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Macrophyte Development and Habitat Characteristics in Sweden's Large Lakes

The four largest Swedish lakes, Vänern, Vättern, Hjälmaren, and Mälaren, were surveyed by means of aerial IR-color photography in the 1970s. Along small slope gradients in all lakes the emergent communities extended to a width of hundreds of meters, while the extent on steeper slopes was a few meters. Because of the fractionate shape, L. Mälaren has a very long shoreline, which promotes vegetation growth in the transition zone between land and water. Sheltered conditions are numerous and water lilies and other floating leaved and freely floating plants are abundant. Emergent as well as submerged macrophytes grow vigorously in the northernmost part of the oligotrophic lake Vättern. In L. Vänern exposed shores predominate, but sheltered bays and archipelagos are overgrown with reeds. In the shallow lake Hjälmaren monospecific stands of *Phragmites australis* are dominant. Recurrent surveys of L. Mälaren and L. Vänern in the 1990s showed changes that could be connected to the watertable fluctuations, which have been stabilized since the first investigation. Reeds and water lilies expanded in sheltered parts of the lakes, while the distribution of reed stands growing at their deep limit decreased.
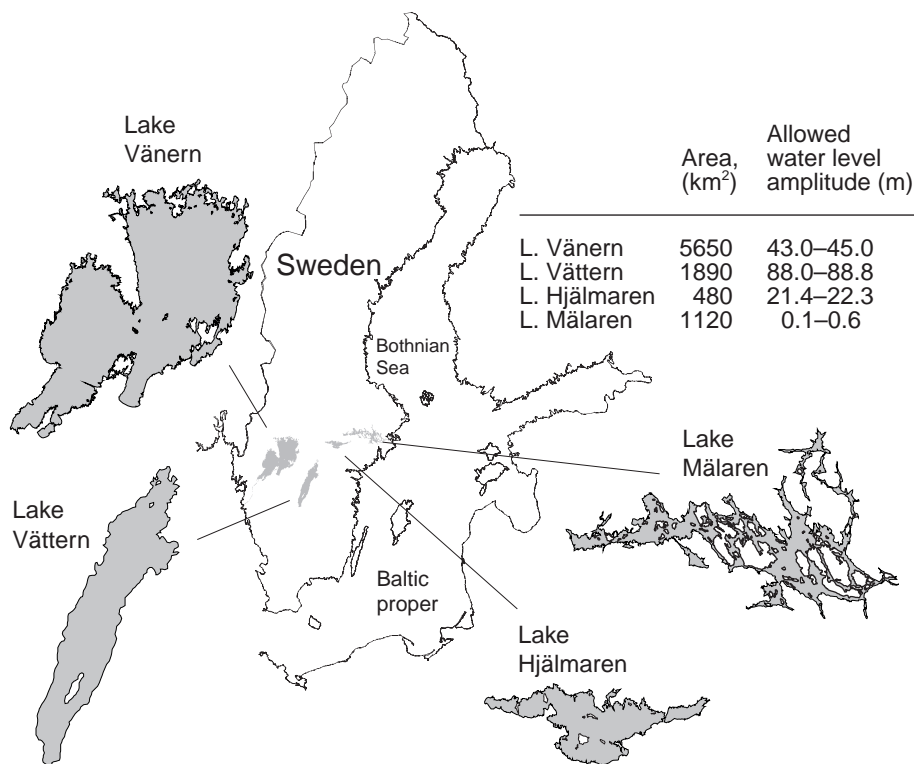
	Area, (km^2)	Allowed water level amplitude (m)
L. Vänern	5650	43.0–45.0
L. Vättern	1890	88.0–88.8
L. Hjälmaren	480	21.4–22.3
L. Mälaren	1120	0.1–0.6

Figure 1. Map of Sweden with the central large lakes Vänern, Vättern, Hjälmaren, and Mälaren.

INTRODUCTION

The vegetation of the terrestrial-freshwater transition zone is extremely well developed in most regions of the world (1). This is true also for the large Swedish lakes Mälaren, Hjälmaren, and the shallow parts of Vänern and Vättern (Fig. 1). A wide range of human activities may, however, lead to deterioration of inland surface waters either directly or indirectly. An obvious effect being overgrowth by aquatic macrophytes along the lake margins caused by increased nutrient levels in water and/or changes in the hydrological regime through drainage and water regulation (2). Overgrowth by reeds became a problem in the large Swedish lakes in the late 1960s, and a monitoring program for observing distribution and biomass of reeds and floating-leaved vegetation was initiated. Recurrent observations in Mälaren and Vänern led to revised processing of data, which are now discussed in view of the changes in the hydrological regime and the ecotone concept.

THE LAND-WATER TRANSITION ZONE

As a zone of contact between different ecosystems the land-water ecotone can be regarded as part of the edge of these ecosystems and as an individual system entity, characterized by a special structure and mode of operation conditioned by land-water coupling. Today, land-water ecotones are recognized as ecological systems of specific and variable abiotic and biotic characteristics, different from adjacent ecosystems (3). The change from terrestrial to freshwater environments is usually gradual and characterized by relatively mild physical and chemical gradients, allowing the development of a permanent cover of species-rich plant communities on the shores of most freshwater habitats. In this transition zone, macrophytic plant species have maintained a semiaquatic life form, enabling them to grow and survive both in air and in water (4).

Aquatic macrophyte vegetation is an key element in aquatic ecosystems and lake vegetation has also often been used as a classification tool because the geographical position, morphology, and catchment character are reflected by the species distribution and community composition (5). Large vascular plants whether rooted or free-floating, submerged or emergent, provide habitat areas for aquatic or semiaquatic organisms (Fig. 2). Lake shallows overgrown by emergent vegetation normally described as littoral, eulittoral, wetland, etc. can also be considered as ecotone habitats (6).

Littoral zone vegetation is a prime area for spawning fish species and is also used as food source by the animals that frequent aquatic environments. In addition, aquatic vegetation serves to anchor soft sediments, to stabilize underwater slopes and to remove suspended particles from the overlying water. Thus, a healthy, natural aquatic plant community is important (2). However, through eutrophication or invasion of alien species, aquatic plant communities may grow to excessive proportions and alter biological conditions. Both the development of plant growth up to the surface, and excessive amounts of plant material,

Figure 2. Ecotonal zone between the terrestrial and limnetic zones. Wetland plants grow between the mean and high water levels, e.g. *Carex acuta, Iris pseudacorus* and *Typha latifolia* ①. Members of the reedbed are *Phragmites australis, Schoenoplectus lacustris* and/or *Typha angustifolia* ②. Floating-leaved vegetation consists mainly of *Nuphar lutea, Nymphaea candida, Potamogeton natans* and *Persicaria amphibia* ③. Submerged caulescent species belong to *Potamogeton, Myriophyllum, Ceratophyllum* or *Elodea* ④. Submerged rosette species are *Lobelia dortmanna, Littorella uniflora* and *Isoëtes lacustris* ⑤ and on deeper levels mostly *Nitella* spp. and mosses ⑥.
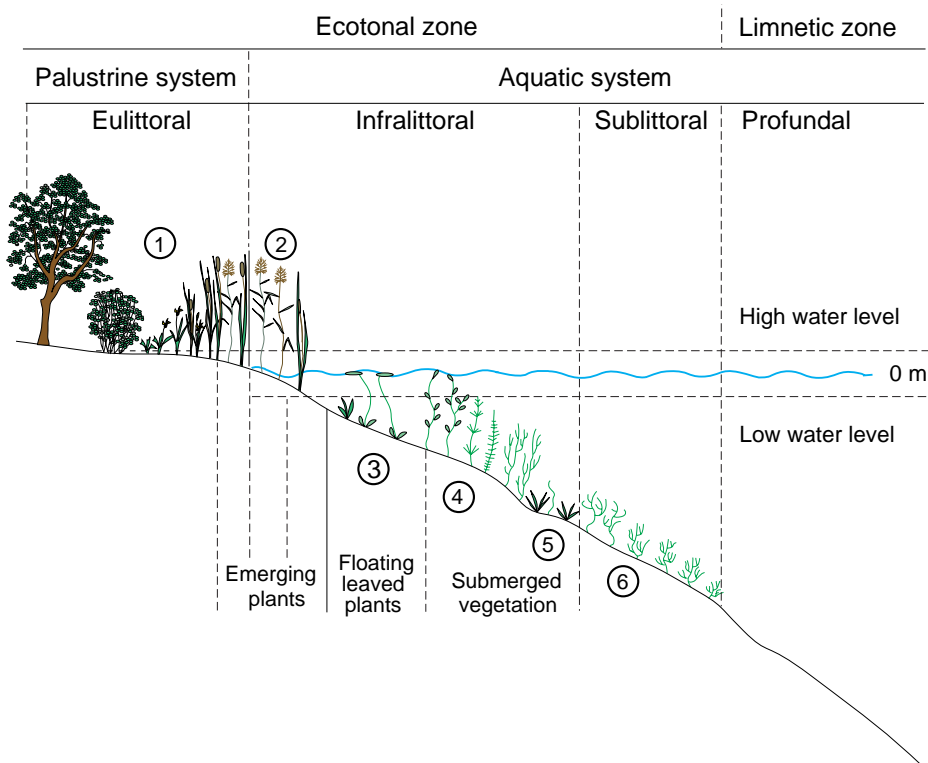
contribute to nuisance problems such as impairment of recreational activities (e.g. swimming, fishing, boat traffic), and a decrease in aesthetic quality (7).

