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COMMENTED LIST OF MACROPHYTE TAXA OF LAKE PEIPSI

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Abstract. A list summarizing data on all 128 taxa of macroflora that different researchers found in Lake Peipsi in 1962–98 and a brief characterization of the habitats of the majority of the species with their frequency are presented. Comparison of the composition of the macroflora of L. Peipsi with that of L. Võrtsjärv, L. Ladoga, and other large lakes located on the northwestern edge of the Russian Platform (eight lakes) yielded 19 species that occurred in all the lakes studied and 12 that were absent in one or two lakes only. Because of the expansion of emergent vegetation (primarily reeds) to new areas several shallow-water species characteristic of L. Peipsi are receding. The recent composition of macrovegetation gives evidence of the eutrophic character of this waterbody.

Key words: frequency, common species, specific features, anthropogenic eutrophication.

INTRODUCTION

The list of the macroflora of one of the largest lakes in Europe, L. Peipsi (area 3555 km^2), is quite long. Far more than 100 species of macrophytes have been counted, among them 50 species of hydrophytes and amphibious plants. Besides these and typical emergent plants a number of hygrophytes and ruderal plants occur there. The flora of the coastal area of L. Peipsi comprises several species that do not belong to the lake's flora but that occur frequently in its depression, e.g. *Symphytum officinale* L. and *Achillea cartilaginea* Led. Obviously, defining the macroflora of L. Peipsi in regard to hygrophytes is quite subjective and it was not the goal of the present study. The species (or higher taxa not determined in greater detail) registered by various researchers at different times are listed here; some cases are marked as doubtful. The present list can be considered almost complete regarding hydrophytes and amphibious plants (excluding Characeae and Bryopsida); however, in our opinion determination of the species of the genera *Carex* and *Juncus* and evidently also of the family Poaceae suffers from essential inadequacy. It should be pointed out that in recent decades the diversity of macroflora and possibly also floristic diversity have notably decreased. These changes seem to be persistent.

The aim of this paper, besides the listing of species, was to present a brief outline of the progression of the macrovegetation of L. Peipsi in the 20th century, as well as to compare its floristic composition with that of other large lakes in neighbouring areas, and to discuss changes in the occurrence of several species. It is hoped that our contribution will improve the knowledge on the ecology of several species.

GENERAL DESCRIPTION OF LAKE PEIPSI

Lake Peipsi (or L. Peipsi *sensu lato,* or Pskovsko-Chudskoe *ozero* in Russian; in older literature L. Peipus) consists of three parts: L. Peipsi *sensu stricto* (2611 km^2, mean depth 8.3 m, max depth 12.9 m), L. Lämmijärv (236 km^2, mean depth 2.5 m, max depth 15.3 m), and L. Pihkva (709 km^2, mean depth 3.8 m, max depth 5.3 m) (Kuptsov & Arukaevu, 1983). The lake belongs to the basin of the Gulf of Finland of the Baltic Sea. Lakes Peipsi *s.s.* and Pihkva are characterized by a more uniformly sloping bottom, whereas L. Lämmijärv with its shallows and deeps resembles a big river. The length of the lake along the north–south axis is 152 km. The depression covers outcrops of different bedrock. The northern coast and the northwestern corner are lying on the outcrop of Ordovician dolomites; the middle part (main part) is lying on the outcrop of Devonian sandstones, siltstones, clays, and marls; the southern end is lying on the outcrop of Devonian dolomites (Raukas, 1978). The lake developed in a pre-Quaternary depression modified by glaciers. The thickness of the Quaternary cover exceeds 50 m in the central part of the depression, while Holocene deposits form only 0.5–4.0 m of this or are absent in places (Miidel & Raukas, 1999).

Bottom deposits near the coast consist mainly of aleurite sand or sandy aleurite (Miidel & Raukas, 1999), in places bottom is stony or peaty (Fig. 1). The northeastern coast of Peipsi *s.s.*, where the terrace-type sandy shore (Tavast, 1999) is continuously changing and the depth of water is in places 4 m already at a distance of 200 m from the shore, is the most unfavourable for plant growth (e.g. at the observation point of Katase).

The southern parts of L. Peipsi *s.s.*, L. Lämmijärv, and L. Pihkva have a more indented shoreline and can be considered quite different from the rest of L. Peipsi *s.s.* also with respect to their higher levels of trophy and abundance of vegetation. The lake is divided into northern and southern parts along the Varnja–Spitsyno line. The southern part of the lake is surrounded with extensive swampy areas and a peaty water's edge is a characteristic feature of long shore stretches.

