (102 km^2) has been regulated for hydroelectric purposes since 1951 with a maximal range of 4.4 m. At the beginning of the regulation, the summer water level was raised by over one metre compared to the original summer water level by damming the outlet with a hydroelectric power station (see paper I for details). Lake Ontojärvi is a typical regulated lake in northern Finland with a raised water level during the summer and increased water level draw down during the winter. The water level fluctuation before regulation was quite similar to that in Lake Lentua. The two study lakes are meso-oligotrophic, but Lake Ontojärvi has a slightly higher trophic status.

Lake Oulujärvi (944 km^2) is the largest lake in the Oulujoki basin (Fig. 1). It has been regulated since the beginning of the year 1951 with a yearly maximum range of 2.7 m (see paper V for details). The regulation included a water level draw down by 1 m during the winter and also eliminated the spring flood, which caused a lowering of the water level by 0.4 m during the open water period (Keränen 1985). The lowered water level was promoted by a need to decrease the large scale shore erosion, which was typical for Lake Oulujärvi in natural state. After some dry years with low water levels during the 1970s, a less intensive regulation practice with higher target levels during the ice-free period was introduced in the 1980s (Kaatra & Marttunen 1993). Lake Oulujärvi is mesotrophic due to point and non point source pollution.

Lake Kostonjärvi (45 km^2) is situated in the Iijoki watercourse (Fig. 1). Its water level has been regulated since 1964 for the production of hydropower by a maximal range of 5 m and a water level raise of 0.5 m (see paper V for details). The water level is lowered by 4 m during the winter. Lake Kostonjärvi is oligotrophic with quite low humic contents.

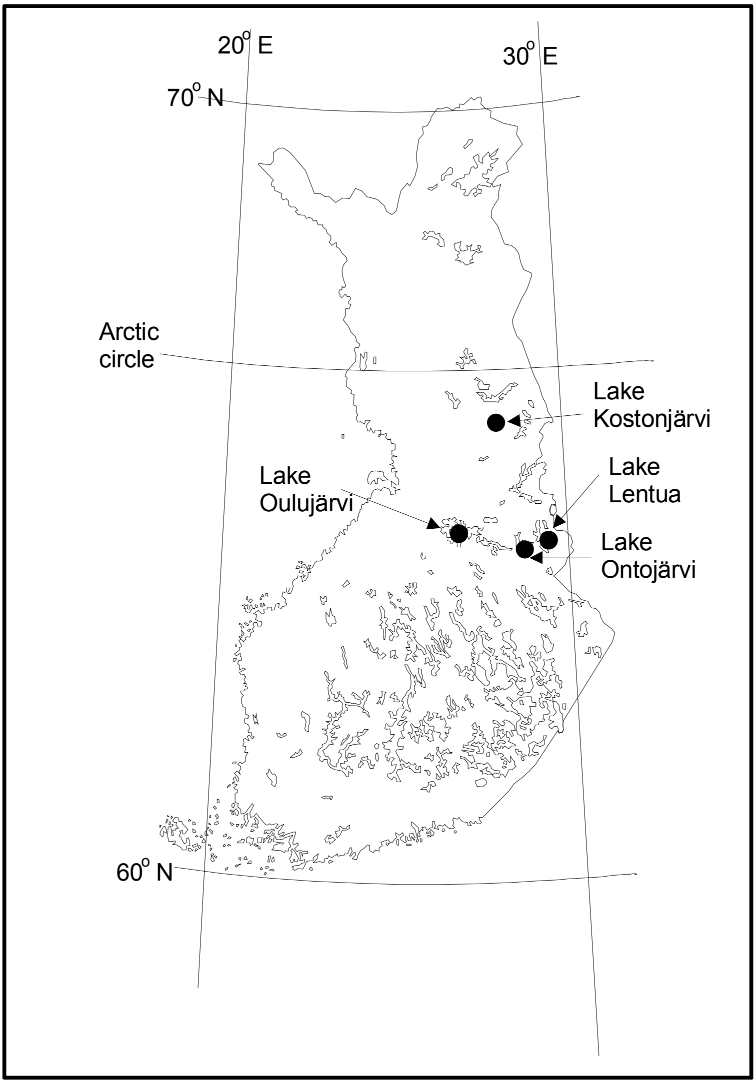

Fig. 1. Location of the study area in northern Finland. The research lakes are marked with filled dots.

2.2 Environmental factors (I, II, III)

The water levels were recorded daily during the study period with an official water gauge. The median water level of the ice-free period (W_{om}) was used as a datum level. The elevations (z) (in metres) and depths (D) presented in this study were calculated from W_{om}. The water level fluctuation zones were determined by the duration (d_w) of the water level during the ice-free period. The eulittoral zone consisted of upper (10% < d_w ≤ 25%), middle (25% < d_w ≤ 50%) and lower eulittoral zones (50% < d_w ≤ 75%). The sublittoral was divided into an upper (75% < d_w ≤ 95%) and a lower zone (95% < d_w ≤ 100%).

The estimation of the underwater light climate was based on the penetration of photosynthetically available radiation (PAR) calculated for some lakes of Central Finland (Eloranta 1978). The extinction coefficient of red light (E_r), was calculated on the basis of water colour. In this study, 4.5% of incident red light was used as an indicator of the lowest limit of productive littoral (Eloranta & Marja-aho 1982). The depth of the zone (D_r) reached by 4.5 % of incident red light (627 nm) and the light zones were assessed according to the Lambert-Beer law (see paper I for details).

The thickness of the frost layer was measured with frost tubes along 5 - 6 different transects in both research lakes. The number of measuring tubes was 40 - 44 in Lake Ontojärvi and 18 - 21 in Lake Lentua during the winters 1984-85 and 1985-86, respectively. The state of the surface sediment was checked through holes drilled in the ice cover in March 1985 and 1986. This procedure was carried out at 13 sites in Lake Ontojärvi and 9 sites in Lake Lentua during both research years.

Bottom stability was measured using sediment samplers managed by scuba divers during the summers 1984 and 1985. The depth of sedimentation (D_s) was determined as the boundary at which bottom quality changed from sand or stone to muddy sand or mud. The relative erosion rate (R) of the bottom sediment was calculated using the SMB method, which estimated sediment erosion (g m^{-2} d^{-1}) in the different quadrats (see I for details).

The slope (S) of the littoral was calculated as an inclination (%) between the different depths. Exposure was assessed by the effective fetch (F_e), which refers to the free water surface over which wind may act upon waves (Håkansson & Jansson 1983). The shape (C) of the shoreline was measured as an angle by setting the centre of a circle with a 2.5 cm or 5 cm radius on the shore line (Palomäki 1992). The shape (C) was presented as degrees using a 0.5 km ($C_{0.5}$) or 1 km (C_1) circle.

Discriminant analysis was used to estimate the relative importance of the different environmental factors affecting the formation of bottom quality classes. The method of Moss *et al.* (1987) was used to predict the probability of the presence of each bottom class at the chosen test site.

2.3 Transect studies (I, II)

Transect studies were carried out in Lake Ontojärvi and Lake Lentua in 1984-86 (Hellsten *et al.* 1989, I, II). On the basis of the distribution of different shore types and exposure, 52 transects were selected from Lake Ontojärvi and 53 from Lake Lentua. The entire material consisted of 6,303 quadrats (1 m^2) situated at one or two-metre intervals, depending on the homogeneity of the bottom or the vegetation. The bottom substrate was visually classified into six classes: peat, stone, gravel, sand, muddy sand and mud. Macrophyte data were collected along transects by using quadrats (1 m^2), but for deeper areas an underwater scope was used. Isoetid-dominated vegetation was analysed with the aid of a bucket equipped with a 3-m handle (Mäkirinta 1978). A rake was also used to determine the species composition of elodeids and water mosses (Maristo 1941). The number of quadrats was 2,717 in Lake Ontojärvi and 3,585 in Lake Lentua, of which 1884 and 1945 were without vegetation in Lake Ontojärvi and in Lake Lentua, respectively. In each quadrat, both species composition and coverage were determined. The coverage percentage data were transformed to the enhanced scale of Braun-Blanquet: + = 1, 1 % = 2, 2% = 3, 3-4 % = 4, 5-10% = 5, 15-25% = 6, 30-45% = 7, 50-75% = 8, 80-100% = 9. In addition to macrophyte data, coverage by stones (K) was transformed to a 1-9 scale.

In this study the term "macrophyte" was used very broadly to apply to both aquatic species and species present in the shore vegetation (e.g. *Carex* vegetation), including freshwater sponge (*Spongilla lacustris* L.). Some plants difficult to identify were treated collectively (e.g. *Sparganium* sp.). The nomenclature of vascular plants was accordant with Hämet-Ahti *et al.* (1998) and that of bryophytes with Koponen *et al.* (1995).

Macrophyte data of separate plots were analysed by using Canonical Correspondence Analysis (CCA) (ter Braak 1986). Classification of the vegetation data was done by TWINSPAN (Hill 1979). The classification was partly concordant with the typology of Mäkirinta (1978, 1989). Discriminant analysis was used to predict the distribution of different vegetation types (Moss *et al.* 1987).

2.4 Permanent plots (III)

The study was done in Lake Ontojärvi and Lake Lentua in 1984-88. 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 (see paper III for details). The sampling quadrats (0.5 by 0.5 m) were marked permanently by steel rods in 16 different shore areas selected on the basis of the results of the transects studies (I). The number of analysed quadrats varied yearly as follows:

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

The observations were made 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 abundance values were calculated from the presence of each species in the different sub-squares (0, 4, 8,...,100 %) and the frequency as a mean frequency of all the quadrats observed. Only the quadrats with continuous time series were included in the analysis.

The annual changes in vegetation were measured by comparing the dissimilarities in species composition between the different research years within each square (Nilsson & Keddy 1988). The mean values of all the observations on a given quadrat were used as an indicator of dynamics (D_o or D_l). Dissimilarity values were also calculated between the lakes ($D_{o/l}$). The total number (N_{sto} or N_{stl}) of observed species in the lake and the mean number (N_{sm}) of observed species on a given quadrat were used as an indicator of diversity.