The contact areas between terrestrial and aquatic ecosystems along lake margins are limited by maximal high- and minimal low-water levels. In most natural lakes, this periodically flooded zone is relatively narrow. It is, however, wider in large post-glacial lakes with extensive shallow areas (8). Water depth, substrate characteristics and environmental disturbances, e.g. wind and wave action, are extremely important in regulating species composition and for their effects on the within-lake distribution of shoreline plants. Exposure is related to the wave height, which is a function of fetch (the distance over which waves can build up), wind speed, and wind duration. Waves affect vegetation, directly by uprooting seedlings or damaging mature plants, and indirectly by eroding fine sediments and preventing litter deposition. Mechanical impact on reed stands varies with bottom configuration (Fig. 3).

Aquatic vegetation in large lakes on the European continent is heavily disturbed by urbanized coastlines and litter, which strengthen the wave impact (9). A method to use measurements of effective fetch for ranking stretches of shoreline along an exposure gradient seems biologically meaningful (10), however, when applied to 7 lakes in southern Sweden, the relationship was acceptable only for sites with relatively soft substrate (11). The Swedish results suggest that distribution of emergent vegetation in moderately wave-exposed eutrophic lakes can be predicted largely from substratum character and water depth (11).

LAKE CHARACTERISTICS

The four large Swedish lakes, Vänern, Vättern, Hjälmaren, and Mälaren are situated in the southern coniferous forest region or the boreo-nemoral (hemi-boreal) vegetational zone (Fig. 1). The lakes are all of glacial origin, and extensive shallow areas occur in some parts of the lakes, e.g. along the northern shores of Mälaren and Hjälmaren. There are shallow bays and archipelagoes in L. Vänern and the northernmost part of L. Vättern. L. Mälaren and L. Hjälmaren are characterized as eutrophic, L. Vänern as an oligotrophic lake with brownish water and L. Vättern as a deep, oligotrophic, clearwater lake.

In the late 1930s, Vänern was dammed up, to form a long-term regulated hydroelectric reservoir. The amplitude was limited to 2 m, but the water-level rhythm was reversed from high to very low in spring and early summer. The maximum level now comes in late summer and/or autumn. Reeds were readily established from seeds on bare shores, and on some local sites the common reed, *Phragmites australis,* was planted to prevent bottom erosion. Vegetation distribution thus changed from a sparse distribution of reeds in the 1920s to vast vegetated areas in sheltered bays and archipelagoes in the 1950–1960s. Nutrient load increased due to untreated wastewater discharges concurrent with water regulation and this intensified the growth effect. Discharges of ligneous silt from cellulose mills colored the water brown, however, effluent reductions have faded the water color considerably.

In L. Vättern, the lake margins are steep without conspicuous littoral zones, except in the northern part. The water is very clear, which is a prerequisite for the vigorous growth of submerged plants.

The topography of L. Mälaren is composed of separate basins, divided by islands and forelands linked by straits. The outlets are regulated in order to impede saline water inflow from the Baltic Sea. The permitted water-level amplitude is about 1 m. The westernmost basin, Galten, is very eutrophic with high phosphorus content (> 50 µg P L^{-1}). The nitrogen supply to this basin was very high when a fertilizer plant was located, but this nutrient input decreased considerably when new treatment methods were introduced at the plant during the 1970s. Decreasing phosphorus concentrations have been measured all over the lake. Nitrogen concentrations, except in Galten, however, have remained high, and even increased, especially in the northernmost basin. The eastern parts of L. Mälaren are deep and have a moderate nutrient content (~ 20 µg P L^{-1}).

In L. Hjälmaren, the water surface has been permanently lowered twice, in 1882 and 1886. The lowering was extensive, and totals about 2 m. A large number of skerries and rocky islets arose from the water. Some of the newly-formed islets were objects of studies already in 1886, and investigations were recurrent (12). Conditions for the original aquatic vegetation deteriorated, but new areas for colonization were created. Without lowering of the water surface, the aquatic macrophytes would have

been located in the accession areas (Fig. 4). The original coves had been clogged with vegetation but ice and waves as well as human activity would have left parts of them open. Some sounds would also have been kept passable. The accession of land was small along the steep, southern shores, and before lowering of the water surface the vegetation was extremely sparse. There is still not much vegetation on the southern shores of the eastern part of the lake, in contrast to the northern shores and the western basins, where extensive belts of *Phragmites australis* occur.

REMOTE SENSING AND FIELD MEASUREMENTS

To obtain an overview of the huge land-water ecotones along the coastline of the lakes, remotely-sensed images were needed. Air photography, from a height of 1500 m, with near infrared color film (IR) was chosen in 1969–1975 for the survey of the vegetated lake areas. The IR-technique combining aerial photography with multiband sensing was still in the research phase, with civilian use, mainly limited to forestry and agricultural purposes. The technique is now used in Sweden as a surveying tool for mapping native wild plants. Subunits of both terrestrial and aquatic ecotones are resolved reasonably well when photographs are taken at a scale of 1:10 000. With satellites the resolution is too low so remote sensing by aerial photography, even at a reduced scale, can still be a useful solution (13).

Only IR-material was used for the main part of the aerial photographs, and no true color information exists. Therefore, no information is available for distinct species below the water surface. Emerging and floating-leaved plant species show different signatures in the near infrared spectral bands and field observations were conducted to facilitate interpretation of key species on the photos (14, 15). The aquatic vegetation in the littoral area consists largely of stands dominated by single species of *Phragmites australis, Schoenoplectus lacustris, Typha angustifolia* and *Nuphar lutea*. These could easily be identified on the photographs (Fig. 5). Interpretations

A

T = Drift   Mechanical impact   Water surface

Subsudal of waves in reedbed stands on the shore

B

Wave 1. Subdued by friction

Wave 1. (big)   Wave 2. (small)

H_1 H_2

L_1 L_2 $d_1 = L_{1/2}$ d_{lk} $d_2 = L_{2/2}$

Wave 1 Breakpoint   Wave 2. Subdued by friction

C

Wave 1. Without friction

$d < d_{lk}$ d_2
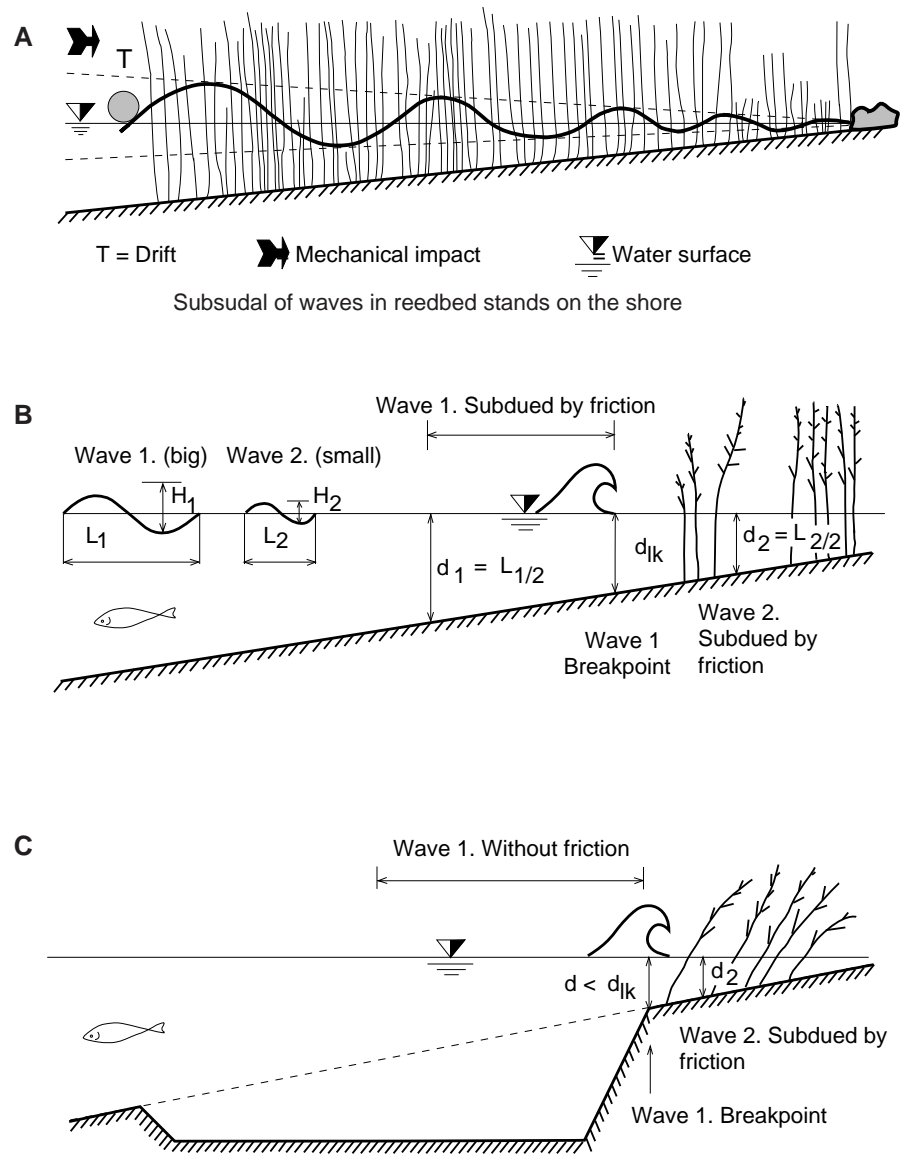
Wave 2. Subdued by friction

Wave 1. Breakpoint

Figure 3. Wave effect on different lake coastlines. A) In natural shore conditions the waves are continuously moderated within the reedbed zone (broken line). Litter is deposited on land. B) Another situation on natural lake shores. The waves transport water from a depth d_1 (big waves) to d_2 (small waves). If the depth is smaller than the wave height the friction against the bottom surface leads to a loss of wave energy. Wave 1 breaks at the critical depth d_{lk}. The smaller Wave 2 is reaching further into the reedbed without bottom friction. However, this wave loses force within the reedbed and becomes more harmless the longer the distance; i.e. on gently sloping bottoms the energy is lost totally before land connection and litter may be deposited within the reeds. If bottom configuration is steep, more strength remains in the waves. C) Influence of a depression in the bottom surface. The depression (not according to scale) has no influence on wave 2, because this wave is affected at a smaller depth. However, Wave 1 is unprevented from reaching the reedbed beyond the depression, where the depth suddenly becomes too shallow for this wave, therefore, it breaks on the depression edge and causes severe impact on the reeds. Presence of gaps in the reedbed zone can be explained by impact of such forces. Redrawn from Lachavanne et al. (9).