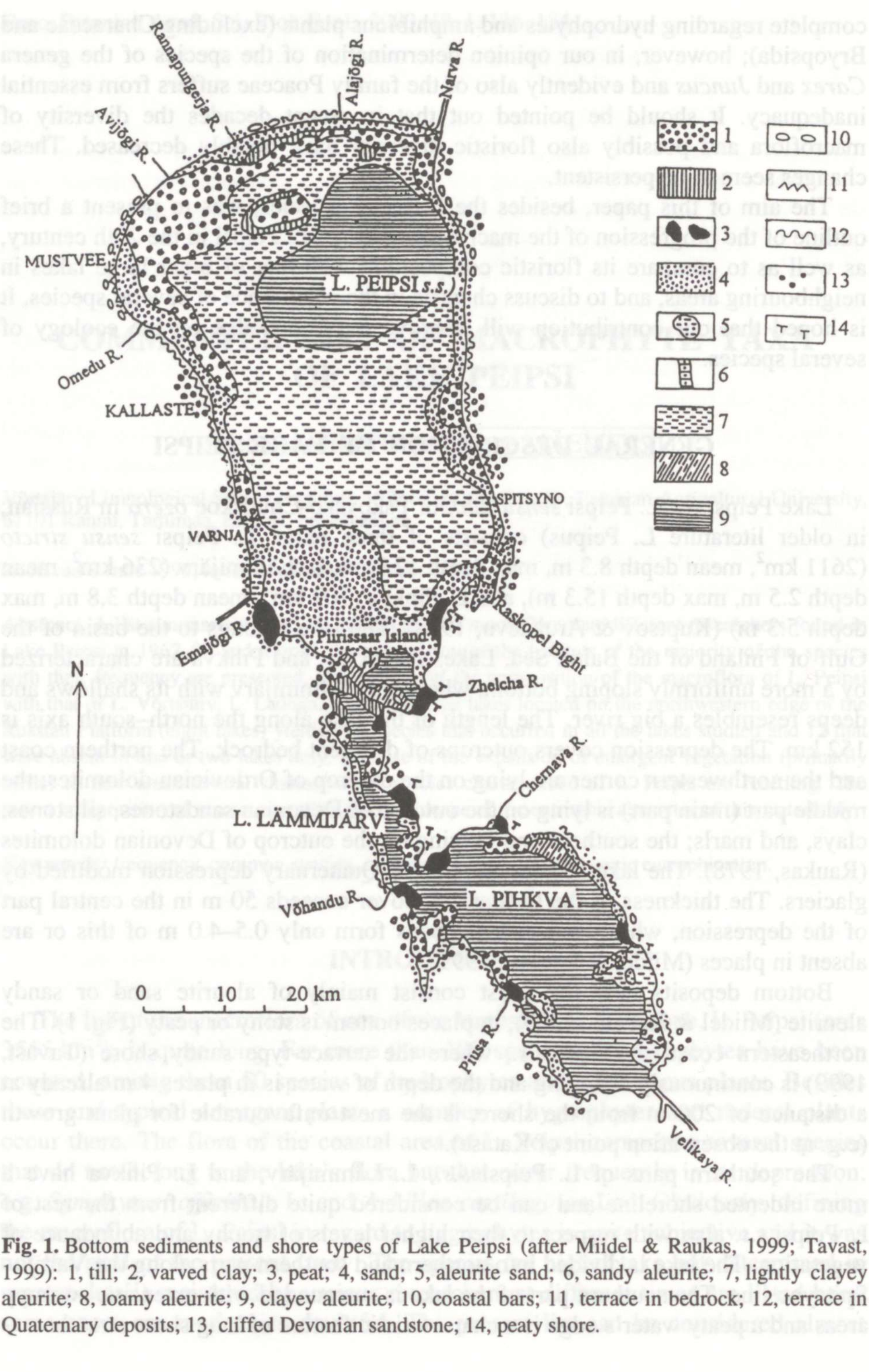

Fig. 1. Bottom sediments and shore types of Lake Peipsi (after Miidel & Raukas, 1999; Tavast, 1999): 1, till; 2, varved clay; 3, peat; 4, sand; 5, aleurite sand; 6, sandy aleurite; 7, lightly clayey aleurite; 8, loamy aleurite; 9, clayey aleurite; 10, coastal bars; 11, terrace in bedrock; 12, terrace in Quaternary deposits; 13, cliffed Devonian sandstone; 14, peaty shore.

The bulk of drain (66%) and pollution (70–80%) (Loigu et al., 1991) originates from two rivers, the Velikaya (catchment area 25 200 km^2) and the Emajõgi (catchment area 9740 km^2). The outflow through the Narva R. falls into the Gulf of Finland. The water turnover period lasts nearly two years. The mean HCO_3 content of water is 138 g m^{-3} (Eipre, 1983; Kaputerko, 1983). Water is the clearest (Secchi depth sometimes up to 5.80 m) in the northern part of the lake, especially in the northwestern corner where also the chlorophyll content is the lowest (Möls et al., 1996). In the southern part, the Secchi depth in mid-summer was 0.25–0.5 m at the end of the 1980s (Sudnitsõna, 1990). The values of total P and N, chlorophyll content, COD_{Mn}, COD_{Cr}, and other parameters increase southwards, indicating a higher trophic level. Some yearly means of hydrochemical parameters are presented in Table 1.