2.5 Experimental revegetation (IV)

Open (O) and sheltered (S) experimental areas were established on the sandy eroded shores of Lake Ontojärvi (IV). The open areas were divided into non-protected areas and areas protected by groins made of stones. One area on a sheltered shore was also left without protection, while another was protected by a chain of floating timbers. Each of the study areas was divided into six subareas (6 * 10 m), of which the first was a non-treated control area, the second was treated by fertilised peat, the third was sowed with rapidly growing oat (*Avena sativa* L.), the fourth had peat treatment with oat and the fifth subarea was covered with bunches of willows (mainly *Salix phylicifolia*) bound together into a carpet (Bagemann & Schiechtl 1986). In the sixth subarea an erosion carpet (Rejtex©) was used.

All the shore plants that were planted in the subareas were erosion-resistant species collected from close to the experimental plots. *Carex rostrata*, *Juncus filiformis* L., *Phragmites australis* (Cav.) Trin. ex Steudel and *Calamagrostis* sp. were planted as pieces of turf or as seedlings in 2-4 rows with a planting depth of 5 to 15 cm. Some typical shore bushes *Salix phylicifolia* and *Alnus incana* (L.) Moench were planted as seedlings. In the willow carpet subarea, only tall (1.5-3 m) cuttings of *Salix phylicifolia* were planted near the shoreline.

The experimental areas were prepared during May 1990, and the planting was done during June 1990. The areas were analysed twice per month in 1990, monthly in 1991 and once in 1992 (IV). The areas were re-assessed in 1994 and in 1998.

2.6 Ecological regulation practices (V)

The methods of ecological regulation practices (ERP) were mostly based on the results of the studies I and II, originally presented in Hellsten *et al.* (1989) and in Alasaarela *et al.* (1989a, c). These practices were based on voluntary work by the permission owners and the water authorities. Regulation was developed within the allowed water level fluctuation regime without changing the legal permissions. In this study, ERP methods were applied to Lake Kostonjärvi and Lake Oulujärvi (for details, see paper V). In the ERP procedure, the responses of the littoral to the water level fluctuation were analysed carefully, and the following measurements were then made.

During the o*pen water period* there was a tendency towards a declining water level in Lake Kostonjärvi, where, due to the raised water level, the littoral was bare and unstable. In addition to the mean water level, special attention was paid to the dynamics of the water level, which should follow the natural lowering trend during the summer, offering optimal possibilities for proper development of the emergent vegetation. On the other hand, the beginning of regulation in Lake Oulujärvi resulted in a lowering of the water level, which led to a rapid invasion of shore vegetation on the gently sloping sandy or silty shores (Keränen *et al.* 1992). Therefore, the main aim of ERP after the lowest water level was to lift the water as early as possible and to keep it at a sufficient level to reduce the plant invasion.

Another aim was to minimise the effects of the lowering of water level *during the winter* by shifting the lowest level towards the spring. The final goal of the procedure was to keep the productive littoral partly non-frozen (I, II). This was considered especially important for Lake Kostonjärvi, where the productive part of littoral was completely frozen. This aspect was also taken into account in Lake Oulujärvi.

The annual range of water level fluctuation was also used together with the Secchi disk transparency values to estimate the production of the macrozoobenthos biomass (B_m, mg m^{-2}) in the 0-3 m depth zone according to Palomäki (1994). This calculation method was used to compare the differences between the different regulation practices.

3 Results and discussion

3.1 Environmental factors and aquatic macrophytes in the littoral zone of regulated lakes

3.1.1 Differences in scales and responses

Regulation of the water level does not introduce any new environmental factors affecting the lake littoral; all the factors present in unregulated lakes also exist in regulated lakes (I). There are, however, significant changes in their amplitude and timing, which usually results in a more vulnerable environment for aquatic macrophytes (Rørslett 1988a, I). My results, which were obtained by comparing two different lakes, support the comparability of the two lakes and are largely applicable to other lakes in Fennoscandia. As pointed out in the papers I and II, the environmental factors can be divided into three groups: lake-, shore- and site-specific factors (Fig. 2).

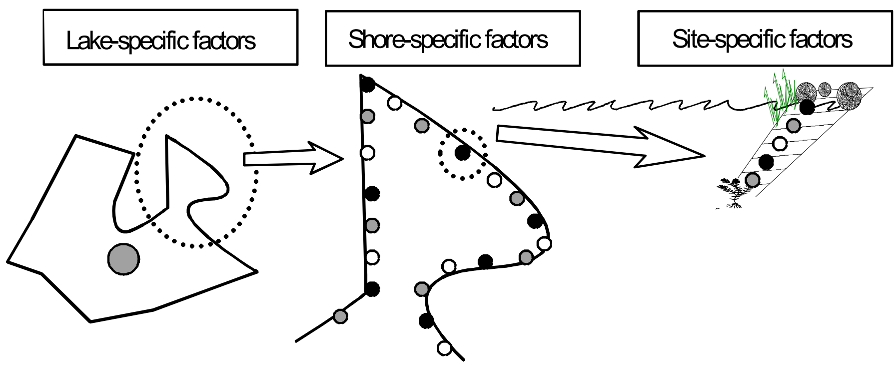

Figure 1. Determination of lake-, shore- and site-specific scales in the littoral zone.

Lake-specific factors are similarly distributed within each lake; water level fluctuation and the related ice factors are a typical example (Figs. 2-3). In general, water quality is also lake-specific, but it may vary widely in a large lake divided into sub-basins. The elevation of water level at the beginning of regulation is also a lake specific background factor, which affects the stability of the shoreline. *Shore-specific* factors consist of geomorphological factors, which vary depending on the exposure within the lake. These mainly horizontally oriented factors are driven by geomorphological processes, which are only partly dependent on water level regulation. *Site-specific* factors are highly dependent on bottom quality, which correlates with geomorphological factors, exposure and depth.

My results showed that the *lake-specific factors* related to water level fluctuation can be divided into several sub-factors. Water level fluctuation during the open water period divides the littoral into different water level duration (d_w) zones (I). These zones called supra-, eu- and sublittoral explains largely the living areas of different life-forms. The supra- and eulittoral represents the living range of emergent plants, especially sedges (*Carex* spp.) (II). This vertical gradient is well known (Pearsall 1920, Lillieroth 1938, Vaarama 1938, Maristo 1941, Segal 1971, Eurola 1965, Andersson 1973, Hutchinson 1975, Spence 1982, Coops *et al.* 1996), but rarely described as duration zones (but see Pieczynska 1972, Mark & Johnson 1985, Blanch *et al.* 1999). The duration zone approach was used to estimate the expected living range of sedges with a relatively good fit (Hellsten *et al.* 1997, Riihimäki & Hellsten 1997, Nykänen 1998, Hellsten 2000). Real aquatic macrophytes (hydrophytes) always prefer the zone (sublittoral) below the median water level of the open water period (den Hartog & Segal 1964).

It seems that at least *Carex rostrata* may benefit from the delayed flood in lake Ontojärvi (II). The high environmental tolerance of *C. rostrata* is presumably related to its two-year life cycle (Bernard 1976), and the species achieves good resistance against flooding with the aid of aeronchymal tissues (Walker & Wehrhahn 1970, Bernard 1973, Elveland 1984, Fagerstedt 1992, Huttunen *et al.* 1996, Nykänen 1988). On the other hand, it decreases in abundance if the water level is raised (Nilsson 1977, Sjöberg & Danell 1983) and it can also grow without a high flood (Weiher & Keddy 1995). The responses of different graminoids are variable; *Galamagrostis*-species benefit from irregular water level (Gill 1973, Nykänen 1998), whereas *Molinia caerulea* (L.) Moench is completely lacking due to its sensitivity to prolonged flooding (Kotilainen 1958, Wassen 1966, Nilsson 1981b, Fraisse *et al.* 1997).

Large helophytes (*Equisetum fluviatile* L., *Phragmites australis*) are also typical of the fluctuation zones, but due to their higher stems, they are able to survive at a deeper level (II). Their frequency has clearly declined in Lake Ontojärvi due to the marked erosion. *E. fluviatile* does not suffer from a high water level during dormancy (Pearce & Cordes 1988), but a high water level during the growing season causes a permanent decline of this species (Rintanen 1976, Anttonen-Heikkilä 1983, Toivonen & Nybom 1989, Wallsten & Forsgren 1989, van den Brink *et al.* 1995). The changed water level dynamics together with abundant erosion create difficult living conditions for *E. fluviatile*, causing a sudden decline in *Equisetum* stands.

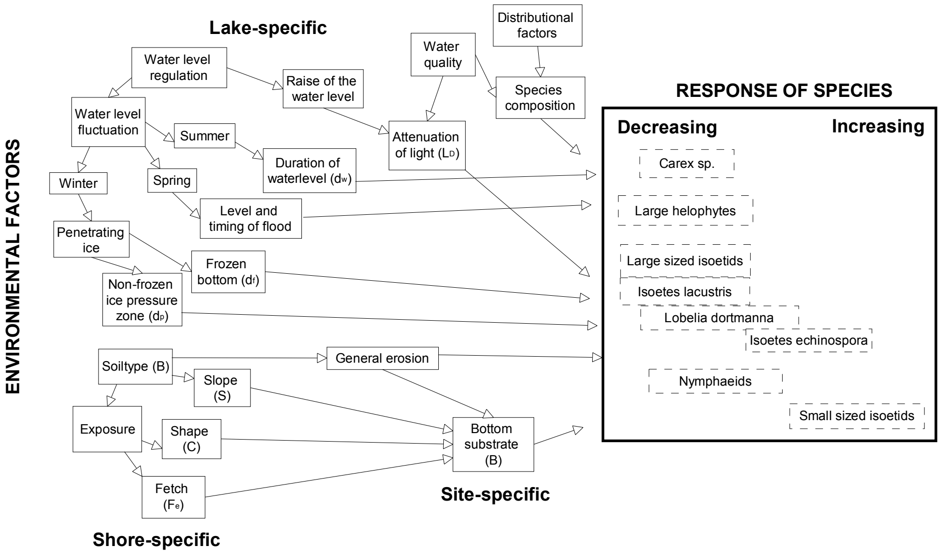

Figure 2. Schematic view of abiotic environmental factors affecting aquatic macrophytes.