Figure 4. Land accession after lake surface lowering 1882–1886, Hjälmaren.

0   5   10   15 km

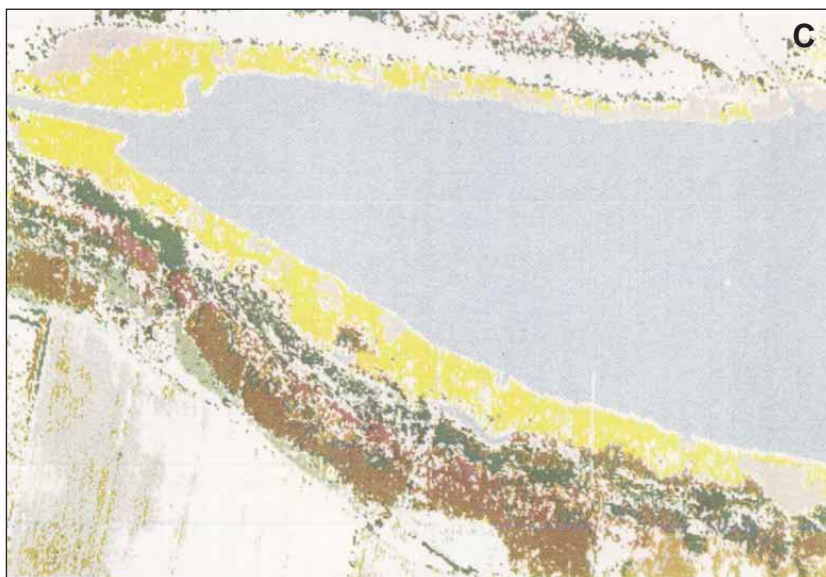© Royal Swedish Academy of Sciences 2001
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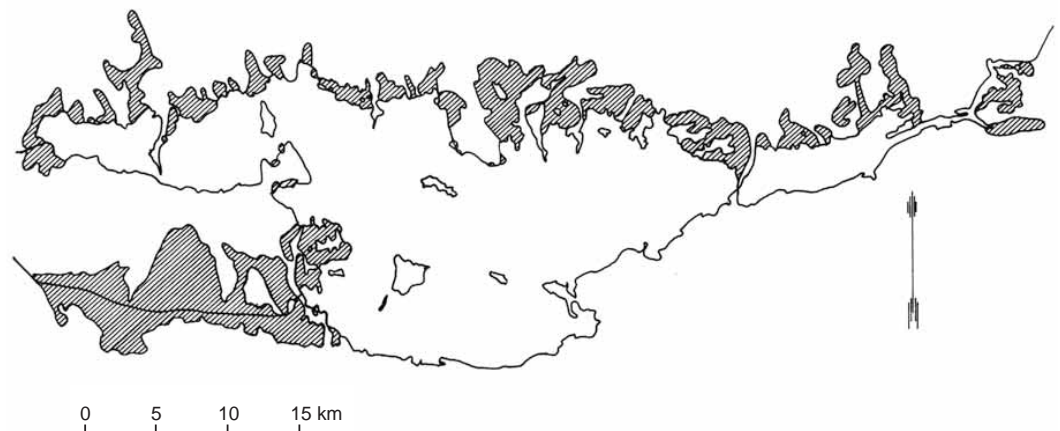
Figure 5. A) Aerial IR-color photograph of the innermost part of Lårstaviken, in northern Mälaren. B) The vegetation map is constructed from interpretation of the photographs from 1975. C) Computer classification map showing results from a simultaneous multispectral scanner registration from an aircraft.
Yellow = *Nuphar lutea*; dark green = *Phragmites australis*; light green = *Glyceria maxima*; brown = *Carex* spp.; lilac = *Schoenoplectus lacustris*; brownish = *Equisetum fluviatile*; black = dead vegetation; blue = water.
Air photo: Copyright National Land Survey, Gävle, Sweden M2001/5200. Permission for distribution approved by the Security Officer, National Land Survey of Sweden 2001-09-17.

were performed successfully and distribution maps of emergent and floating-leaved vegetation were drawn for all of the Mälaren and Hjälmaren, as well as parts of the other two lakes, Vänern and Vättern, during the period 1969–1975. Species in more complex communities, such as *Potamogeton natans, Nymphaea candida* and *Persicaria amphibia* could also be identified on IR-color photos (15). *Equisetum fluviatile* and *Typha latifolia*, which are readily identified on true color photo (16), are close to *Schoenoplectus* in the near infrared and therefore careful field-work is necessary for successful interpretation.

The interpreted shoreline length of L. Mälaren was 2218 km (17, 18), of L. Hjälmaren 366 km (19), and of L. Vättern (the northernmost part) 328 km (20). In L. Vänern, 9 selected areas (Fig. 6) were photographed and interpreted along a summarized shorelength of 1604 km (21). A repeated aerial documentation of L. Vänern was performed in 1999 with the aim of detecting changes in the ecotone (22). Water level was 0.6 m higher at date of the repeated air photography (July 1999) than it was on the first occasion (July 1975), a factor to consider when interpreting cause-effect relationships of changes in species composition and distribution.

Species composition and biomass data on emergent and floating-leaved littoral plants were analyzed in the field by stratified sampling of vegetation in all lakes. The measurements were made along randomly selected transects, perpendicular from the bank and out to the depth limit of vegetation, by analyzing quadrats (1 x 1 m) every 5th meter. The most thorough investigations were performed in L. Mälaren with analyses of all together some 100 transects 1970–1972 (17, 18). Especially in the northern basins, extending from the capital of Stockholm and northwards, numerous sites were chosen. A smaller number of transects were investigated in the other lakes during 1971–1976, 20 in L. Hjälmaren (19), 16 in L. Vänern (21), and 15 in L. Vättern (20). Follow-up observations were made on a restricted number of sites in L. Mälaren in 1975, 1977, and 1980 (23). All sites in the main part of the lake and a few sites in the northern basins were reinvestigated in 1996 (24). The investigations in Lake Hjälmaren were repeated on a re-

Figure 6. Mapped areas of Vänern and aerial IR-color photograph representing, Lurö archipelago. Air photo: Copyright National Land Survey Gävle Sweden M2001/5200. Permission for distribution approved by the Security Officer, National Land Survey of Sweden 2001-09-17.
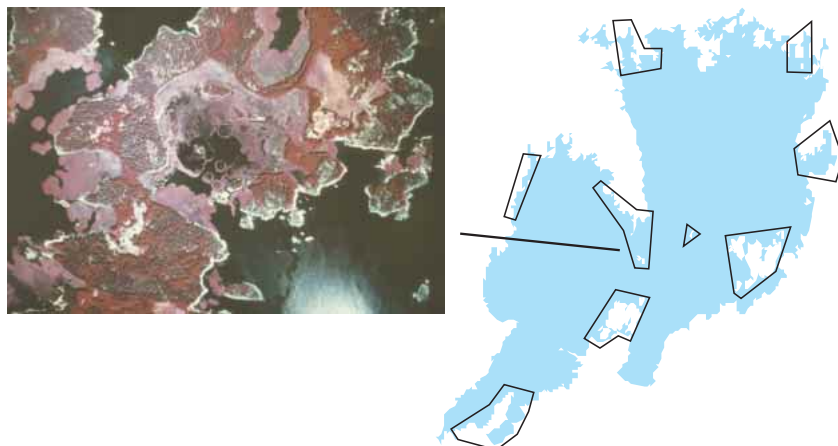
stricted number of sites in 1976 and 1977 (23).

Initially, in 1969, an attempt to investigate submerged vegetation by SCUBA diving was performed in the northern basin of L. Mälaren. Scarce occurrence of submerged macrophytes, however, interrupted this attempt, but a re-investigation was later made in the eastern parts of the main lake (23). The investigated northern part of L. Vättern has vigorous submerged vegetation, which was studied by field observations in 1973 by means of a viewing tube in shallow water and a rake in deeper water. In this lake, earlier investigations of species richness were available from 1939 (25).