Table 1. Overall means and extreme values of the yearly means of some hydrochemical parameters of Lake Peipsi from 1985 to 1994 (after Möls et al., 1996)

	TP, mg P m^{-3}	TN, mg N m^{-3}	Chl, mg m^{-3}	COD_{Cr}, mg O L^{-1}	COD_{Mn}, mg O L^{-1}	SD, m	pH	O_2, mg L^{-1}	O_2, %
Overall mean	39.1	626	12.8	30.6	13.7	1.8	8.3	9.8	106
Min	29.9	411	11.3	26.4	12.7	1.6	8.2	9.2	99
Max	58.1	738	15.9	35.4	15.8	2.0	8.7	10.9	112

MATERIAL AND METHODS

The first inventory of the macroflora of the whole of L. Peipsi was made in 1962–63 (Tuvikene, 1966). From the earlier period, there existed only a few floristic data pertaining mostly to the southern part of the lake (Võrumaa, 1926; Setumaa, 1928; Sirgo, 1935; Petrov, 1947; Ivanov, 1950). Detailed inventories followed in the years 1966–70, compiled by Nedospasova (1974), and in the years 1970–71 and 1980, compiled by A. Mäemets (Myaémets, 1983; Mäemets, 1983). During 1988–89 Sudnitsyna worked mainly on L. Pihkva and L. Lämmijärv (Sudnitsõna, 1990; Sudnitsyna, 1990). A. Mäemets studied the macrovegetation of the inflows of the lake on the Russian side in 1970, 1971, and 1980 and on the Estonian side in 1986–87 (Mäemets, 1990). During 1997–99 the Estonian part of the shore was studied by H. Mäemets (Mäemets & Mäemets, 1999).

Opportunities permitting, macroflora was studied more thoroughly at the lakeward side of the littoral zone (by Tuvikene, A. Mäemets, Sudnitsyna) or close to the shore (H. Mäemets in 1997–98). As a result, the established numbers of species, particularly those regarding the plants of the flooded shore zone, were different. Frequencies for most species, based on the data of 87 observation sites (32 of them studied repeatedly) were calculated by A. Mäemets. Of the taxa listed 54 were registered by Tuvikene, 71 by Nedospasova, 91 by A. Mäemets, and 37 by Sudnitsyna. The latest data are not included in the table (Table 2), as these

Table 2. List of macrophyte taxa of L. Peipsi and their occurrence in different periods; occurrence in L. Võrtsjärv and presence in macrophyte associations in some large lakes of the northwestern part of the Russian Platform (Raspopov, 1985).

H.T., Tuvikene (1966), separate estimates for northern (N) and southern (S) part (demarcation along the Varnja–Spitsyno line); G.N., Nedospasova (1974); A.M., A. Mäemets; H.M., H. Mäemets; T.F., T. Feldmann. * conventionally placed under this group; P, L. Peipsi *s.s.*; L, L. Lämmijärv; Pi, L. Pihkva; N, S, SW, etc., directions of the compass; EF, *Eesti floora*, 1953–1984; ab, abundant(ly); B, b, bay(s), bight(s); bound, boundary; bott, bottom; char, characteristic; decr, decreasing; dom, dominating; earl, earlier; eutr, eutrophic; est, estuary; ext, extinct; fl, flooded; fr, frequency, frequent(ly); grd, growth depth; incr, increasing; infl, inflow; l, lake; lrg, large; mass, in masses; p, part; pl, places; R, r, river(s); rel, relatively; rl, rivulet(s); sc, scattered; sh, shore; shal, shallow; shel, sheltered; sm, some; sts, stands; w, water; z, zone. Frequency (4 points): x – rare; xx – occasional; xxx – frequent; xxxx – very frequent