The disappearance of *Phragmites australis* is also well known in regulated water courses (Nilsson 1978, Granberg & Hakkari 1980, Hellsten & Joronen 1986, II). It benefits from the low water levels during the early summer (Coops & Van der Velde 1995), and stabilisation of the water level will cause a decline in its distribution (Coops *et al.* 1996). It also suffers from organic rich bottom quality (e.g. Ostendorp 1989, Weisner 1991, Coops *et al.* 1996, Clevering 1999). From the water level fluctuation and bottom quality point of view, there should be luxuriant growth of *Phragmites* in my research lakes. On the other hand, it does not tolerate high exposure (Coops *et al.* 1991, Coops *et al.* 1994) and is also sensitive to ice erosion (e.g. Luther 1951a). The permanent plots (III) and planting experiments in Lake Ontojärvi (IV) showed that *Phragmites*, being a good competitor, is able to retain its growing areas, but unable to expand its living range. Obviously, bottom instability combined with continuous ice and wave erosion restricts new occurrences.

My study also showed the essential need to differentiate between observed depth (moving Lagrangian co-ordinate) and depth calculated from the open-water mean (fixed Eularian co-ordinate) as proposed by Rørslett (1984, 1985a, 1987a, b, 1988a). Especially in regulated lakes with fluctuating water levels, the use of an exact datum level is a basic assumption in calculations.

The effect of ice expanding to the bottom can be divided into two strikingly different factors: *the frozen bottom zone* is situated in the upper part of the littoral and characterised by frozen sediment up to 40 cm in thickness (I). This is typical of minerogenic shores, where the lowest level of the frozen bottom zone can be predicted by the date when the lowering ice touches the bottom. Most of the peat bottoms and bottoms with high organic contents remain non-frozen, as also noted by Palomäki & Koskenniemi

(1993) and Koskenniemi (1994). This date in the first week of February is relevant in the northern part of Finland, but it also seems to be applicable in the western part of Finland (Hellsten *et al.* 2000). Comparable values can be noticed from northern Swedish reservoirs and rivers too (Nilsson 1981a, Erixon 1979,1981, Renman 1989,1993, I). Functionally, the same phenomenon has been described as an ice scouring function by Rørslett (1984, 1985a, 1987b, 1988a). The zone below the frozen zone is only affected by the mechanical pressure of ice and can be called *an ice penetration zone*. In this zone, the ice merely presses down on the bottom, but the surface of sediment is not frozen. These two zones can be described in terms of the duration of the frozen (d_f) and ice penetration (d_p) zones (I).

The responses of the species can be divided into three basic types. Helophytes, which are bounded to the upper zone, and small isoetids (*Ranunculus reptans, Eleocharis acicularis*) are relatively tolerant against bottom freezing and prefer the frozen zone (II). The second group consists of large isoetids, such as *Lobelia dortmanna* and *Isoetes echinospora* Durieu, which avoid the frozen zone but are able to grow in the ice penetration zone (II). The third group is characterised by *Isoetes lacustris* and some large nymphaeids (*Potamogeton natans* L.*, Nuphar lutea* (L.) Sibth. & Sm), which avoid the ice pressure zone (II).

Small isoetids are well adapted to the vulnerable environment present in the upper zone of the lake and are therefore much more common in Lake Ontojärvi than Lake Lentua (II). Due to their flexible growth strategies, they can spread rapidly over the entire littoral (e.g. Rørslett 1989). It has been even stated that *Ranunculus reptans* benefits from being broken up by ice into small pieces capable to spread vegetatively (Renman 1989). These two species are found in extreme environments with water level fluctuation up to 20 meters (Nilsson 1978, 1981a, Granberg & Hakkari 1980, Renman 1986, Wilcox & Meeker 1991, Hill *et al.* 1998). However, Rørslett (1989) noted that *R. reptans* was lacking in a lake with 14.4 meter regulation, but was able to return to the bare exposed littoral of the regulated reservoir Meltingen (21 meters of regulation) after the addition of fertilisers (Rørslett & Johansen 1996).

Large isoetids clearly suffer from the effects of ice (II). The most sensitive species, *Isoetes lacustri*s*,* even avoided the zone of penetrating ice due to its growth form, which is characterised by hard leaves (Aulio 1985, Rørslett & Brettum 1989). Its sensitivity to ice has been described in several studies (Quennerstedt 1958, Nilsson 1978, Renman 1989, Rørslett 1984, 1985a, b, 1987b, c, 1988b, 1989, Rintanen 1996). On the other hand, *Isoetes echinospora* with its flexible habitus with bendable leaves is able to survive in Lake Ontojärvi very well (II). It is notably ice-resistant (Luther 1951a, Nilsson 1978, Rørslett & Brettum 1989) and obviously benefits from the disappearance of *I. lacustris* in the lower littoral. On the other hand, the absence of helophytes in the upper littoral zone may stimulate its growth in Lake Ontojärvi.

The distribution of *Lobelia dortmanna* is very limited in Lake Ontojärvi (II). Its decline has been demonstrated in several regulated lakes (Rørslett 1985ab, 1987c, 1989). It usually prefers minerogenic bottoms with low nutrient contents (e.g. Kurimo 1970, Szmeja 1987, Toivonen & Huttunen 1995) due to its large root system specialised to CO_2 intake (Wium-Andersen 1971). On the other hand, it cannot escape to deeper area by increasing the amount of chlorophyll (Kansanen & Niemi 1974). Minerogenic shore areas are also easily frozen (Palomäki & Koskenniemi 1993, I), and the damage to the root system is therefore obvious.

Another group sensitive to ice consists of large nymphaeids, such as *Potamogeton natans* and *Nuphar lutea* (Luther 1951b, II). *P. natans* prefers soft bottoms, which are usually not frozen, and it can therefore be found even in the littoral of Lake Ontojärvi and regulated reservoirs (Koskenniemi 1987, Erixon 1981). The distribution of *N. lutea* was quite similar to that of *P. natans*; a soft unfrozen bottom enabled it to occupy the ice pressure zone. In general, the decrease in the frequency of *N. lutea* is very clear (Nilsson 1978, Erixon 1979).

In addition to the water level fluctuation and ice extension, the attenuation of light forms a depth related pattern which restricts the lowest level of aquatic macrophytes (I, II). In my study, it is described by the intensity of red light (L_D). A typical example of light limited distribution is the distribution of *Isoetes lacustris*, which is almost lacking in Lake Ontojärvi (II). The relationship between red light and the lowest depth limit of *I. lacustris* was compatible with the 4-6 % observation of Eloranta & Marja-aho (1982). The ecological niche of *I. lacustris* between the ice disturbance and the lack of light has been described in detail in several studies of Rørslett (1984, 1985a, b, 1987b, c, 1988b, 1989).

All of these factors are clearly related to elevation (z) or depth (D), which means that their values remain constant at same vertical level of the littoral within a given lake (Fig. 2). These factors are heavily affected by the water level fluctuation. Their values can be easily used to evaluate the effects of different water level regulation practices (V).

The *shore-specific factors* consist of geomorphological factors (slope S, shape C) and effective fetch (F_e), which fluctuate quite randomly within a given lake (I, Fig. 3). These horizontal shore-specific factors are mainly driven by geomorphological processes, which are only partly dependent on water level regulation. It should been noted that the changes in water level greatly affect the significance of fetch, because the stability of bottom decreases if the water level is raised or lowered (Sundborg 1977, Granberg & Hakkari 1980, Nilsson 1981a, Hellsten & Alasaarela 1984, Newbury & McCullogh 1984, Hellsten & Joronen 1986, Mark 1987, Mark & Kirk 1987). The rise in water level, as seen in Lake Ontojärvi, launches abundant erosion, and the sandy shores of Lake Ontojärvi were much steeper compared to Lake Lentua, which shows the unstable nature of shores (I). On the other hand, the lowering of water level starts the increase of aquatic plants, as shown in Lake Oulujärvi (Nykänen 1998).

The response of macrophyte species to exposure is flexible. Aquatic macrophytes can partly escape into deeper water, while some species can arise their position to a higher level (Keddy 1982, Spence 1982). Exposure affects the distribution of helophytes and nymphaeids by mechanical force and indirectly via changes in bottom quality (e.g. Keddy 1982). My oligotrophic lakes showed no significant relationship between their presence and the exposure factors, but their presence is, however, quite clearly related to the bottom substrate (II). The diversity of macrophytes was slightly higher on sheltered shores (III, Nilsson 1981a, Keddy 1983). On the other hand, Rørslett (1987c) and Nilsson & Keddy (1988) were unable to find any significant effect of exposure on the stability of vegetation.

It should also be noted that exposure values calculated as effective fetch (F_e) and shape (C) correlate significantly with each other (I, Palomäki & Hellsten 1996). The use of shape according to Palomäki (1992) divides the shores into erosional minerogenic cape areas and accumulative soft bottom bay areas, providing a clear insight of these discrete environments.

The inclination of shoreline or slope is assumed to be a significant factor affecting the diversity of the littoral flora (Duarte & Kalff 1986). Slope affects the distribution of bottom substrate (e.g. Håkanson & Jansson 1983), but there was only a weak correlation between slope and sedimentation level in my research lakes (I). There was therefore no correlation between the different species and continuous slope, but there were slightly more species on the mildly sloping shores (II, III).

Site-specific factors are illustrated by bottom quality, which itself is related to slope (S), shape (C) and fetch (F_e), but most clearly to water depth (Fig. 3). The shores of Lake Ontojärvi were steeper than those of Lake Lentua, which affected the distribution of bottom types, sandy bottoms being more common in Lake Ontojärvi than in Lake Lentua (I). The softness of the bottom usually increases along with increasing depth and decreasing exposure. The sedimentation level only correlated with the slope and was not predicted by fetch or shape. The distribution of bottom quality is difficult to predict. The main environmental factors from the two lakes were used in a discriminant analysis to predict the bottom type distribution of the littoral. Although the statistical significance of the predicted types was quite low (r^2 = 0.41), it showed the possibility to predict the bottom quality by environmental data. In addition to these factors, the general soil types (moraine, glaciofluvial deposits, peatland, cliffs) of the area and the quality of water affect the formation of bottom quality.