THE HYDROLOGICAL REGIME AND MACROPHYTES

Generally, shrub thickets with species intolerant to flooding may dominate the upper landward part of a lake margin. Wet meadow vegetation develops between the maximum high and mean water level and occurs wherever slope and substrate conditions are not too steep or rocky. Wet meadows are diverse wetland communities, often dominated by sedges (*Carex* spp.) and grasses (e.g. *Glyceria maxima, Deschampsia caespitosa, Calamagrostis* spp. and *Phalaris arundinacea*) and supported by rushes (*Eleocharis* spp.), horsetails (*Equisetum* spp.) and additional herbaceous species. During low water conditions, herbaceous and woody plants are able to invade this area but may be killed when flooded during long-lasting high water phases. Where slopes are very gentle, shoreline wet meadows can cover vast areas, e.g. in sheltered bays of Mälaren and Vänern.

Between the mean water level and the extreme minimum is the zone in which emergent aquatic vegetation is best developed. The emergent aquatics can survive permanent flooding, but many require occasional low water levels to expose the lake bottom in order for seedlings to establish. Some emergent vegetatively spreading aquatics (reeds), however, can permanently grow in water as deep as 1.5–2.2 m beneath the low water level, which is the zone where submerged aquatic vegetation survives continuously (Fig. 2).

In most areas of the large lakes, the major dominant species is common reed, *Phragmites*
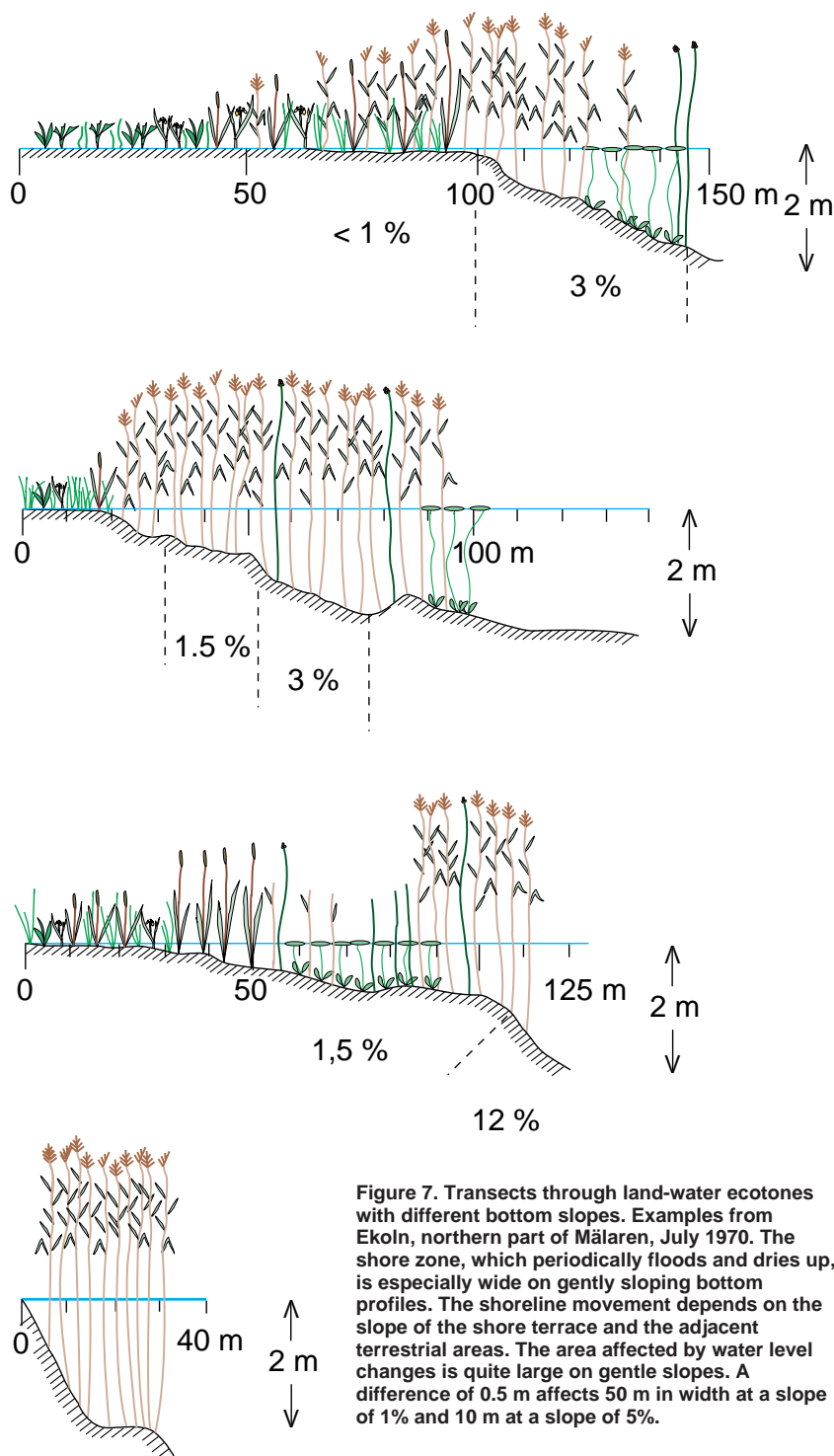

Figure 7. Transects through land-water ecotones with different bottom slopes. Examples from Ekoln, northern part of Mälaren, July 1970. The shore zone, which periodically floods and dries up, is especially wide on gently sloping bottom profiles. The shoreline movement depends on the slope of the shore terrace and the adjacent terrestrial areas. The area affected by water level changes is quite large on gentle slopes. A difference of 0.5 m affects 50 m in width at a slope of 1% and 10 m at a slope of 5%.

australis. Locally, in Vättern and Mälaren *Typha angustifolia* and *Schoenoplectus lacustris* also dominate extensive areas. In shallow water (< 15 cm deep) *Carex acuta, Equisetum fluviatile, Glyceria maxima, Iris pseudacorus, Sparganium erectum, Typha latifolia*, as well as some species among the genera *Alisma, Bidens, Eleocharis, Juncus, Lycopus, Lysimachia, Ranunculus*, and *Sagittaria* may dominate or be mixed with the dominating species.

At or just above the water line, seasonal water level fluctuations and waves cause erosion and deposition. This repeated disturbance produces a strand zone with sparse vegetation. Low litter deposition and abrupt slopes on the landward zone sometimes create a gap with open water between strand and perennial reed species, which occur at depths where the disturbance is less pronounced (Fig. 7). In the gaps, small stands of some species with different life strategies sometimes can survive.

The submerged and floating-leaved aquatic plants grow in water deeper than the maximum depth tolerated by emergent species. They also occur in shallow water, in openings within the emergent plant zone and as an occasional 'understorey' to emergent aquatic vegetation. Among the most important are *Potamogeton* spp., *Myriophyllum* spp., *Ceratophyllum demersum, Utricularia vulgaris, Elodea canadensis, Nuphar lutea, Nymphaea alba* (coll.).

During low water periods several changes of the littoral vegetation can be expected. Soil chemistry may change when oxygenated, and some plant species alter their growth form to accommodate to dryer conditions (1, 26). Low water periods allow many species and vegetation types to regenerate from buried seeds, and emergent species will propagate vegetatively under shallow water. However, both emerging seedlings and vegetative propagules cannot withstand deeper water and will gradually die out under rising water levels. High water periods also kill dominant species, thereby creating gaps, which other species can colonize during low water periods (27). Also woody plants are extinguished by permanent high water levels thereby extending aquatic species landward. Fluctuating water levels increase the area of shoreline vegetation, and the diversity of vegetation types and plant species. Any stabilization of water levels would likely reduce the ecotone area, as well as vegetation and plant species diversity.

However, the natural flooding of the Swedish large lakes is modified by water regulation, especially in Vänern and Mälaren. Additionally, the interest in increased shipping capacity has, during the latter decades of the 20th century, resulted in agreements minimizing annual water-level amplitudes around the mean water level, as determined by the water-rights court.

In L. Vänern the annual water-level amplitude has been reduced as a result of negotiations between different water tenants. Since the 1980s, monthly mean-level amplitude has been small, 0.8 m most of the time, in relation to the allowed regulation range of 2 m (Fig. 8). Mean levels of < 44.0 m and levels > 44.8 m became very rare. The frequency of extreme values decreased from 15% to 3%. Thus, the constantly flooded zone increased in area and deepened in recent decades.

Normally, in the late 1960s and early 1970s the shores of L. Mälaren were flooded in springtime, and minimum water level occurred in August. Within this period the fluctuations between high and low water levels frequently exceeded 40 cm, but later during the 1980s the water regime was stabilized because low water levels were kept 15–25 cm higher than the long-term normal low water level. Since spring flooding has been rare in the 1990s, due to very small amounts of snow in winter, the water level has been extremely stabile, with the fluctuation amplitude often < 30 cm (Fig. 8). When the low water level and the high water level are close to the mean, a narrower area is dried up in late summer and a relatively small area is seasonally flooded. Thus, the entire fluctuating area is narrowed by regulation, so ecotone habitats may lose heterogeneity.