Taxon	Growth areas in L. Peipsi (if known)	1962–63 H.T. N p NB! 3 points	1962–63 H.T. S p NB! 3 points	1966–70 G.N. 4 points	1970–80 A.M. 4 points	1997–99 H.M. 4 points	Frequencies: whole lake (%)	Frequencies: Peipsi *s.s.*/ Lämmijärv/ Pihkva (%)	Võrtsjärv 1965–66 A.M.	Võrtsjärv 1997 T.F.	Ladoga	Onega	Ilmen	Beloe	Kubenskoe	Vozhe	Lacha
SUBMERGED PLANTS																	
Chara spp.	fr changed, recently NW p		x	xx	xx	x	47	69/16/41	xx				x			x	
Nitella spp.	Raskopel B 1970																
Nitellopsis obtusa	mouth of Omedu R 1970																
Drepanocladus aduncus						x											
Amblystegium riparium						x											
Bryophyta (indetermined)					xx	x	20	22/0/28	x		10						
Fontinalis antipyretica DC.	recently more in N p		x	xx	x	xx	3	6/0/3									
Isoëtes echinospora Durieu	Raskopel B, ext		x	x								1					
Ranunculus aquatilis L.					x		1	0/0/3			4	11					
R. circinatus Sibth.	more eutr pl at settlements		x	xxx	x	xx	11	11/16/9	xx	x	x	2					
R. trichophyllus Chaix (*s.l.*)	sc, not ab	x	x	xx	xx	xx	28	33/11/31									
Elatine hydropiper L.	in sm b		x	x	x		8	11/0/9			10	4					
Ceratophyllum demersum L.	more eutr pl at settlements			xx	x	xx	3	6/0/3	x	xxx	4	1		2			
Myriophyllum spicatum L.	mainly sc, sts in sm b	x	xx	xx	xx	xxx	30	25/21/41	xx	xxxx	33	23			1	11	15
M. verticillatum L.					x		1	0/0/3		xx		7					

Table 2 continued

Taxon	Growth areas in L. Peipsi (if known)	1962–63 H.T. N p NB! 3 points	1962–63 H.T. S p NB! 3 points	1966–70 G.N. 4 points	1970–80 A.M. 4 points	1997–99 H.M. 4 points	Frequencies: whole lake (%)	Frequencies: Peipsi s.s./ Lämmijärv/ Pihkva (%)	Võrtsjärv 1965–66 A.M.	Võrtsjärv 1997 T.F.	Ladoga	Onega	Ilmen	Beloe	Kubenskoe	Vozhe	Lacha
Callitriche spp.	rl mouths, pools				x	x			x	?	3	4					2
Hottonia palustris L	rl mouths			xx		x			x	?							
Utricularia vulgaris L.	rl mouths, pools, canals					xx			x	x	30	9					1
Elodea canadensis L.	at infl, mainly at settlements		x	xxx	xx	xx	31	8/21/41	xx	?	41	32			2	1	14
Stratiotes aloides L.*	creeks & tributaries, in pl ab		xx	xxx	xx	xx	28	17/26/41	x	?	26	5	6		3		2
Potamogeton berchtoldii Fieb.	in rl Smolnitsa 1997					x					1						
P. crispus L.	rarely				x	x	1	0/0/3	x		x						
P. filiformis Pers.	earl fr at E sh of P				x	x	15	36/0/0	x		x						
P. friesii Rupr.	sc		x	xx	x	x	2	3/0/3	x			1					
P. gramineus L.	fr in shal w and pools	x	xx	x	xxx	xxx	60	81/63/34	xx	xx	42	36	7	7	15	6	4
P. lucens L.	S p of the l, changing fr		xxx	xxxx	x	x	11	6/21/13	xx	xx	3	23	1	4	2	6	1
P. obtusifolius Mert. et Koch					x		1	0/0/3									
P. pectinatus L.	sc, fr in NW; at Velikaya R	xx	x	xxx	xxx	xxx	51	56/37/53	xx	xx	1	1	1		2		3
P. perfoliatus L.	**dom in all l**, earl grd to 5 m, even 1.5 km from sh	xxx	xxx	xxxx	xxxx	xxxx	92	86/100/94	xxxx	xxx	41	45	14	13	10	12	18
P. praelongus Wulf.	S p of the l					x											
P. pusillus L., incl. *P. berchtoldii* by G.N.	sc, mass in B Krupp 1971		x	xx	xx		23	39/11/13			x	3		1	4	2	4
P. rutilus Wolfg.	ab in sm eutr and muddy b				x		5	6/5/3									1
P. trichoides Cham. et Schlecht.	very rare in Estonia; 1970 at Mustvee, 1998 at Kolkja				x	x	1	3/0/0									
P. zosterifolius Schum.	sc		x	xx	x	x	3	3/0/6	x	x	22	6	1	2			
P. filiformis × *P. pectinatus*	earl fr at E sh of P and Pi				x		5	8/0/3									
Zannichellia palustris L.	not ab, mainly in P			x	x	x	16	31/5/6									