The effect of bottom quality on aquatic macrophytes is partly an artefact (II). *Carex* species are always found on peaty bottom, but they actually prefer sheltered, mildly sloping shores and themselves produce peat. On the other hand, nymphaeids mainly grow on soft bottoms, which exist in sheltered bays suitable for species with floating leaves sensitive to wave action. The same also applies to large isoetids, whose correlation with soft bottom is related to the fact that soft bottom is typical of deeper areas (I, II). My observations are largely concordant with those of Rørslett (1985b), who was not able to find any relationship between bottom quality and macrophytes. The importance of bottom substrate has been shown by several other researchers (Pearsall 1920, Spence 1982, Barko & Smart 1983, Duarte & Kalff 1986, Wisheu & Keddy 1989). The inconsistent conclusions are mainly due to the different points of view, but at least in my research, the lake bottom substrate is a consequence of exposure and depth rather than an independent environmental factor in itself.

Despite the different environmental regimes, several common vegetation types were found in a TWINSPAN analysis (II). Most of the types were present in both lakes, but due to the harsh environment in Lake Ontojärvi, their ecological niches were very limited. This was especially true of ice-sensitive, large isoetids, such as *Isoetes lacustris* and *Lobelia dortmanna*. In general, the analysis indicated a similar structure in the vegetation in both lakes, although the different ecological regimes were reflected on the distribution of different types.

The disciminant analysis according the method of Moss *et al.* (1987) was used to predict the vegetation type distribution of the littoral (II). The analysis classified 50.1 % and 45.1 % of the vegetation types correctly in Lake Ontojärvi and Lake Lentua, respectively. Although the hit percentage was relatively low, it should be noted that the original TWINSPAN classification was very detailed, including 12 types in Lake Ontojärvi and 14 types in Lake Lentua. In general, the predicted types were ecologically close to the observed types, and a simplification of typology would have improved the results. It was concluded that this prediction method provides useful tool for analysing the effects of water level regulation.

3.1.2 Dynamics of the littoral vegetation

The littoral is always partly unstable, as waves and currents cause erosion in the upper zone, whereas eroded material accumulates in the lower, deeper zone of the littoral (I). Furthermore, the differences between hydrological years cause differences in the environmental conditions of the upper zone. The rise of water level at the beginning of regulation also brings about a specific factor causing unbalance in vegetation. Nilsson *et al.* (1997) demonstrated that the abundance of species tends to decrease in storage reservoirs 30-40 years after their construction. Obviously, the same tendency is also present in regulated lakes in northern Finland, which are rarely affected by eutrophication.

In my study, the stability of vegetation was investigated using a permanent plot design (III). A follow-up of four years showed that 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 increased ecological stress was visible in the littoral zone; the number of species was lower in Lake Ontojärvi than in Lake Lentua. The lesser diversity is consistent with the observations of Grime (1979) and Rørslett (1989).

In Lake Ontojärvi, the area that is almost permanently submersed (sublittoral) showed higher dissimilarity (D_m) and lower diversity (N_{sm}) values compared to Lake Lentua (III). On the other hand, dissimilarity in the eulittoral zone was higher in Lake Ontojärvi compared to Lake Lentua. The stability of the water level during the open water period explains the high stability of vegetation in Lake Ontojärvi compared to the Swedish reservoirs of fluctuating water level of open water period (Nilsson 1981a, Nilsson & Keddy 1988).

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 the sheltered shores. This agrees with the observations of several researchers (Keddy 1982, 1983, Nilsson 1981a). The gently sloping shores carried higher diversity, as also noted by Duarte & Kalff (1986). The peaty bottoms were the most stable environments, as also noticed by Koskenniemi (1987) and Nilsson (1981a). On the other hand, the muddy bottoms were unstable in our research lakes; these bottoms are situated at the deepest area of littoral, where the mortality of individuals is also high (Rørslett 1985b).

Generally speaking, the vegetation in Lake Ontojärvi is equally stable as that 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. This does not mean that the succession is at its final stage, because the abundance of species is probably increasing and the differences between different hydrological years cause some unforeseen changes in the ecological environment (cf. Nilsson *et al.* 1997).

3.1.3 General overview

In general, the environment in the littoral of a regulated lake is much more vulnerable than that of a lake in its natural state (I, II). The most visible effects of water level regulation were related to the raised water level, which yielded erosion of sandy shores at the beginning of the regulation (I). Another direct effect of regulation was the altered fluctuation of the water level, which led to bottom instability and increased the area of the frozen and ice penetration zones. The effect of ice penetration was also easy to recognise on the shores of Lake Ontojärvi, where the surface sediment was frozen to a greater depth and across wider areas than in Lake Lentua. Below the freezing zone, the ice merely pressed down on the sediment. The vertical reduction of light was estimated on the basis of water colour.

The littoral area acts as an ecocline between the terrestrial and aquatic environments and serves as the habitat of aquatic macrophytes. The composition of vegetation in the littoral is difficult to predict. Environmental factors along with biogeographical factors (e.g. Whittaker 1977), herbivory (e.g. Jutila 1997) and competition (e.g. Grime 1977) constitute the basic patterns that affect the general distribution of plant species. Water level regulation incorporates a set of pronounced changes, which, in turn, complicate the interactions in the littoral ecosystem (Rørslett 1989, I, II, III).

3.2 Possibilities to alleviate harmful effects

3.2.1 Alternatives to restoration

The littoral environment of a regulated lake is under ecological pressure due to erosion caused by ice and waves. Erosion processes are stimulated by the altered water level and enhanced by the water level fluctuation (I, II, III). In general, there are three alternatives to mitigate the negative effects in the littoral zone (Table 1). The first possibility is to trust in natural succession, which ultimately leads to stabilisation through sedimentation and settling down of the eroded shores (Rørslett & Johansen 1996). This alternative includes several benefits: there are no costs and no need for guidance. For example, the follow-up in Lake Kemijärvi, which has been regulated by 7 meters since 1966, shows that the abundance of species was higher in 1998 than in 1983 (Hellsten *et al.* 1999). Another example of Swedish storage reservoirs showed similar enrichment, although the trend was downward again after 30-40 years (Nilsson *et al.* 1997). It has been shown in III that succession in the short run does not change the set of species already present in the littoral. The second choice is to apply active restoration methods, including mechanical protection of shores, shoreline modification and planting of new tolerant species (IV). The third route includes changes in the regulation practice, which improve the environment of the littoral subjected to water level fluctuation (V).

All of these methods or strategies of shore management have both positive and negative effects (Table 1). From the lake managers point of view, a combination of different methods is the most suitable way to improve the littoral ecosystem of a regulated lake. It should be noted that, without changes in the regulation practices, the possibility to achieve the desired recovery of littoral is limited (cf. Nilsson 1996).

3.2.2 Revegetation studies

As shown in the previous chapters, the littoral environment of Lake Ontojärvi is bare and vulnerable due to the water level fluctuation. Therefore, the planting experiments carried out on the shore were quite risky since the beginning (IV). After the first summer, the average survival rates were about 45 %, because the seedlings tended to dry up due to the low water level, which was almost 50 cm below the normal. The survival rate was slightly higher in the sheltered area with a lower elevation, where 60 % of the plants were alive. As a result of freezing and ice erosion 10-15 % of the plants died during the first winter. The second year was characterised by extraordinarily high water levels causing a sudden drop in the survival rates. Only in the sheltered area protected by floating timbers did the survival rate stay above 20 %.

In the uppermost part of the littoral, the possibility of drying is also obvious due to regulation (Rørslett 1984, I, II). The effect of extending ice during the wintertime also causes scouring and freezing of the bottom sediment, as has been described for several lakes and rivers (Rørslett 1984, 1987c, Erixon 1981, I). Thus, the rapid decline of planted species was quite expected in the case of Lake Ontojärvi.

The difference between the different soil treatment plots was relatively small; only the erosion carpet provided a better survival rate during the first summer, but the second-year erosion caused a rapid decrease in survival (IV). Oat as a protective plant provided the lowest survival rates for planted helophytes, because wild ducks grazed on the young oat seedlings and concurrently plucked planted individuals (cf. Bache & MacAskill 1984). The bottom substrate is one of the most important factors affecting aquatic macrophytes (e.g. Barko & Smart 1983). Substrate can be improved by erosion barriers (see Allen *et al.* 1984) or by adding fertilisers or organic matter (e.g. Fowler & Maddox 1974, Broome *et al.* 1988). In the case of Lake Ontojärvi, both of these methods failed due to the high water level during the second year. This concerns also erosion carpets, which were covered by eroded sand (cf. Allen *et al.* 1984).

Table 1. Strategies of remediation of littoral vegetation in regulated lakes. The references refer to methods, not to results.

Method	References	Advantages	Disadvantages
No measures	III, many others	No costs No reverses Natural "method"	Slow Limited species composition High patchiness, uneven zones
Active restoration: Revegetation measures Mechanical barriers Shore protection Slope modifications	Allen *et al.* (1984), Bache & MacAskill (1984), Allen & Klimas (1986), Bagemann & Schiechtl (1986), Lester *et al.* (1986), IV, Rørslett & Johansen (1996), Fraisse *et al.* (1997)	Increased biodiversity Fast recovery Desired by lakeutilisers	High costs High probability of failures Unexpected species composition Patchiness, limited zonation
Changed regulation practice (ERP)	Wilcox & Meeker (1992), V, Rørslett & Johansen (1996), Nykänen (1998)	Environmentally friendly Permanent results Desired by lakeusers Enhanced zonation	Very high costs Slow recovery Easily affected by exceptional years Need of research Individual solutions for each lakes

The best results were obtained for the helophyte *Carex rostrata*, of which 30 % were struggling against erosion (IV). Tall willows (*Salix phylicifolia*) were also erosion-resistant with a survival rate of 80 %. *Phragmites australis* and *Juncus filiformis* disappeared quite soon, even though the latter is quite resistant against erosion (II). The latter helophytes are typical C-strategists, which are good in competition, but slow in extending their living areas (see Grime 1977, Murphy *et al.* 1990). All the species with good resistance against erosion are small R-strategists (e.g. *Ranunculus reptans*, *Eleocharis acicularis*), which are difficult to use as experimental plants and do not provide any natural protection against erosion.

One of the most promising results was achieved with tall willow seedlings (cf. Comes & McCreary 1986). Willows are easily collected and resistant against flooding. On the other hand, the willow carpets dried or eroded during the first year of our study, whereas many other studies have shown it to be a good method (Bache & MacAskill 1984, Bagemann & Schiechtl 1986). Re-design of the shore could also have been a solution against erosion as proposed by Allen & Klimas (1986).