In L. Hjälmaren, the dominant water-level fluctuations are similar to those in L. Mälaren. The main amplitude is ~ 30 cm, amplitude that frequently was more extended in the 1970s (Fig. 8). The patterns in L. Vättern seem to be somewhat different, with a dry period and low water levels in the beginning of the

Figure 8. Yearly water levels given as percentiles (10, 50 and 90%). Data since 1940 in Vänern, 1965 in Mälaren and since 1975 in Vättern and Hjälmaren. Figures on the Y-axis show m a.s.l.
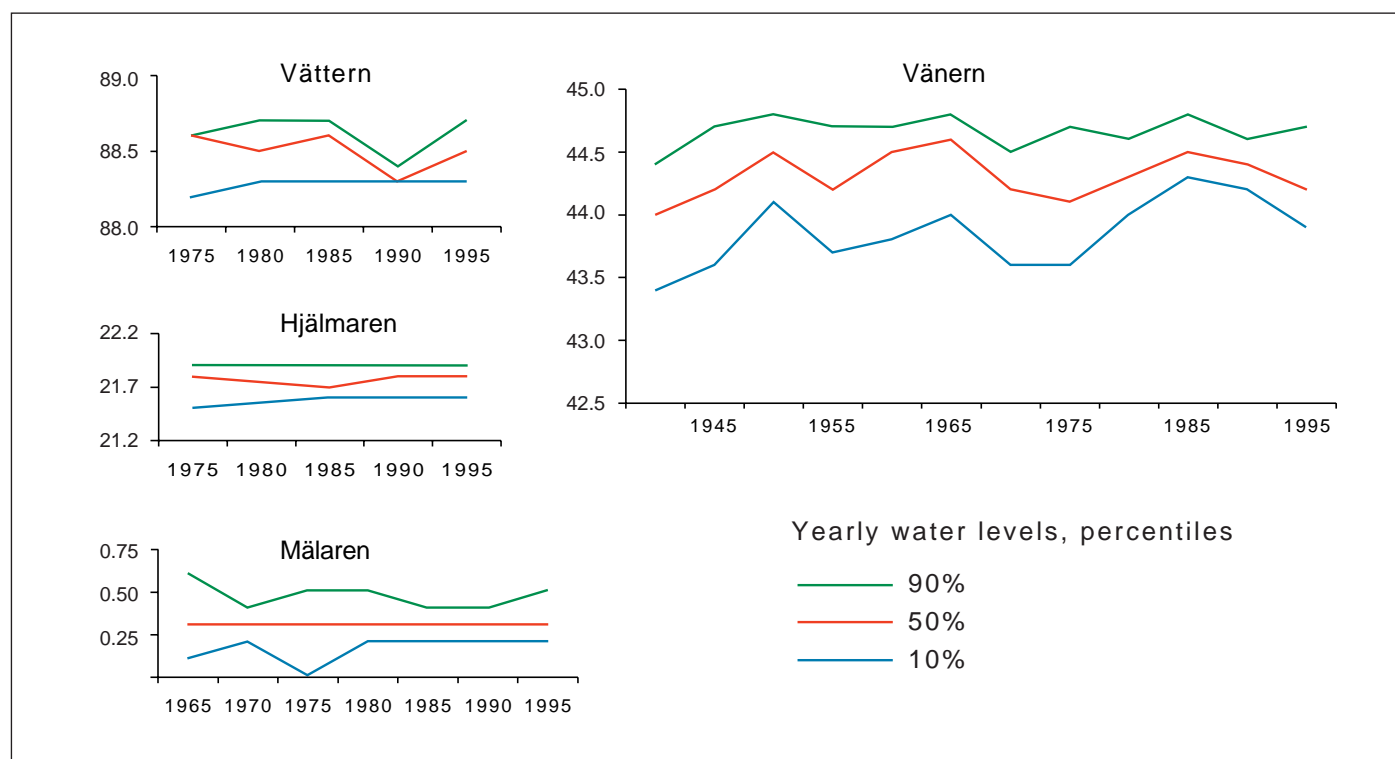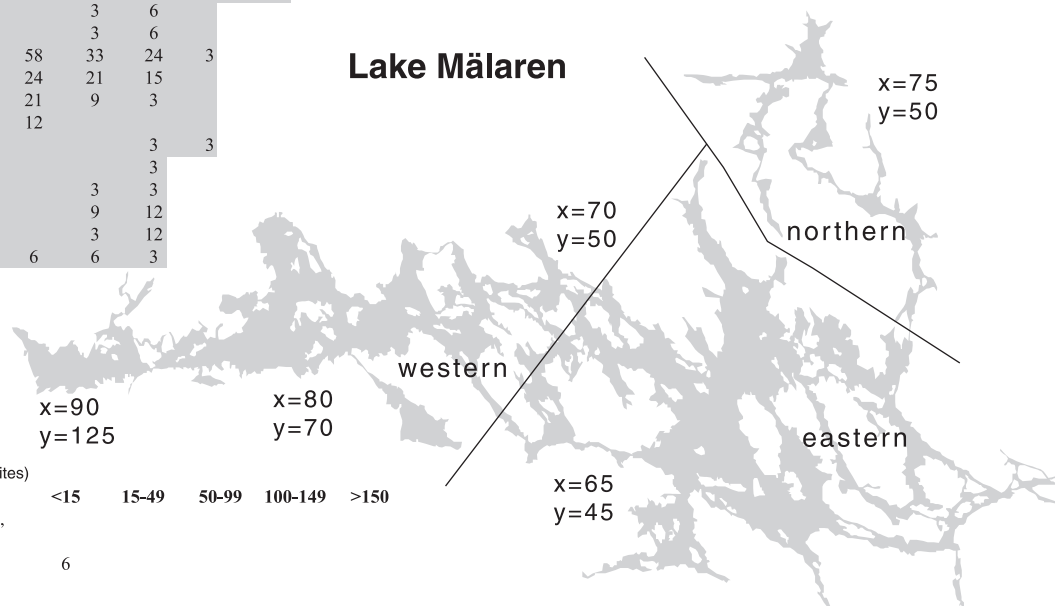
Figure 9. Depth distribution of registered species on sampling sites (%) in different parts of Mälaren, 1970–1972. Emergents are listed above the grey area, floating-leaved and submerged species within the grey area. Lists of species observed outside transects are valid for the whole lake. Figures representing x = distribution of emergent vegetation in proportion to the shore length (%), and y = vegetated zone width (m).

Northern L. Mälaren (33 sampling sites)

Depth cm	<15	15-49	50-99	100-149	>150
Peucedanum palustre (L.) Moench,					
Potentilla palustris (L.) Scop.	3				
Acorus calamus L., Hippuris vulgaris L.,					
Sium latifolium L.	6				
Rorippa amphibia (L.) Bess	9				
Oenanthe aquatica (L.) Poir	12				
Alisma plantago aquatica L.,					
Iris pseudacorus L., Lysimachia vulgaris L.	15				
Carex acuta L.	30				
Solanum dulcamara L.	6	3			
Lysimachia thyrsiflora L.	21	3			
Glyceria maxima (Hartm.) Holmb.	36	3			
Rumex hydrolapathum Huds.	9	6			
Epilobium palustre L.	15	6			
Bidens tripartita L.	36	9			
Typha latifolia L.	18	15			
Sagittaria sagittifolia L.		3	3		
Lycopus europaeus L.	12		3		
Butomus umbellatus L.	3	9	6		
Cicuta virosa L.	24	12	6		
Sparganium erectum L.	15	18	21	3	
Equisetum fluviatile L.	18	18	21	6	
Typha angustifolia L.	9	21	18	12	3
Schoenoplectus lacustris (L.) Palla	18	21	15	12	3
Phragmites australis (Cav.) Trin ex Steud	45	55	61	45	24
Nuphar lutea (L.) Sibth et Sm.		6	45	42	24
Persicaria amphibia (L.) Gray		3	6		
Potamogeton natans L.		3	6		
Lemna minor L.	58	33	24	3	
Hydrocharis morsus ranae L.	24	21	15		
Ricciocarpus natans (L.) Corda	21	9	3		
Spirodela polyrrhiza (L.) Schleid.	12				
Potamogeton lucens L.			3	3	
Potamogeton perfoliatus L.			3		
Potamogeton obtusifolius L.		3	3		
Ceratophyllum demersum L.		9	12		
Stratiotes aloides L.		3	12		
Utricularia vulgaris L.	6	6	3		

Eastern L. Mälaren (31 sampling sites)

Depth cm	<15	15-49	50-99	100-149	>150
Epilobium palustre L., Lycopus europaeus L.,					
Peucedanum palustre (L.) Moench,					
Potentilla palustris (L.) Scop., Ranunculus lingua L.	3				
Hippuris vulgaris L., Oenanthe aquatica (L.), Poir					
Solanum dulcamara L.	6				
Glyceria maxima (Hartm.) Holmb.,					
Sium latifolium L., Typha latifolia L.	10				
Iris pseudacorus L.	16				
Carex acuta L.	29				
Lysimachia thyrsiflora L.	42				
Butomus umbellatus L.	3	3			
Sparganium erectum L.	6	3			
Typha angustifolia L.	16	29	23	3	
Equisetum fluviatile L.	19	29	32	16	
Schoenoplectus lacustris (L.) Palla	26	29	32	16	3
Phragmites australis (Cav.) Trin ex Steud	61	87	94	87	45
Nuphar lutea (L.) Sibth et Sm.		10	10	19	10
Persicaria amphibia (L.) Gray		3	10	19	6
Hydrocharis morsus ranae L.	10	3			
Lemna minor L.	13				
L. trisulca L., Ricciocarpus natans (L.) Corda	3				
Utricularia vulgaris L.	6				
Potamogeton lucens L.	3	3			
Potamogeton perfoliatus L.				3	6