Table 2 continued

Taxon	Growth areas in L. Peipsi (if known)	1962–63 H.T. N p NB! 3 points	1962–63 H.T. S p NB! 3 points	1966–70 G.N. 4 points	1970–80 A.M. 4 points	1997–99 H.M. 4 points	Frequencies: whole lake (%)	Frequencies: Peipsi *s.s.*/ Lämmijärv/ Pihkva (%)	Võrtsjärv 1965–66 A.M.	Võrtsjärv 1997 T.F.	Ladoga	Onega	Ilmen	Beloe	Kubenskoe	Vozhe	Lacha
FLOATING & FLOATING-LEAVED PLANTS																	
Ricciocarpus natans (L.) Corda	1999 at Tammispää					x					7						
Hydrocharis morsus-ranae L.	in eutr shel pl			xx	x	xx	11	11/16/9	x	x	22	10		7			
Lemna minor L.	in eutr shel pl				x	xx	11	14/16/6	x	?	16	2		12			2
L. trisulca L.*	S p of P, b of Pi, fr incr		xx	xxx	xx	xxx	25	19/11/41	x	?	21	4	3	12	8	x	15
Spirodela polyrrhiza (L.) Schleid.	in eutr shel pl, fr incr		x	xx	x	xx	10	11/1/9	x	?	4			9			
Nuphar lutea (L.) Sm.	r mouths, shel pl		xx	xxx	xx	xx	29	11/37/44	xx	xxx	32	35	1	1	1	5	8
N. pumila (Timm) DC.	small amounts in sm b		x	x	x		6	8/0/6			15	5					2
Nymphaea alba L.	r mouths, sm b		x	xx	x	x			x	xx	2	1					
N. candida C. Presl	r mouths, sm b		x	xxx	x	x	al+ca 7	6/5/9			15	26	1		2	3	2
Polygonum amphibium L.*	P mainly S p., sts in L, Pi	x	xx	xxxx	xxx	xxx	72	53/89/81	x	xx	44	38	10	16	20	3	5
Potamogeton natans L.			x	xxx	x		3	8/0/0	xx	x	33	24		4		1	
Sparganium emersum Rehm.	main at infl	x	x	xx	xx	x	24	22/21/28	x	xx	27	14	10	6	1	3	4
EMERGENT PLANTS																	
Equisetum fluviatile L. em. Ehrh.	lrg sts in sm b, r mouths		xx	xxxx	xxx	xx	51	42/74/47	x	?	44	47	11	3	11	2	2
E. palustre L.						x											
Caltha palustris L.	mainly Pi, shal w, w bound				x	x			x		9	5	1	x	6	1	1
Ranunculus lingua L.			x	xx	x	x	3	3/11/0	x	?	4	7			3		1
R. reptans L.*	earl char for E sh of P			xx	xxx	xx	52	58/58/41	xx	?	13	16			11	1	3
R. sceleratus L.	in fl sh z					x					6			1			
Comarum palustre L.						x			x		9	8				2	
Potentilla anserina L.					x				xx	xx							
Lythrum salicaria L.	marshes		x	xx	xx	xx	32	31/37/31	xx	xx	11	7	2	1	3	2	

Table 2 continued

Taxon	Growth areas in L. Peipsi (if known)	1962–63 H.T. N p NB! 3 points	1962–63 H.T. S p NB! 3 points	1966–70 G.N. 4 points	1970–80 A.M. 4 points	1997–99 H.M. 4 points	Frequencies: whole lake (%)	Frequencies: Peipsi s.s./ Lämmijärv/ Pihkva (%)	Võrtsjärv 1965–66 A.M.	Võrtsjärv 1997 T.F.	Ladoga	Onega	Ilmen	Beloe	Kubenskoe	Vozhe	Lacha
Peplis portula L.						x											
Epilobium palustre L.					x	x					8	1	x	1	1		
Cicuta virosa L.				xx	x	xx			x	?	1	1		1			
Oenanthe aquatica (L.) Poir.	more fr southwards			xx	x	x	13	0/11/28	xx	xx	3	2		1			
Sium latifolium L.	more fr southw., not ab	x	xx	xx	xxx	xxx	60	42/63/78	xx	xx	27	6	8	5	11	5	3
Galium palustre L.						x			x	x	8	4			3		
Menyanthes trifoliata L.				xx	x				x	?	x	5			1		
Myosotis scorpioides L.	rel fr in reeds of S p				xx	x			x	?	11	7			7	1	1
Symphytum officinale L.	marshes, r valleys					x											
Solanum dulcamara L.					x	x											
Scutellaria galericulata L.						x				x	3	3					
Lycopus europaeus L.					x				x	?	5						
Mentha spp. (incl. *M. x verticillata* L., *M. aquatica* L.)					x	x			x	x		2	x				
Stachys palustris L.	marshes, in pl fr					xx			?	x	11	6		2			
Hippuris vulgaris L.						x			x	x						1	2
Cardamine spp.						x											
Rorippa amphibia (L.) Bess.			x	xx	?	xx	?		x	?	2	2	5	2	10	2	3
R. palustris (L.) Bess.	fl sh z				x	x					x	x	x		x		
Subularia aquatica L. *	Raskopel B, N sh of Piirissaar, extinct?		x	x	x		5				20	13			1		
Bidens cernuus L.	fl sh z					x					3						
B. radiata Thuill.	after EF in S p																
B. tripartitus L.	fl sh z					xx					7	x		1			1
Senecio paludosus L.						x							1		1	1	