The experimental areas were re-studied again in 1994 and in 1998 (Fig. 4). The observations, those made eight years after the planting, confirmed the results of IV. The tall willows were still alive, but they had not expanded their living area and their survival rate was less than 40 %. On the other hand, the survival of *Carex rostrata* had increased and was more than 40 %. It seems that wave erosion had transported planted species to the upper part of the eulittoral, where the environment was more stable. It should also be noted that small *Phragmites australis* individuals were still present (<5 %) near the shoreline, which proves their tolerance against freezing if the erosion is not too severe.

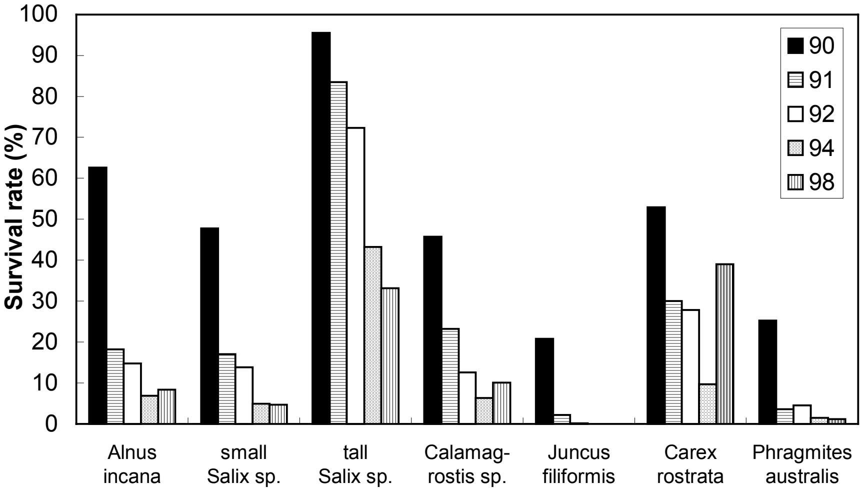

Figure 3. Mean survival rates of different species at the end of the different research years.

According to the 1998 results, the average survival rate of the planted species was 9.3%. There were no significant differences between the different treatments, except the slightly higher (17.5 %) survival rate in the peat treatment. The survival rate was also some what higher (13.4 %) on sheltered shores compared to value of 5.3 % on open shores. The follow-up proved the adaptive nature of *Carex rostrata*, which is also one of the few helophyte species more common in Lake Ontojärvi than in Lake Lentua (II).

3.2.3 Changes in the water level fluctuation regime – ecological regulation practice (ERP)

Changes in water level due to hydropower regulation cause extensive changes in shore processes. The replanting of shore vegetation is not effective without any mechanical wave-protecting barriers, although some species can survive in hard environmental conditions (IV). The effects of different soil improvement methods also seem to be quite unimportant in the area of abundant erosion. Also, the removal of aquatic weeds in a lake with a lowered water level is usually only an emergency measure for the problems caused by altered shore processes. The situation can be changed only by an elevation of the water level or by small-scale dredging operations in the outermost zone of the shore (Keränen 1985, Nykänen 1998).

Ecologically-based regulation (ERP) requires careful investigations and interpretation of the results before any recommendations can be given (e.g. Marttunen & Hellsten

1997). In the case study of Lake Kostonjärvi, the efforts were aimed at a reduction of the area affected by bottom freezing, which covered the whole productive zone in the lake (V). In the ERP, the water was kept at a higher level during the early winter compared to the old regulation practice. Consequently, the water level was lowered during the late winter to minimise the frozen bottom area. Moreover, the minimum water level in the early summer was set to a level, which allowed spring-spawning fishes to reach their spawning grounds. The water level of the open water period was not altered significantly, because the rocky shores were already adapted to the higher water level and the proportion of sandy shores was only 4 % of the total shoreline (V).

The ecologically-based regulation practice should reduce the area of frozen bottom by 24 %, which should increase the growing area of large isoetids with a positive impact on the zoobenthos and the autumn-spawning fishes (V). From the viewpoint of hydropower production, however, the effects were quite significant and caused significant losses during the winter, when discharge was limited. The value of fishery was not calculated in this study, but, apart from its indirect effects, the ecologically-based regulation practice would definitely also increase the area available for winter fishing as well as the fishing of spring-spawning fishes. The value of recreational use was not estimated in this case study.

In spite of the high costs of the ERP, these water level guidelines have been voluntarily followed by the hydropower company (PVO Group Ltd) since 1992 (V). For the following 3 years, the water level successfully remained between the ERP targets with the exception of the year 1994, when the winter water level dropped rapidly due to the dry autumn 1993. The extremely wet summer 1992 caused the water level to be very high in July and August. The short field investigations at Lake Kostonjärvi during the summer 1998 showed that there were some positive changes in the shore biota. Ice-sensitive *Isoetes lacustris* was found on one sheltered shore, and the presence of erosion- sensitive *Equisetum fluviatile* indicated an enhanced littoral environment (unpublished data). On the other hand, the exceptional years will probably greatly disturb the succession of isoetids (e.g. Rørslett 1985b).

Another case study at Lake Oulujärvi was designed to decrease the emergent vegetation expanding on the littoral due to the lowered summer time water level (V). In a preceding research the impacts of hydropower production, recreational use, flooding and fishery were estimated (Marttunen & Kaatra 1993). The annual loss caused by the current water level regulation for recreational use was US $ 0.34 million, whereas in the planned ERP it would have been US $ 0.26 million due to the excessively high summertime level (Aittoniemi 1993).

Due to the notable loss in energy production and partly also to the high level of recreational use, the ERP was rejected at Lake Oulujärvi and an intermediate water level regulation plan was developed with a target level of 122.5 m on the 20th of June instead of the beginning of July (V). The target had been reached during 3 of the 4 years, with the exception of the year 1992. During the very dry summer of 1993, the water level dropped below the target level in August. The water level during the summer did not completely prevent the spread of emergent vegetation and more attention should be given to the other management and rehabilitation methods, including the removal of the vegetation from the shores of Oulujärvi under intensive recreational use (Keränen *et al.* 1992). The small-scale dredging of vegetation was, however, quite useless, because the vegetation returned quite rapidly. The method is economically suitable only to relatively limited shore areas.

Despite the rejected ERP, the tendency towards high summer water levels since the 1980's has led to improvements in the littoral environment. Nykänen (1998) noted, in a vegetation follow-up, that vegetation has decreased after the raise of the water level. A strategy analysis of aquatic vegetation showed that there was a slight change from competition-oriented to stress-oriented vegetation (Nykänen 1998). The change in succession status showed that the stability of vegetation is slowly increasing.

4 Conclusions

Water level regulation in northern lakes constitutes a typical environmental problem as far as its acceptability is concerned. At *the first stage* following the beginning of regulation, the ecological changes are often noticed only by local fishermen as changes of fish stocks (e.g. Sundborg 1977). It should be noted that most of the lake regulations were carried out during the 1950s and the early 1960s without any environmental impact assessment (Marttunen & Hellsten 1997). Only very few *a priori* studies concerning the status of fishery can be found, or the assessment studies have been focused mainly on mapping the pre-regulation situation (e.g. Wassen 1966). The situation before the period of environmental awareness was more or less the same in the other Nordic countries (Sundborg 1977, Nilsson & Brittain 1996, Rørslett & Johansen 1996). On the other hand, the sensitivity of littoral biota to water level fluctuation was not widely known, because of the pelagial-oriented research tradition.

At *the second stage*, the changes in public attitude and general environmental awareness caused several environmental studies of acidification, global change and, ultimately, water level regulation (Alasaarela *et al.* 1989b). The project ECOREGU largely answered to the general questions of the effects of water level regulation in boreal lakes (Alasaarela *et al.* 1989c, Hellsten *et al.* 1989, Huusko *et al.* 1989, Tikkanen *et al.* 1989). The same process of identifying environmental problems in regulated lakes has taken place earlier in Sweden (e.g. Sundborg 1977) and in Norway (e.g. Rørslett 1984). As a results of these studies, the ecological status of heavily regulated lakes is relatively well known in the Nordic countries.

The present study revealed the sensitivity of the littoral against water level fluctuation (I, II, III). The raising of water at the beginning of regulation caused long-lasting erosion processes affecting aquatic macrophytes. Enhanced erosion and unstable bottom especially limited the occurrences of emergent large helophytes (e.g. *Phragmites australis*, *Equisetum fluviatile*), but promoted the spread of small isoetids (e.g. *Ranunculus reptans*, *Eleocharis acicularis*). Apart from erosion, most of the *Carex* species were also limited by the delay of spring flood as a consequence of regulation. The distribution of large isoetids (*Isoetes lacustris*, *Lobelia dortmanna*) was largely restricted by the lowering ice cover in the regulated lake. The division of the littoral into frozen and ice pressure zones demonstrated the differences in the tolerance of different macrophytes against the water level draw down in regulated lakes. It was also noted that the vegetation was equally stable in the regulated Lake Ontojärvi as in Lake Lentua with natural water level fluctuation. The long-lasting regulation in Lake Ontojärvi has resulted in the selection of a species pool adapted to harsh environmental conditions.

In addition to these obvious differences in the environmental conditions and the distribution of aquatic macrophytes in regulated lakes, the changes can be imperceptible. Especially in the cases of slight changes in the water level dynamics, the response of the littoral is slow, and the effects therefore appear gradually after several decades (e.g. Marttunen & Järvinen 1999, Hellsten 2000). Such water level regulations usually exist in southern Finland, where most of the regulations are carried out for flood protection purposes without significant changes in the amplitude of water level fluctuation (Marttunen & Hellsten 1997).

The third stage in the process of the development of lake regulation was littoral rehabilitation by active methods or by changes in the regulation practice (IV, V). In Finland, these projects focused on new restoration methods, which were mainly applicable only on a small scale (Keränen *et al.* 1992, Alasaarela *et al.* 1993, Kaatra & Marttunen 1993, IV). In Norway, the replanting experiments showed promising results, but they were applied only to limited areas (Rørslett & Johansen 1996). In Sweden, oligotrophic regulated lakes are managed by adding fertilisers to water (e.g. Milbrink & Holmgren 1981). This method is also commonly applied to reservoirs in North America (e.g. Stockner & MacIsaac 1996). This method, which does not focus on the restoration of littoral vegetation, usually also incorporates increased production of the littoral zone (Stockner & MacIsaac 1996). It should be noted, however, that there is a trend towards habitat improvements in river restoration schemes before fish stocking (e.g. Mäkipetäys 1999). This trend of habitat improvement is obviously getting more and more attention in the restoration of regulated lakes.