Lake Mälaren

x=75
y=50

northern

x=70
y=50

western

x=90
y=125

x=80
y=70

eastern

x=65
y=45

Western L. Mälaren (17 sampling sites)

Depth cm	<15	15-49	50-99	100-149	>150
Galium palustre L., Hippuris vulgaris L.,					
Peucedanum palustre (L.) Moench,					
Sagittaria sagittifolia L.	6				
Cicuta virosa L., Lycopus europaeus L.,					
Glyceria maxima (Hartm.) Holmb.,					
Potentilla palustris (L.) Scop.,					
Rumex hydrolapathum Huds.,					
Solanum dulcamara L.	12				
Typha latifolia L.	18				
Lysimachia vulgaris L.	24				
Iris pseudacorus L.	29				
Carex acuta L.	41				
Lysimachia thyrsiflora L.	53				
Acorus calamus L.	12	6			
Sparganium erectum L.	12	6			
Equisetum fluviatile L.	24	12	12		
Typha angustifolia L.		18	18	6	
Butomus umbellatus L.				6	
Schoenoplectus lacustris (L.) Palla	6	24	18	24	6
Phragmites australis (Cav.) Trin ex Steud	59	82	82	76	24
Nuphar lutea (L.) Sibth et Sm.	6	29	41	53	29
Nymphaea alba (coll.)L.		6	6	12	6
Potamogeton natans			6	6	
Persicaria amphibia (L.) Gray			6		
Hydrocharis morsus ranae L.	41	6			
Lemna minor L.	24				
L. trisulca L., Ricciocarpus natans (L.) Corda	12				
Ceratophyllum demersum	12	12	12	6	
Utricularia vulg aris L.	6				
Stratiotes aloides L.			6		
Potamogeton perfoliatus L.					6

Species outside sampling sites:

Emergent species: *Calla palustris* L., *Carex elata* All., *C. pseudocyperus* L., *C. riparia* Curt., *C. rostrata* Stokes, *C. vesicaria* L., *Eleocharis palustris* L., *Juncus effusus* L., *Lythrum salicaria* L., *Mentha* spp., *Menyanthes trifoliata* L., *Myosotis scorpioides*, *Pedicularis palustris*, *Phalaris arundinacea*, *Ranunculus sceleratus* L., *Rorippa amphibia* (L.) Bess., *Rumex aquaticus* L., *Scutellaria galericulata* L., *Sparganium ermersum* Rehman, *Stachys palustris* L., *Veronica scutellata* L.

Species with floating leaves: *Glyceria flutians* (L.).R Br., *Sparganium angustifolium* Michx., *S. minimum*

Submerged species: *Eleocharis acicularis* (L.) Roem. et Schoult., *Elodea canadensis* Michx., *Fontinalis antipyretica* (L.) Hedw, *Hottonia palustris* L., *Isoëtes lacustris* L., *Littorella uniflora* L., *Myriophyllum alterniflorum* DC, *M. spicatum* L., *M. verticillatum* L., *Potamogeton gramineus* L., *P. compressus* L., *Ranunculus circinatus* L., *R. peltatus* Schrank, *Scorpidium scorpioides* (Hedw.) Limpr., *Subularia aquatica* L.

Species added during the monitoring in 1996
Elodea nuttallii (Planch.) St John, *Nymphoides peltata* (Gmel.) Kunze, *Potamogeton berchtoldii* Fieber, *P. crispus* L., *Ranunculus aquatilis* L., *Callitriche* spp., *Nitella* spp.,

1990s, later on the water levels seem to be back to normal (Fig. 8).

MACROPHYTE COMMUNITIES OF THE LAKES

Lake Mälaren

The transition zone between terrestrial and freshwater habitats is extremely well developed along shallow margins of L. Mälaren. The aquatic emerged and floating-leaved vegetation is distributed along 74% of the shoreline and comprises an area of 100 km^2—which is about 9% of the entire lake area (Fig. 9). The aboveground biomass was estimated to 0.460 kg dw m^{-2}. Nonvegetated shores are common along the eastern parts of the lake (36% of the shoreline length), and less common along the shallow western basins (12% of the shoreline length). Steep strand zones causing open-water space of 3–10 m width between land and the reedbed occurred at 30% of the randomly selected sites.

The mean width of the vegetated zone was 60 m, but at gentle slopes (slope < 1 %) the emergent plant zone may exceed 90 m (Fig. 9). In addition to that a zone of 80 m was occupied by floating-leaved vegetation. The ecotonal variation is greatest on these gently sloping sites resulting in occurrence of 30–40 semiaquatic and amphibious species. Increasing steepness results in narrower reedbed zones and fewer species. Hence, a reedbed at a slope of 3–4% is about 50 m and the species amount to 10. Few species are seen at a slope of 5–10%, and the width of the vegetated zones are usually 15–25 m. With greater steepness no emergent vegetation occurs (Fig. 7).

The overall dominant species, *Phragmites australis* (common reed), occurs on 95% of all investigated sites and occupies 65% of the vegetated area. *Phragmites* is a plant with extreme tolerance for wave exposition and steep bottom conditions. Wet meadows, dominated by *Carex acuta* and *Glyceria maxima*, comprise 15% of the area and about 10% are floating-leaved plants, especially the yellow water lily*, Nuphar lutea*. In the

northern part of L. Mälaren, common reed is still predominating (60%), but water lilies occupy large areas (25%).

The number of species in the littoral zone gradually increases from about 2-m depth landward (Fig. 9). Few species grow in water deeper than 1.5 m. Besides, the prominent common reed 2 other reeds, *Schoenoplectus lacustris* and *Typha angustifolia*, as well as yellow and white water lilies occur at the outer fringe. Those species are common at all depths, and at depths < 1 m also *Equisetum fluviatile* and *Sparganium erectum* are frequent inhabitants. Further landward (< 0.5-m depth), herbaceous plants can be seen, but they, like species floating on the water surface, e.g. *Hydrocharis morsus-ranae* and *Lemna minor*, are mainly members of the innermost zone (< 15 cm). More than 30 emergent species occasionally occur in shallow water (Fig. 9).

The most prominent results of the reinvestigation performed in 1996 compared with results from the 1970s show that *Phragmites*-stands had become narrower. An increased frequency of water lilies was observed in 1996, as well as increased occurrence of *Typha angustifolia* and *Schoenoplectus lacustris* at depths exceeding 0.5 m. Increased frequency was also observed for *Iris pseudacorus* and herbaceous species, e.g. *Lysimachia* spp., *Lycopus europaeus, Lythrum salicaria, Cicuta virosa, Sium latifolia*, and the shore liana *Solanum dulcamara* at the shallowest landward zone (zone 1; Fig. 2). The floating species *Hydrocharis morsus-ranae* occurred at a greater distance lakeward than in 1972 and also the mace-reed *Glyceria maxima* had expanded lakeward, now rather frequently down to 1 m deep water. An increasing number of species were noticed in the landward zone, 48 in 1996 compared with 39 in 1972. The new species were mainly herbaceous wetland species, which appeared occasionally on a few sites, but 2 species are recent introductions. One of them is *Nymphoides peltata*, which is invasive and vegetatively spread through a tributary to the southwestern basin of L. Mälaren. The other new species, also nonindigenous, is *Elodea nuttallii*, first observed in 1992; it is spread along the northern and eastern parts of the lake.