Table 2 continued

Taxon	Growth areas in L. Peipsi (if known)	1962–63 H.T. N p NB! 3 points	1962–63 H.T. S p NB! 3 points	1966–70 G.N. 4 points	1970–80 A.M. 4 points	1997–99 H.M. 4 points	Frequencies: whole lake (%)	Frequencies: Peipsi s.s./ Lämmijärv/ Pihkva (%)	Võrtsjärv 1965–66 A.M.	Võrtsjärv 1997 T.F.	Ladoga	Onega	Ilmen	Beloe	Kubenskoe	Vozhe	Lacha
Myosoton aquaticum (L.) Moench	fl sh z					x											
Sagina nodosa (L.) Fenzl	fl sh z					x											
Stellaria palustris Retz.					x												
Montia fontana L.	after EF in Pi																
Polygonum lapathifolium L.	harbours, fl sh z					x											
Rumex aquaticus L.				xx	x												
R. confertus Willd.				xx?													
R. hydrolapathum Huds.	more fr in S p	?	?	?	xx	xx	34	22/47/41	x	?	?						
R. maritimus L.	fl sh z, more fr at W c				x	x	11	17/0/13	?	x	4	1					
Lysimachia thyrsiflora L.					x	x			x	?	27	25	2	1	4		
L. vulgaris L.	more fr southwards		x	xx	x	x			?	x	7	5	x	2	3		1
Alisma gramineum C. Ch. Gmel.*	shal w, fr decr	x	x	xx	xxx	x	53	56/47/53									
A. plantago-aquatica L.	fr, but sc	x	x	xxx	xx	xx	39	50/37/28	x	xx	29	27	3	4	7	5	3
Sagittaria sagittifolia L.	**dom**, lrg sts in r mouths; L	x	xxx	xxx	xxxx	xxx	78	67/89/84	xx	xx	35	18	11	11	12	7	12
Iris pseudacorus L.	sc, more fr in S p	?	x	xx	xx	x			x	?	13	5					
Butomus umbellatus L.	fr, most ab in P	x	xx	xxx	xxx	xx	63		xx	xx	14	6	12	10	13	5	3
Juncus spp. (incl. *J. ambiguus* (coll.) Guss., *J. bufonius* L., *J. articulatus* L., *J. filiformis* L., *J. nodulosus* Wahlenb.)	fl sh z, fr in NW of P	?	?	x	xx	xx	15		xx	?	14	7					
Cyperus fuscus L.	N and NW sh of P, rarely					x											
Eleocharis acicularis Roem. et Schult.	fl sh z, fr at E coast of P	?	?	xx	xx	xx	45	44/42/27	xx	?	11	10	4		15	5	8
E. mamillata H. Lindb.	after EF on the sh of P																
E. ovata (Roth.) Roem. et Schult.				xx?													