The changes in regulation practices are quite new phenomena in the environmental policy in Finland. The amendments of the Water Act in 1994 significantly increased the opportunities to modify the old regulation practices if the effects of regulation were harmful or the use of lakes had changed. At the end of 1997 there were more than 50 Finnish lakes where regulation was under a critical review (Vähäsöyrinki 1997). It should be noted, however, that most of these cases did not lead to any extensive changes in the regulation practice. Alterations in regulation may not cause flood damage or significant losses in hydropower production. In several cases, ecological regulation procedures based on the studies of I and II were applied (Hellsten *et al.* 1997, Riihimäki & Hellsten 1997, Marttunen & Järvinen 1999, Hellsten *et al.* 2000). The estimation method was also applied in 1998 in a Delphi exercise to the Lower Kananaskis Lake in Canada, to search for the best regulation practices in a heavily modified water course (unpublished data). In addition to many ERP applications, the forthcoming water policy directive of the European Union emphasizes the status and follow-up of the littoral environment, which, in turn, underlines the importance of the relationships between environmental factors and aquatic macrophytes.

The first follow-up results of the lakes under ecological regulation showed only slight positive changes in the aquatic vegetation. In most cases, hydrologically wet years have caused high water levels promoting littoral erosion, which has degraded the recently settled vegetation (IV). On the other hand, the vulnerable sublittoral is incapable of providing suitable habitats for new plants. This is especially the case in lakes without any seed banks in the upper lake chain (e.g. Nilsson *et al.* 1989). It is well known that the littoral of large reservoirs in northern Finland is without any vegetation due to the perennial regulation practice and the lack of a seed bank (Hellsten *et al.* 1993). An example from Lake Hartevatn in Norway show that a change of the regulation amplitude from 7 meters to 2 meters provided a possibility for aquatic macrophytes to recover (Rørslett & Johansen 1996). There are some small lakes in northern Finland, where the water level regulation has been completely cancelled, but without environmental follow-up. From a scientific and partly also a management point of view, complete cancellation of water level regulation could offer a good possibility to follow the recovery of the disturbed shore areas. Another key question, i.e. the effects of exceptional years and speed of succession, could also be studied in an experimental set-up of that kind.

References

Aittoniemi P (1993) Vesistön säännöstelyn vaikutukset rantojen virkistyskäyttöön - arviointimenetelmä ja sovelluksia Kainuun järvillä. Imatran Voima Oy, Tutkimusraportteja IVO-A-01/93, Vantaa 135 pp. + 3 app. (In Finnish).

Alasaarela E (1988) Ekologiset näkökohdat Pohjois-Suomen järvien säännöstelyssä. Vesitalous 2/1988: 16-19. (In Finnish).

Alasaarela E, Hellsten S & Tikkanen P (1989a) Ecological aspects of lake regulation in northern Finland. In: Laikari H (ed) River Basin Management 5, Pergamon Press PLC, Oxford.

Alasaarela E, Hellsten S, Huusko A & Tikkanen P (1989b) Ekologiset näkökohdat joidenkin Pohjois-Suomen järvien säännöstelyssä. Osa 1. Yleistutkimukset. (Ecological aspects of lake regulation in Northern Finland. Part 2. General results.) VTT Research Notes 926. Espoo. (In Finnish).

Alasaarela E, Hellsten S, Huusko A & Tikkanen P (1989c) Ekologiset näkökohdat joidenkin Pohjois-Suomen järvien säännöstelyssä. Osa 5. Säännöstelykäytäntö ja ekologiset vaikutukset. (Ecological aspects of lake regulation in Northern Finland. Part 5. Regulation practices and ecological effects) VTT Research Notes 929. Espoo. (In Finnish).

Alasaarela E, Hellsten S, Keränen R, Kurttila T & Riihimäki J (1993) Säännöstelyjärvien rantojen kunnostuksen ja hoidon periaatteet - esimerkkinä Oulujoen vesistö. (Principles for the restoration and management of the shores of regulated lakes – Examples from the Oulujoki watercourse). Vesi- ja ympäristöhallituksen julkaisuja 145. Helsinki. (In Finnish).

Allen HH & Klimas CV (1986) Reservoir shoreline revegetation guidelines. Technical report E-86-13, US Army engineer waterways experiment station. Vicksburg, Miss. 87 pp.

Allen HH, Webb JW & Shirley SD. (1984) Wetlands development in moderate wave-energy climates. Proc. dredging '84, Waterway, Port, Coastal and Ocean division, American Society of Civil Engineers, November 14-16, 1984, Clearwater, Fla., pp 943-955.

Andersson L (1973) Vegetationzoner och vattenståndsvariation vid sjön Mjörn. Svensk Bot Tidskr 67: 201-207.

Anttonen-Heikkilä K (1983) Säännöstelyn vaikutuksista Oulujärven ranta- ja vesikasvillisuuteen. Vesihallituksen tiedotuksia 231. Helsinki, 75 pp. (In Finnish).

Aulio K (1985) Biomass and chlorophyll contents of Isoetes lacustris as related to water depth in the Lake Pyhäjärvi, SW Finland. Aqua Fennica 15:127-131.

Bache DH & MacAskill IA (1984) Vegetation in civil and landscape engineering. Granada, London. 317 pp.

Bagemann W & Schiechtl HM (1986) Ingenieur biologie: Handbuch zum naturnachen Wasser- und Erdbau. Bauverlag GMBH, Wiesbaden und Berlin. 216 pp.

Barko JW & Smart RM (1983) Effects of organic matter additions to sediment on the growth of aquatic plants. J Ecol 71: 161-175.

Bernard JM (1973) Production ecology of wetlands sedges: the genus Carex. Pol Arch Hydrobiol 20:207-214.
Bernard JM (1976) Life history and population dynamics of shoots of Carex rostrata. J Ecology 64:1045-1048.
Blanch SJ, Ganf GG & Walker KF (1999) Tolerance of riverine plants to flooding and exposure indicated by water regime. Regulated rivers: research and management: 15:43-62.
Braak Ter CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179.
Brink Van den FWB, van der Velde G, Bosman WW & Coops H (1995) Effects of substrate parameters on growth responses of eight helophyte species in relation to flooding. Aquatic Botany 50:79-97.
Broome SW, Seneca ED & Woodhouse WW (1988) Tidal salt marsh restoration. Aquatic Botany 32: 1-22.
Clevering O (1999) The effects of litter on growth and plasticity of Phragmites australis clones originating from infertile, fertile or eutrophicated habitats. Aquatic botany 64:35-50.
Comes RD & McCreary T (1986) Approaches to revegetate shorelines at Lake Wallula on the Columbia River, Washington-Oregon. Technical report E-86-2, US Army Engineer Waterways Experiment Station, Vicksburg, Miss.
Coops H & Van der Velde G (1995) Seed dispersal, germination, and seedling growth of six helophyte species in relation to water-level zonation. Freshwater biology 34:13-20.
Coops H, Boeters R & Smit H (1991) Direct and indirect effects of wave attack on helophytes. Aquatic Botany 41:333-352.
Coops H, Geilen N & van der Velde G (1994) Distribution and growth of the helophyte species Phragmites australis and Scirpus lacustris in water depths gradients in relation to wave exposure. Aquatic Botany 48:273-284.
Coops H, Geilen N & van der Velde G (1996) Helophyte zonation in two regulated estuarine areas in the Netherlands: vegetation analysis and relationships with hydrodynamic factors. Estuaries 22:657-668.
Duarte CM & Kalff J (1986) Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. Limnol Oceanogr 31: 1072-1080.
Eloranta P (1978) Light penetration in different types of lakes in Central Finland. Holarct Ecol 1:362-366.
Eloranta P & Marja-aho J (1982) Transect studies on the aquatic macrophyte vegetation of Lake Saimaa in 1980. Biol Res Rep Univ Jyväskylä 9:35-65.
Elveland J (1984) Degeneration of wet hay-meadow vegetation caused by inundation at the stubble. Svensk Bot Tidskr 78:45-58.
Erixon G (1979) Environment and aquatic vegetation of a riverside lagoon in Northern Sweden. Aquat Bot 6:95-109.
Erixon G (1981) Aquatic macrophytes and their environment in the Vindelälven river, northern Sweden. Wahlenbergia 7:61-71.
Eurola S (1965) Beobachtungen Über die Flora Und Vegetation am südlichen Ufersaum des Saimaa-Sees in Südostfinnland. Aquilo Ser Botanica Tom 2: 1-56.
Fagerstedt KV (1992) Development of aerenchyma in roots and rhizomes of Carex rostrata (Cyperaceae). Nordic J Bot 12:115- 120.
Foote AL & Kadlec JA (1988) Effects of wave energy on plant establishment in shallow lacustrine wetlands. J of Freshwater Ecology 4(4):523-532.
Fowler DK & Maddox JB (1974) Habitat improvement along reservoir inundation zones by barge hydroseeding. J Soil Water Conserv 22: 263-265.
Fraisse T, Muller E & Decamps O (1997) Evaluation of spontaneous species for the revegetation of reservoir margins. Ambio 26: 375-381.
Gaboury MN & Patalas JW (1984) Influence of water level drawdown on the fish populations of Gross Lake, Manitoba. Can J Fish Aquat Sci 41: 118-125.
Gill D (1973) Modification of northern alluvial habitats by river development. Can Geogr 17:138-153.

Granberg K & Hakkari L (1980) Säännöstelyn vaikutuksista eräiden Kainuun järvien limnologiaan. Vesihallituksen tiedotuksia 187. 95 pp. (In Finnish).

Granberg K & Ruohonen K (1985) Saimaan vesikasvit ja sedimentit In: Saimaan ekologinen tutkimus vuosina 1980-1983. Vesihallituksen tiedotuksia 255:31-82. (In Finnish).

Grimås U (1961) The bottom fauna of natural and impounded lakes in northern Sweden. Rep Inst Freshwat Res Drottningholm 42:183-237.

Grimås U (1962) The effect of increased water level fluctuation upon the bottom fauna in Lake Blåsjön, northern Sweden. Rep Inst Freshwat Res Drottningholm 44:14-41.