x=95
y=120

x=100
y=80

x=72
y=80

x=78
y=65

x=93
y=100

x=78
y=60

x=43
y=45

x=17
y=30

x=84
y=130

x=34
y=50

Figure 10. Hjälmaren. View of the westernmost part in the vicinity of Örebro, as well as the northern and southern shore of the eastern lake basin. Figures representing x = distribution of emergent vegetation in proportion to the shore length (%) and y = vegetated zone width (m). Photos: S. Åhrberg.
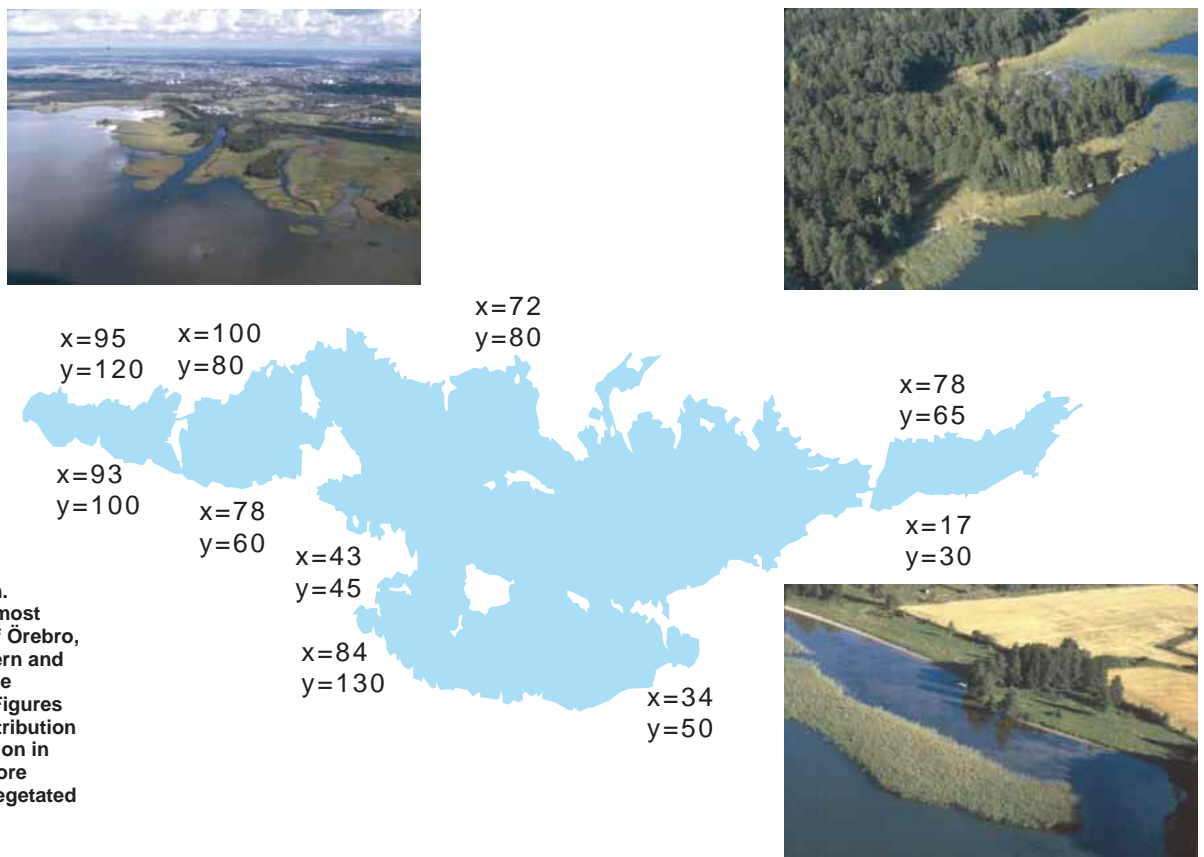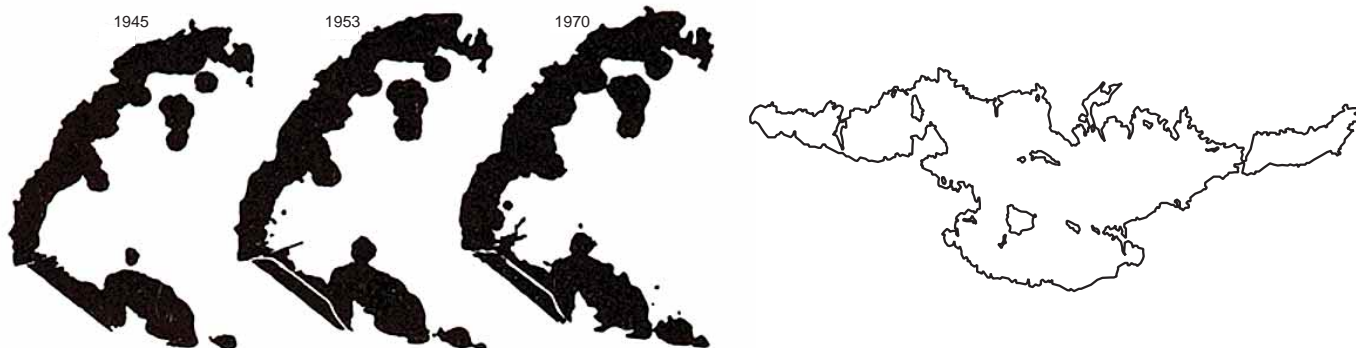
Figure 11. Expanding reed vegetation in westernmost part of Hjälmaren. The difference in the vegetated area between 1945 and 1970 was 13 ha.

The difference between mean and low water levels has been reduced since the earlier investigations of L. Mälaren. Therefore, the normally dry area below the mean water level, suitable for grazing of livestock in late summer, is more often flooded by deeper water, which negatively affects the effectiveness of grazing. On many sites, the grazing has also ceased for other reasons. This may explain why the grass *Glyceria maxima* and also herbaceous species are more frequent in L. Mälaren in 1996 compared with 1972. The lakeward zone of the reedbed seems to have been affected by the increased low water level as well. Constantly deeper water on the lakeward margin makes it hard to survive in the deepest part of the reedbed. Thus, the *Phragmites*-stands were significantly wider in 1972; 40 m in median width compared with 25 m in 1996. The narrowness in 1996 is accentuated by wider and more frequent gaps on the landward side of the stands.

Submerged species often occupy natural gaps and also man-made gaps along piers and fairways through the reeds. Within thinner reed stands and floating-leaved communities submerged plants can move in below the surface. The species most often recorded in this environment are *Ceratophyllum demersum, Stratiotes aloides, Elodea candensis, Utricularia vulgaris* (Fig. 9), and some members of the genus *Potamogeton* (e.g. *P. lucens, P. perfoliatus*). Because of decreased nutrient loading, water transparency in L. Mälaren has increased since the 1970s resulting in more abundant findings of submerged vegetation in 1996, also in deeper water outside the transition zone. Submerged rosette species, e.g. *Isoëtes lacustris* and *Littorella uniflora* can be found preferably on hard bottoms located in the southeastern part of the lake (23, 24). In L. Mälaren there are at least 3 submerged species, which are regarded as rare or threatened. On the 2000 Red List of Swedish species (28), *Alisma wahlenbergii* is considered endangered (EN), *Potamogeton compressus* as vulnerable (VU), and *Crassula aquatica* as near-threatened (NT).

Lake Hjälmaren

In 1970, the emergent vegetation covered 18.8 km^2 and the aboveground biomass was estimated to 0.740 kg dw m^{-2}. As shown in Figure 4 the northern shores were most affected by the lowering of the water surface, and they are also overgrown by reeds. Emergents occupied about 20–35% of the southern shoreline and 75% of the northern shoreline in the central and eastern basins, while the comparable share was almost 100% in the western basins. The reed vegetation (Fig. 10) and the earlier expansion rate of the reedbeds are shown in aerial photographs from 1945, 1953 and 1970 (Fig. 11).

The vegetated areas are gently sloping, ≤ 3% on the majority (75%) of investigated sites and the greatest depth at the outer fringe of the reedbed was ≤ 1.7 m. The species listed for L. Mälaren are also found in L. Hjälmaren, but many with sparser occurrence. *Carex acuta* and *Potentilla palustris* were far more abundant on the wet meadows of L. Hjälmaren compared to L.

Mälaren and, on the contrary, *Glyceria maxima* was hardly found. *Phragmites australis* entirely dominated (86%) the reedbeds, which on the average for the whole lake was 80 m in width. The few emergent species, that regularly co-dominate, were infrequent and only floating species like *Hydrocharis morsus-ranae* and *Lemna minor* occurred more frequently. These species, which indicate eutrophic conditions, were found at greater water depth (1 m) than in L. Mälaren. A great number of Canadian geese have been obstructing development of common reed at the outer fringe by grazing the emerging apical buds in springtime.

Observations of vegetation changes in L. Hjälmaren have not been made since 1977, but a development similar to that in L. Mälaren may be predicted because of similar lake conditions.

Lake Vänern

The vegetation in 1975 was distributed along 64% of the studied shoreline and covered an area of 74.1 km^2. Thus, the mean width of the vegetated zone was 75 m, but varied between 33 m on exposed littoral and 175 m along margins of sheltered bays (21). *Phragmites australis* was predominant, 81% of the dry weight estimated at a mean of 0.5 kg m^{-2} (0.3–0.8). The dominance is outstanding at depths below the low water level, where other species seldom occur. Thus, the species richness is entirely concentrated to the upper landward zone comprising about 30 species.

The results of repeated aerial photography in 1999 partially confirm the subjective observations by people, indicating compositional changes within the littoral zone since 1975. On adjacent land margins, trees were expanding between 1975 and 1999 (22), and probably due to deeper water (less frequency of low water levels) the common reed was revitalized with vigorous growth in the zone near land. This circumstance led to public complaints about the expansion of the reedbed, in spite of the fact that the outer reedbed fringe retained its previous extension. Certainly the constantly flooded reedbeds are broadening landward. Thus, the consequence of a higher water level during what are normally low water periods in summer is that bridges and piers have to be extended, and the reed-cutting machines have larger areas to deal with. Changes within the outer littoral zone are obvious with expanding communities of water lilies partially replacing stands of bulrush *Schoenoplectus lacustris*, and common reed *Phragmites australis*. The bulrush stands have decreased substantially in all documented areas, and the concurrent expansion of water lilies indicate that the exclusion of low water levels may limit the survival of reeds on the outer fringe. Locally, stands of common reed also decreased up to 30%, especially around small islets in archipelago areas of the lake. According to local inhabitants the decrease is a result of grazing by wild geese (22).

Long-lasting and heavy rain during late autumn 2000 caused severe and disastrous flooding in the L. Vänern area. Water lev-

els rose to a peak level 1.3 m above the long-term mean. A follow-up study of the consequences to aquatic macrophytes is necessary and of interest for the future understanding of macrophyte development.