Table 2 continued

Taxon	Growth areas in L. Peipsi (if known)	1962–63 H.T. N p NB! 3 points	1962–63 H.T. S p NB! 3 points	1966–70 G.N. 4 points	1970–80 A.M. 4 points	1997–99 H.M. 4 points	Frequencies: whole lake (%)	Frequencies: Peipsi *s.s.*/ Lämmijärv/ Pihkva (%)	Võrtsjärv 1965–66 A.M.	Võrtsjärv 1997 T.F.	Ladoga	Onega	Ilmen	Beloe	Kubenskoe	Vozhe	Lacha
E. palustris (L.) Brown em. Roem. et Schult.	lrg sts in Pi	x	xx	xxx	xxx	xx	74	64/79/81	xx	x	28	24	11	x	13	2	3
E. uniglumis (Link.) Schult.	mainly in NW corner of P				x				xx	?							
Schoenoplectus lacustris (L.) Palla	**dom,** especially in S p	x	xxx	xxxx	xxxx	xxx	90	78/100/97	xxx	xxx	23	31	13	2	3	9	11
Bolboschoenus maritimus (L.) Palla				x													
Scirpus radicans Schkuhr.	in pl in S p		x	xx	x	x	10	6/0/22									
S. sylvaticus L.					x	x											
Carex spp. (incl. *C. acuta* L., *C. aquatilis* Wahlenb., *C. pseudo-cyperus* L., *C. rostrata* Stok., *C. vesicaria* L., *C. vulpina* L.)	fr but not ab in sh w and at w border; in marshes		x	xx	xxx	xxx	54	53/58/53	xx	xx	35	50	9	9	10	2	2
Phragmites australis (Cav.) Trin ex Steud.	**dom**, most ab in S p of P and in Pi	x	xxx	xxxx	xxxx	xxxx	91	83/100/94	xxxx	xxxx	49	51		11	6	11	10
Calamagrostis neglecta (Ehrh.) Gaertn., Mey. et Scherb.	in pl in marshes					x											
Agrostis stolonifera L.	vegetative sts in sh w	?	?	?	xxx	xxx	51	47/58/50	x	xx							
Glyceria maxima (Hartm.) Holmb.	very fr at settlements		xx	xxx	xxx	xxx	47	33/53/59	x	?	21	2		5	3	4	1
G. fluitans (L.) R. Brown		x	x	xx	xx	xx	13	11/11/16	x	?	4	1					
G. plicata (Fr.) Fr.						x											
Phalaris arundinacea L.	rather fr in marshes	x	x	xx	x	xx			xx	xx	18	9	4	5	6	1	2
Scolochloa festucacea (Willd.) Link.	fr incr southwards		xx	xx	xx	x	24	19/21/31	x	?	26	7		9		3	2
Acorus calamus L.	relatively fr in Pi		xx	xx	xx	x	40	31/32/47	x								
Sparganium erectum L. (coll.)	eutr b, at infl, not ab		x	xx	x	x	14	11/11/19	xx	xx	1	8	3	4	7	2	1
Typha angustifolia L.	eutr b, at infl, fr incr?	x	xx	xx	xx	xx	30	14/26/50	xxx	xxx	9	13		4		4	
T. latifolia L.	pools, muddy creeks		x	xx	x	x	16	19/5/19	x	?	1	1		3			

yield indirect estimates of frequency only for the most common species (i.e. main association forming species). By adding to the above list the species found by H. Mäemets as well as those mentioned in the book *Estonian Flora* (Eesti Floora, 1953–84), the number totals 128, excluding three species considered dubious by A. Mäemets: *Alisma gramineum* subsp. *Wahlenbergii* Holmb., *Catabrosa aquatica* (L.) Beauv., and *Schoenoplectus tabernaemontanii* (C. Ch. Gmel.) Palla. Still, in all probability, some of the species have become extinct or very rare by now. Table 2 presents all taxa registered at different times supplied, as much as possible, with brief comments in regard to habitats, frequencies, and, for comparison, available data on the macroflora of several large lakes in neighbouring areas. The data presented by Raspopov (1985) reflect frequency indirectly (through presence in associations). Taxa among the main groups of life forms are arranged according to families after *Estonian Flora*, while genera and species are arranged in alphabetic order.

RESULTS AND DISCUSSION

Changes in the macroflora of Lake Peipsi in the course of eutrophication

Considering the character of its contemporary macroflora, L. Peipsi is a typical eutrophic waterbody (Mäemets, 1985). The dominant species are *Potamogeton perfoliatus* and *Phragmites australis*, which are southwards supplemented with *Schoenoplectus lacustris* (Fig. 2) and *Sagittaria sagittifolia*. Judging by earlier data, the macrovegetation of L. Peipsi *s.s.* was very scanty in the first quarter of the 20th century (Tartumaa, 1925). It was still scanty in the early 1960s and, according to a description from the 1960s (Tuvikene, 1966), possessed oligo-mesotrophic features at least in the northern part up to the Varnja–Spitsyno demarcation line. The common depth limit for submerged plants was 2–3 m, in exceptional cases 5 m (*Potamogeton perfoliatus*) or even 8 m (mosses) (Tuvikene, 1966). Since the area covered with vegetation accounted for only a few per cent of the lake surface still in the late 1960s (Table 3), it can be supposed that before eutrophication started its proportion could not have been much greater than it is in oligotrophic lakes Ladoga and Onega (Äänisjärv), where it was 0.6% and 0.24% of the surface area, respectively, in the 1980s (Raspopov, 1985).

For comparison, a few examples are presented of the other groups of biota. In zooplankton, the character species of oligo-mesotrophic lakes, *Holopedium giberrum* Zadd., was present up to the early 1960s (the latest record from 1964) (Mäemets et al., 1996). In phytoplankton, the character species of large oligo-mesotrophic lakes, *Aulacoseira islandica* (O. Müller) Sim., is abounding also at present in spring and autumn (Laugaste et al., 1996).