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169-1194.

Håkanson L & Jansson M (1983) Principles of lake sedimentology. Springer, Berlin. 316 pp.

Hämet-Ahti L, Suominen J, Ulvinen T & Uotila P (eds) (1998) Retkeilykasvio (Field Flora of Finland) 4 Ed. Finnish Museum of Natural History, Botanical Museum. Helsinki 656 pp.

Hartog den C & Segal S (1964) A new classification of the water plant communities. Acta Bot Neerl 13:167-393.

Hellsten S (ed) (2000) Päijänteen säännöstelyn kehittäminen. Rantavyöhykkeen tila ja siihen vaikuttavat tekijät. Suomen ympäristö 394. 159 pp. + 9 app. (In Finnish).

Hellsten S & Alasaarela E (1984) Ekologisten näkökohtien huomioon ottaminen Pohjois-Suomen vesistöjen säännöstelyssä. Esitutkimus. VTT Building laboratory Report. 93 pp. + 11 app. Technical Research Centre of Finland, Oulu. (In Finnish).

Hellsten S & Joronen R (1986) Kemijärven litoraalin kasvisto ja kasvillisuus sekä niihin vaikuttavat ekologiset tekijät vuosina 1982-83. Rovaniemi, Kemijoen vesiensuojeluyhdistys ry. 39 pp. (In Finnish).

Hellsten S, Neuvonen I, Alasaarela E, Keränen R & Nykänen M (1989) Ekologiset näkökohdat joidenkin Pohjois-Suomen järvien säännöstelyssä. Osa 2. Rannan geomorfologia ja vesikasvillisuus. (Ecological aspects of lake regulation in Northern Finland. Part 2. Geomorphology and vegetation of the littoral zone.) VTT Research Notes 986, Espoo, 131 pp. + app. 13 pp. (In Finnish).

Hellsten S, Virtanen M, Nenonen O, Kinnunen K & Riihimäki J (1993) Relative importance of internal sources of phosphorus and organic matter in northern Finnish reservoirs. Wat Sci Tech 28: 85-94.

Hellsten S, Palomäki R & Järvinen E (1997) Inarijärven vedenkorkeuden säännöstelystä ja sen vaikutuksista rantavyöhykkeellä. Lapin ympäristökeskuksen moniste 2, Rovaniemi, 75 pp. + app. (In Finnish).

Hellsten S, Hellsten S, Kerätär K, Visuri M, Kääriäinen S & Huttula E (1999) Kemijärven säännöstelyn vaikutusten seurannasta, haitallisten vaikutusten lieventämisestä ja alustavista mahdollisuuksista säännöstelyn kehittämiseen. Lapin ympäristökeskuksen moniste 31: 1-50. (In Finnish).

Hellsten S, Huttu U, Visuri M, Kerätär K, Sinisalmi T, Riihimäki J, Juntura E, Väisänen T & Savolainen M (2000) Ähtärinjärven säännöstelyn kehittämisselvitys - Nykytila ja siihen vaikuttavat tekijät sekä mahdollisuudet säännöstelyn kehittämiseen. Alueelliset ympäristöjulkaisut 148. (In Finnish).

Hill MO (1979) TWINSPAN - A FORTRAN Program for Arranging Multivariate Data in an Ordered Two-Way Table by Classification of the Individuals and Attributes. Cornell University, Ithaca, NY, 48 pp.

Hill NM, Keddy PA & Wisheu IC (1998) A Hydrological Model for Predicting the Effects of Dams on the Shoreline Vegetation of Lakes and Reservoirs. Environmental Management 22(5):723-736.

Hutchinson GE (1975) A Treatise of Limnology. 3. Limnological Botany. Wiley, New York, 660 pp.

Huttunen A, Heikkinen K & Ihme R (1996) Nutrient retention in the vegetation of an overland flow treatment system in northern Finland. Aquat Botany 55:61-73.

Huusko A, Sutela T, Karjalainen J, Auvinen H & Alasaarela E (1988) Feeding of vendace (Coregonus albula L.) fry in a natural-state lake and a regulated lake in Northern Finland. Finnish Fisheries Research 9:447-456.

Huusko A, Sutela T, Karjalainen J, Hellsten S & Hirvonen A (1989) Ekologiset näkökohdat joidenkin Pohjois-Suomen järvien säännöstelyssä. Osa 4. Kalojen mädin ja poikasten selviytyminen. (Ecological aspects of lake regulation in Northern Finland. Part 2. Survival of spawn and juveniles of fishes.) VTT Research Notes 988, Espoo, 131 pp. + app. 13 pp. (In Finnish).

Juntura E, Ylinen H & Virtanen M (1999) Comparison of nearshore wind-wave measurements and model results in the development of a coupled wind-wave, hydrodynamic and sediment transport model for estimating coastal zone erosion. In: Brebbia CA & Anagnostopoulos P (eds) Coastal engineering and marina developments, WIT Press, Southampton, Boston 404-410.

Jutila HM (1997) Vascular plant species richness in grazed and ungrazed coastal meadows, SW Finland. Ann Bot Fenn 34:245-263.

Kaatra K & Marttunen M (eds) (1993) Oulujoen vesistön säännöstelyjen kehittämisselvitykset. (Impact assessment and mitigation in existing lake regulation projects in the Oulujoki river system) Vesi- ja ympäristöhallinnon julkaisuja 140. Helsinki, 157 pp. (in Finnish).

Kansanen A & Niemi R (1974) On the production ecology of isoetids, especially Isoëtes lacustris and Lobelia dortmanna, in Lake Pääjärvi, southern Finland. Ann Bot Fennici 11:178-187.

Keddy PA (1982) Quantifying within-lake gradients of wave energy: Interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. Aquatic Botany 14: 41-58.

Keddy PA (1983) Shoreline effects in Axe Lake, Ontario: Effects of exposure on zonation patterns. Ecology 64: 331-344.

Keränen R (1985) Wave-induced sandy shore formations and processes in Oulujärvi, Finland. Nordia 19: 1-58.

Keränen R, Riihimäki J, Asunmaa A, Madekivi O, Hellsten S, Alasaarela E & Seppänen E (1992) Oulujärven rantojen kasvillisuuden kehittyminen ja käyttöedellytysten parantaminen. (Development of littoral vegetation and possibilities of shore restoration in Lake Oulujärvi). Vesi- ja ympäristöhallituksen monistesarja 382. 67 pp. + 6 app. (in Finnish).

Koponen T, Karttunen K. & Piippo S (1995) Suomen vesisammalkasvio. (Summary: Aquatic bryophytes of Finland). Bryobrothera 3:1-86. (In Finnish).

Koskenniemi E (1987) Development of floating peat and macrophyte vegetation in a newly created, polyhumic reservoir, western Finland. Aqua Fenn. 17:165-173.

Koskenniemi E (1994) Colonization, Succession and Environmental Condition of the Macrozoobenthos in a Regulated, Polyhumic Reservoir, Western Finland. Int Revue ges Hydrobiol. 79: 521-555.

Kotilainen MJ (1958) Siniheinä. In: Jalas, J. (ed) Suuri kasvikirja I:346. Otava, Helsinki. (In Finnish).

Kurimo U (1970) Effect of pollution on the aquatic macroflora of the Varkaus area, Finnish Lake District.. Ann Bot Fennici 7:213-254.

Lester JE, Klimas CV, Allen HH & Shetron SG (1986) Shoreline revegetation studies at lake Texoma on the Red River, Texas-Oklahoma. Technical report E-86-1, US Army Eng. Waterways Experiment Station, Vicksburg, Miss.

Lillieroth S (1938) Die höhere Vegetation des Sees Lammen bei Aneboda. Lunds univ Årsskr N F Avd 2. 34:1-64.

Lindström T (1973) Life in a lake reservoir: fewer options, decreased production. Ambio 5: 145-153

Luther H (1951a) Verbreitung und Ökologie der höheren Wasserpflanzen im Brackwasser der Ekenäs-Gegend in Südfinnland. I Allgemeiner teil. Acta Bot Fennica 49:1-176.

Luther H (1951b) Verbreitung und Ökologie der höheren Wasserpflanzen im Brackwasser der Ekenäs-Gegend in Südfinnland. II Specieller teil. Acta Bot Fennica 50:1-370.

Mäki-Petäys A (1999) Habitat requirements of juvenile salmonids: towards ecologically-based fisheries management in boreal streams. Acta Univ Oul A322: 1-29.

Mäkirinta U (1978) Die pflanzensoziologische Gliederung der Wasservegetation im See Kukkia, Südfinnland. Acta Univ Oulu A75: 1-157.

Mäkirinta U (1989) Classification of South Swedish Isoetid vegetation with the help of numerical methods. Vegetatio 81:145-157.

Marttunen M & Hellsten S (1997) Säännöstelyjen kehittäminen - ympäristövaikutusten arvioinnista monitavoitteiseen päätöksentekoon. Vesitalous 6/1997:4-13. (In Finnish).

Marttunen M & Järvinen EA (eds) (1999) Päijänteen säännöstelyn kehittäminen. Yhteenveto ja suositukset. Suomen ympäristö 357. (In Finnish).

Maristo L (1941) Die Seetypen Finnlands auf floristischer und vegetations-physiognomischer Grundlage. Ann Bot Soc Vanamo 15: 1-314.

Mark AF (1987) Lake Level Control. In: Henriques PR (ed) Aquatic biology and Hydroelectric Power development in New Zealand. p. 113-123. Oxford University Press 1987, Auckland. 280 p.

Mark AF & Johnson PN (1985) Ecologically-derived guidelines for managing two New Zealand lakes. Environmental management 9: 355-363.

Mark AF & Kirk RM (1987) Lake levels and lakeshore erosion. In: Vant, W.N. (ed) Lake Managers Handbook. Water & Soil Miscellaneous publication No 103: 215-222. Hamilton. 230 p.

Milbrink G & Holmgren S (1981) Addition of artificial fertilizers as a means of reducing the negative effects of “oligotrophication” in lakes after impoundment. Drottingholm Rept 59:121-127.

Moss D, Furse MT, Wright JF & Armitage PD (1987) The prediction of the macro-invertebrate fauna of unpolluted running-water sites in Great Britain using environmental data. Freshw Biology 17:41-52.