Lake Vättern

In the northern vegetated parts of L. Vättern, the emergent plant zone was comparatively narrow (mean width 30 m) in 1973, occupying about 50% of the studied shoreline. *Phragmites australis* had a dominant position also in L. Vättern with 73% of the vegetation cover. The nearshore bottom substrate consisted of sand on the majority of the sampling sites and the steepness was striking with a depth of 1 m often attained within 25 m of the land margin. Gaps with open water between land and the reedbed stands were regular in 1973, probably caused by the easily eroded sandy shores. In the field survey carried out during July 1973, the aboveground biomass of emergent species was low, 0.3 kg dw m^{-2}, compared with 0.5–0.7 kg dw m^{-2} measured in the other large lakes. Biomass data from L. Vättern provide illustrative examples of the importance of bottom substrate. When growing on soft bottoms the mean weight of a single reed stem was 15–17 g dw, when growing on sandy sites only 7–9 g. On stony bottoms the weight was intermediate, 11–14 g dw. The low production of dry matter mainly depends on the small shoots, because stem density in the stands is similar to that in the other large lakes.

Other emergent species like *Schoenoplectus lacustris, Typha angustifolia*, and *Equisetum fluviatile* comprised a larger share (22%) than seen in the other studied lakes. *Nuphar lutea* was comparatively scarce (3%), but submerged vegetation was more luxuriant in this lake than in the other large lakes due to the transparent water (Secchi depth ≈ 15 m), and the much lower nutrient concentrations as well as the sandy-bottom substrate. Species richness is far more substantial, e.g. with charophytes and isoetids on the species list. Nine different species of *Potamogeton* were found in 1939 (25), and at least 7 were found in 1973. *Potamogeton rutilus* is one of the threatened species found in L. Vättern—indicated as endangered (EN) on The 2000 Red List of Swedish species (28). Another species on the list is *Pilularia globulifera*, marked as vulnerable (VU).

Half of the 80 observed aquatic and semiaquatic species grew mainly submerged, and 9 were floating or floating-leaved. The charophyte *Nitella opaca* turned out to be one of the most frequent species besides the caulescent vascular plants *Myriophyllum alterniflorum* and *Ranunculus peltatus* and the isoetids, or rosette plants *Lobelia dortmanna, Subularia aquatica* and *Isoëtes lacustris*. Other characteristic species were *Potamogeton gramineus, Stratiotes aloides, Littorella uniflora* and *Ranunculus reptans*.

In comparison to the conditions investigated in the 1930s, an ongoing eutrophication with denser stands of littoral vegetation expanding in the sheltered bays was seen in the 1970s. Changes in community composition, including the appearance of species like *Lemna minor* and *Glyceria maxima* in the 1973 survey confirm some nutrient enrichment since 1939. Present conditions need further investigation.

SPECIES COMPOSITION AND NUTRIENT AVAILABILITY

As metabolic units in the gradient, the emergent macrophytes are the most productive of all of the plant communities (29). However, due to climatic and edaphic conditions, species distribution differs greatly from north to south in Sweden (30). Thus, lakes in different parts of Sweden differ distinctly in the supply and production of organic matter. There is an altitudinal gradient from the extremely nutrient-poor and clear alpine waters to the nutrient-rich lakes in the southern and central parts

of the country. The nutrient-rich lakes are mainly situated below the highest coastal line (the highest level reached by the sea after the last glaciation period).

Unpolluted oligotrophic lakes with transparent water, fairly common in the northern parts of Sweden, are dominated by submerged plants: 5–6 rosette species (isoetids) especially *Isoëtes lacustris* and 4–5 caulescent species (elodeids, e.g. *Myriophyllum alterniflorum*). Floating-leaved aquatics (nymphaeids) are represented by 3–4 species and emergents are few, 6–7. In humic lakes with yellow-brown color, the isoetids are often lacking and elodeids and nymphaeids are limited to 3 of each type. The emergents correspond to the clearwater type. In meso- and eutrophic lakes the emergent plants are numerous (> 20) and submerged plants are represented by elodeids, while isoetids are rarely found. Nymphaeids are of equal number (about 4), but the community is composed of more nutrient-demanding species. Nutrient-rich water also involves presence of lemnids, i.e. free-floating plants on the water surface (30).

Lake area contributes most to explain variation in species richness according to an evaluation of data from of 641 Nordic lakes. After lake-area relationship, pH followed by water-level range, extent of lake lowering, conductivity and elevation were among the top predictors. Upland lakes exhibited proportionally fewer species than lowland sites and submerged bryophytes largely replaced aquatic angiosperms at high elevations (> 1000 m). Lakes in which the water level alternated 1–2 m within a year supported more species than predicted from the area alone. Lakes with permanently lowered levels also showed elevated species richness (31).

The large lakes of Sweden all belong to, or possess elements of, the lowland mesotrophic or eutrophic lake type. Thus, they have all the requirements for high species richness. As described above, the vegetation is characterized by about 10 elodeid submerged species in the water, 3–4 floating-leaved and a couple of free-floating species on the water surface, as well as a varied flora of emergent species along the lake margins. Forty-five species are common to all the lakes, and the majority of those are emergents. The total number of species is greatest in L. Mälaren (88 spp.) (Fig. 9). This richness is probably due to the great variety of habitats in the lake, which range from eutrophic conditions with a rich emergent flora to oligotrophic basins with a great richness of submerged species. Species richness is also great in northern L. Vättern, which has the most varied submerged vegetation (40 spp.) with 11 species occurring only in this lake. The species richness in L. Vänern (65 spp.) and L. Hjälmaren (60 spp.) is also beyond the mean (40 spp.) for this type of lake.

Eutrophic conditions are mainly found in the southern part of Sweden, often strengthened by lowering of water surface, or by nutrient pollution. As described above, the large lakes and their separate subbasins range from highly eutrophic to oligotrophic waters. During the latest 6 decades all of them have been wastewater recipients. In the mid-1970s, sewage-treatment works were supplemented with phosphorus removal. Because nitrogen concentrations remained constant or increased, the N/P-ratio has increased very much since that time. This would support reed growth because experiments of fertilization carried out in natural extensive monospecific stands of *Phragmites australis* showed that nitrogen was the major growth supporting agent (32). The response after fertilization was weak, but the fact that poor availability of N limits reed production is explained by the chemical behavior of N and P. High amounts of particle-bound P are found in littoral sediment accumulation zones which support the most intense macrophyte growth. In addition, P is often kept in solution because of reducing conditions within the sediment. N on the other hand is lost through denitrification from the sediment surface. In a thin stand, the standing crop is readily increased by N-fertilization, but in a dense stand an increase

in standing crop can only be accomplished through a thinning of the stand in favor of increasing shoot weight. A further increase in shoot weight or shoot density would result in excessive shading, resulting in mortality of shoots or abscission of lower leaves (32).

The mean concentrations of nutrients in both aboveground and underground parts of *Phragmites australis* measured in L. Mälaren in late September 1976 was 0.06% P dw^{-1} and 0.4% N dw^{-1} (18). The mean N/P ratio was 7, but lower in the eulittoral ($\approx$ 5) than in the littoral parts ($\approx$ 9). A similar difference in N/P ratio was measured between eulittoral (9.2) and littoral (7.0) in stems collected in June 1973. They also differed in September when the ratio was even higher, 15.0 and 11.6, respectively. The difference is probably due to the denitrification processes promoted by the reducing conditions in the sediment (32).

There seems to be a relationship between the biomass of emergent macrophytes and the trophic state of the lake water. The highest biomass (dw) was recorded in the eutrophic basins Hemfjärden (980 g m^{-2}) in L. Hjälmaren and the basins Dättern-Brandsfjorden (890 g m^{-2}) in the southernmost parts of L. Vänern. Biomass records of the other basins in these lakes ranged between 600–720 g m^{-2}, whereas L. Mälaren basins comprised quite similar records all over the lake from the east to the west (400–460 g m^{-2}). L. Vättern's low biomass (340 g m^{-2}) also seems related to the low nutrient content of the lake. There are, however, eutrophic sites with high reed biomass (920 g m^{-2}) also in L. Vättern, but sparser stands (100–300 g m^{-2}) were still more frequent when investigated in July 1973.

CONCLUSION

The geomorphology of a lake basin is a primary factor for the structure of the interface zone between land and water. The steepness of the lake margins is decisive for the sediment stability along slope gradients, which in turn influences the establishment of the vegetation. The shape of Vättern and Vänern provides adequate sediment substrata for vegetation establishment only in the archipelagoes and in the sheltered bays. In L. Mälaren and Hjälmaren on the other hand, about 65–75% of the entire shoreline length is covered by emergent or floating-leaved macrophytes.

In general, vast areas of emergent macrophytes are established on gently sloping shores (zone width $\geq$ 100 m, species number 30–40). On slightly steeper slopes (3–4%), the zone width is considerably smaller (50 m) and the number of emergent species is reduced to about 10. Small stands and few species grow on steeper ground and are utterly reduced beyond 10% inclination.

The overall species richness in Mälaren and Vättern is considerable because the water transparency allows many submerged species to develop. Monospecific stands of the common reed *Phragmites australis* are abundant in all lakes but most pronounced in the lowered L. Hjälmaren and in several bays of the regulated L. Vänern.

Altered water regime with smaller water-level fluctuations, within the latest 25-yr period, probably caused decreased reed distribution on the deeper parts of the land-water interface zone and increased reed vitality in the shallow near-land zone. Water lilies increased their distribution locally when the reeds and bulrush decreased. On sheltered sites, mace-reed and freely floating species expanded lakeward.

Further changes in the land-water transition zone are expected if the rise in water level continues. Such a state will follow a predicted climate change with increased precipitation. Indicative tendencies in that direction are increasing winter temperatures and heavy rains in late summer and fall which have occurred during the last 10-yr period.

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