Murphy KJ, Rørslett B & Springuel I (1990) Strategy analysis of submerged lake macrophyte communities: an International example. Aquatic Botany 36: 303-323.

Newbury RW & McCullough GK (1984) Shoreline erosion and restabilization in the Southern Indian Lake reservoir. Can J Fish Aquat Sci 41:558-566.

Nilsson C (1977) Älvstrand i förvandling. Svensk Bot Tidskr 71: 23-28.

Nilsson C (1978) Changes in the aquatic flora along a stretch of the River Umeälven, N. Sweden, following hydro-electric exploitation. Hydrobiologia 61:229-236.

Nilsson C (1981a) Dynamics of the shore vegetation of a North Swedish hydro-electric reservoir during a 5-year period. Acta Phytogeographica Suecica. 69.

Nilsson C (1981b) Vegetationsförändringar vid måttlig vattenkraftreglering. Fauna och Flora 76:129-134.

Nilsson C (1996) Remediating river margin vegetation along fragmented and regulated rivers in the north: what is possible? Regulated rivers: research and management 12: 415-431.

Nilsson C & Brittain JE (1996) Remedial strategies in regulated rivers: introductory remarks. Regulated rivers: research and management 12: 347-351.

Nilsson C & Keddy PA (1988) Predictability of change in shoreline vegetation in a hydroelectric reservoir, northern Sweden. Can J Fish Aquat Sci 45:1896-1904.

Nilsson C, Grelsson G, Johansson M & Sperens U (1989) Patterns of plant species richness along riverbanks. Ecology 70:77-84.

Nilsson C, Jansson R & Zinko U (1997) Long-Term responses of river-margin vegetation to water-level regulation. Science 276: 798-800.

Nykänen M (1998) Oulujärven rantakasvillisuuden dynamiikka kaudella 1980-1995 ja siihen vaikuttavista tekijöistä. Unpublished Phil Lic Thesis, Univ Oulu, Dept Biology.

Ostendorp W (1989) Die-back of reeds in Europe- a critical review. Aquatic botany 35:5-26.

Palomäki R (1992) Oulujärven rantatyyppien ja rantahabitaattien suhteellisten osuuksien arviointi. Vesi- ja ympäristöhallituksen monistesarja 385: 1-31. (In Finnish).

Palomäki R (1994) Response by macrozoobenthos biomass to water level regulation in some Finnish lake littoral zones. Hydrobiologia 286:17-26.

Palomäki R & Koskenniemi E (1993) Effects of bottom freezing on macrozoobenthos in the regulated Lake Pyhäjärvi. Arch Hydrobiol 128:73-90.

Palomäki R & Hellsten S (1996) Littoral macrozoobenthos biomass in a continuous habitat series. Hydrobiologia 339: 85-92.

Pearce CM & Cordes LD (1988) The Distribution and Ecology of Water Horsetail (Equisetum fluviatile) in Northern Wetlands. J of Freshwater Ecology 4(3):383-394.

Pearsall WH (1920) The aquatic vegetation of the English lakes. J Ecology 8: 164-201.

Pieczynska E (1972) Ecology of the eulittoral zone of lakes. Ekol Polska 22:637-732.

Pieterse AH & Murphy KJ (1990) Aquatic Weeds. The Ecology and Management of Nuisance Aquatic Vegetation. Oxford University Press, Oxford. 593 pp.

Quennerstedt N (1958) Effect of water level fluctuation on lake vegetation. Verh Internat Ver Limnol 13:901-906.

Raatikainen M & Kuusisto E (1988) Suomen järvien lukumäärä ja pinta-ala. Terra 102(2): 97-110. (In Finnish).

Raspopov IM, Slepukhina TD, Vorontzov FF & Dotzenko ON (1988) Wave effects on the bottom biocenoses in the Onega Lake bays. Arch Hydrobiol 112:115-124.

Renman G (1986) Distribution of littoral macrophytes in a North Swedish river in relation to winter habitat conditions. Aquatic Botany 33: 243-256.

Renman G (1989) Distribution of littoral macrophytes in a north Swedish riverside lagoon in relation to bottom freezing. Aquatic Botany 33:243-256.

Renman G (1993) Frost formation in the ecotonal zone and its role for release of nutrients. Hydrobiology 251:65-72.

Riihimäki J & Hellsten S (1997) Konnivesi-Ruotsalaisen säännöstelyn vaikutusten selvittäminen - Säännöstelyn vaikutukset rantavyöhykkeessä sekä esitys ekologiseksi säännöstelykäytännöksi. Suomen ympäristö 153. (In Finnish).

Rintanen T (1976) Lake studies in eastern Finnish Lapland. I. Aquatic flora: Phanerogams and Charales. Ann Bot Fennici 13: 137-148.

Rintanen T (1996) Changes in the flora and vegetation of 113 Finnish lakes during 40 years. Ann Bot Fennici 33:101-122.

Rørslett B (1984) Environmental factors and aquatic macrophyte response in regulated lakes – a statistical approach. Aquatic Botany 19:199-220.

Rørslett B (1985a) Regulation impact on submerged macrophytes in the oligotrophic lakes of Setesdal, South Norway. Verh Internat Verein Limnol 22:2927-2936.

Rørslett B (1985b) Death of submerged macrophytes-actual field observations and some implications. Aquatic Botany 22:7-19.

Rørslett B (1987a) Statistics of the underwater light field: an empirical model. Int Revue ges Hydrobio 72:1-25.

Rørslett B (1987b) A generalized spatial niche model for aquatic macrophytes. Aquatic Botany 29:63-81.

Rørslett B (1987c) Niche statistics of submerged macrophytes in Tyrifjord, a large oligotrophic Norwegian lake. Arch Hydrobiol 111:283-308.

Rørslett B (1988a) An integrated approach to hydropower impact assessment. I. Environmental features of some Norwegian hydro-electric lakes. Hydrobiologia 164:39-66.

Rørslett B (1988b) Niche extension of aquatic macrophytes in hydrolakes: Predictive assessments of enviromental impacts. Int Revue ges Hydrobiol 73:129-143.

Rørslett B (1989) An integrated approach to hydropower impact assesment. II. Submerged macrophytes in some Norwegian hydro-electric lakes. Hydrobiologia 175:65-82.

Rørslett B & Brettum P (1989) The genus Isoetes in Scandinavia: an ecological rewiew and perspectives. Aquatic Botany 35:223-261.

Rørslett B & Johansen SW (1996) Remedial measures connected with aquatic macrophytes in Norwegian regulated rivers and reservoirs. Regulated rivers: Research & Management 12:509-522.

Segal S (1971) Principles on structure, zonation and succession of aquatic macrophytes. Hidrobiologia 12:89-95.

Selin P & Hakkari L (1982) The diversity, biomass and production of zooplankton in Lake Inarijärvi. Hydrobiologia 86:55-59.

Sjöberg K & Danell K (1983) Effects of permanent flooding on Carex-Equisetum wetlands in northern Sweden. Aquatic Botany 15:275-286.

Spence DNH (1982) The zonation of plants in freshwater lakes. Adv In ecol Res 12:37-125.

Stockner JG & MacIsaac EA (1996) British Columbia Lake Enrichment Programme: Two Decades of Habitat Enhancement for Sockeye Salmon. Regulated rivers: Research and management 12:547-561.

Sundborg Å (1977) River, hydropower, environment – environmental effects of hydropower development. Motala, Statens naturvårdsverk, 150 pp.
Szmeja J (1987) The structure of a population of Lobelia dortmanna L. along a gradient of increasing depth in an oligotrophic lake. Aquatic Botany 28:1 13.
Tikkanen P, Niva T, Yrjänä T, Kuusela K, Hellsten S, Kantola L & Alasaarela E (1988) Effects of regulation on the ecology of the littoral zone and the feeding of whitefish, Coregonus spp., in lakes in Northern Finland. Finnish Fisheries Research 9: 457-465.
Tikkanen P, Kantola L, Niva T, Hellsten S & Alasaarela E (1989) Ekologiset nakökohdat joidenkin Pohjois-Suomen järvien säännöstelyssä. Osa 3. Järven pohjaeläimistö ja aikuisten kalojen ravinto (Ecological aspects of lake regulation in Northern Finland. Part 2. Macrozoobenthos and feeding of fish.) VTT Research Notes 988, Espoo, 131 pp. + app. 13 pp. (In Finnish).
Toivonen H & Nybom C (1989) Aquatic vegetation and its recent succession in the waterfowl wetland Koijärvi, South Finland. Ann Bot Fenn 26:1-14.
Toivonen H. & Huttunen P (1995) Aquatic macrophyted and ecological gradients in 57 small lakes in southern Finland. Aquatic botany 51:197-221.
Vaarama A (1938) Wasservegetationstudien am Grossee Kallavesi. Ann Bot Soc Vanamo 13(1):1-314.
Vähäsöyrinki E (1997) Vesistön säännöstelyt ja niiden tarkistaminen. Vesitalous 6/1997: 1-3. (In Finnish).
Walker BH. & Wehrhahn CF (1970) Relationships between derived vegetation gradients and measured environmental variables in Saskatchewan wetlands. Ecology 52:85-95.
Wallsten M & Forsgren PO (1989) The effects of increased water level on aquatic macrophytes. Journal of Aquatic Plant Management 27:32—37.
Wassen G (1966) Gardiken. Vegetation und Flora eines Lappländischen Seeufers. K Sven Vetenskapsakad Avhandl Naturskydds 22:1-142.
Weiher E & Keddy PA (1995) The assembly of experimental wetland plant communities. Oikos 73: 323-335.
Weisner SEB (1991) Within-lake patterns in depth penetration of emergent vegetation. Freshwater Biology 26:133-142.
Whittaker RH (1977) Evolution of species diversity in land communities. Evol Biol 10: 1-67.
Wilcox DA & Meeker JE (1991) Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota. Can J Bot 69:1542-1551.
Wilcox DA & Meeker JE (1992) Implications for faunal habitat related to altered macrophyte structure in regulated lakes in northern Minnesota. Wetlands 12(3): 192-203.
Wisheu IC & Keddy PA (1989) Species richness - standing crop relationships along four lakeshore gradients: constraints on the general model. Can J Bot 67:1609-1617.
Wium-Andersen S (1971) Photosynthetic uptake of free CO_2 by roots of Lobelia dortmanna. Physiol Plant 25:245-248