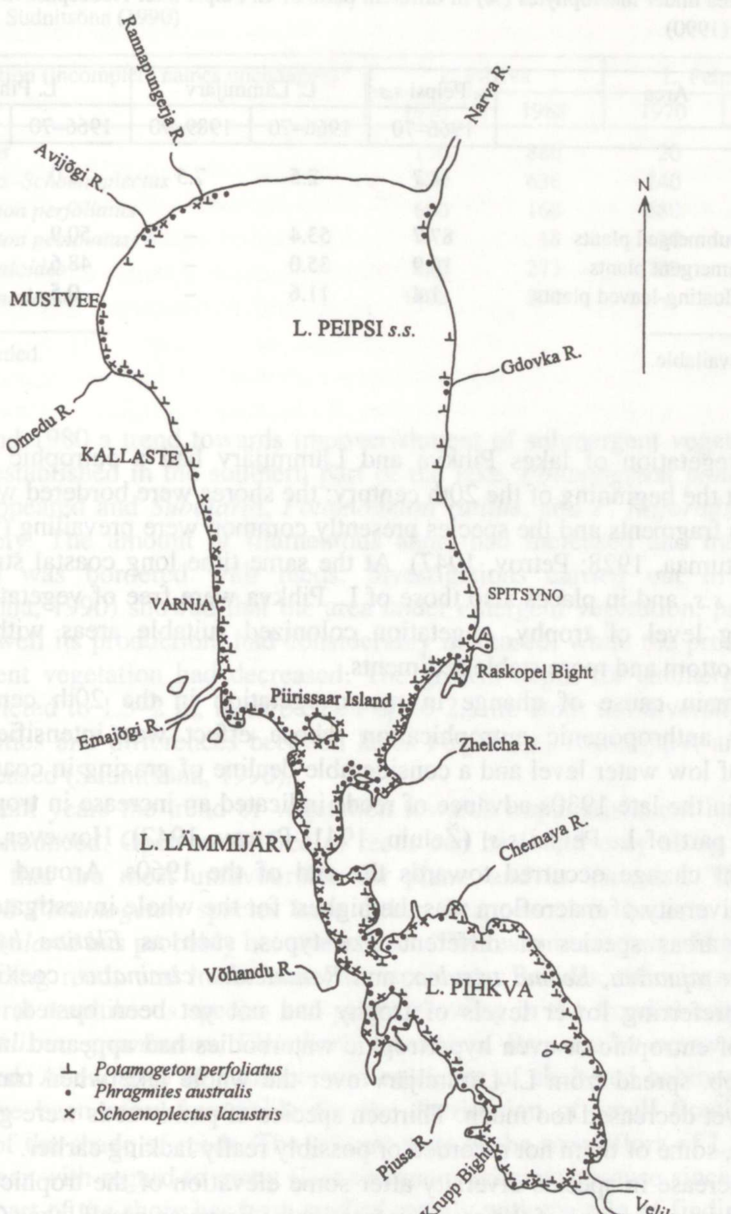

Fig. 2. Growth areas of some dominant macrophytes in Lake Peipsi on the basis of investigations in 1970, 1971, and 1980 (after A. Mäemets).

Table 3. Area under macrophytes (%) in different parts of L. Peipsi after Nedospasova (1974) and Sudnitsõna (1990)

Area	L. Peipsi *s.s.*	L. Lämmijärv		L. Pihkva	
	1966–70	1966–70	1989–90	1966–70	1989–90
Total area	1.7	2.5	7.5	5.0	7.9
Of this					
under submerged plants	87.7	53.4	–	50.9	–
under emergent plants	10.9	35.0	–	48.6	–
under floating-leaved plants	1.4	11.6	–	0.5	–

– No data available.

The vegetation of lakes Pihkva and Lämmijärv had a eutrophic character already at the beginning of the 20th century: the shores were bordered with a reed belt or its fragments and the species presently common were prevailing (Võrumaa, 1926; Setumaa, 1928; Petrov, 1947). At the same time long coastal stretches of L. Peipsi *s.s.* and in places also those of L. Pihkva were free of vegetation. With increasing level of trophy, vegetation colonized suitable areas with a more sloping bottom and more stable sediments.

The main cause of change in macrovegetation in the 20th century was evidently anthropogenic eutrophication whose effect was intensified during periods of low water level and a considerable decline of grazing in coastal areas. Already in the late 1930s advance of reeds indicated an increase in trophy in the southern part of L. Peipsi *s.s.* (Želnin, 1941; Petrov, 1947). However, the most significant change occurred towards the end of the 1960s. Around 1970, the species diversity of macroflora was the highest for the whole investigated period. In some areas species of different lake types, such as *Elatine hydropiper*, *Subularia aquatica*, *Lemna trisulca*, and *Ranunculus circinatus*, coexisted. The species preferring lower levels of trophy had not yet been ousted, while the species of eutrophic or even hypertrophic waterbodies had appeared in the lake. *Chara* spp. spread from L. Lämmijärv over the whole lake when transparency had not yet decreased too much. Thirteen species of pondweeds were growing in L. Peipsi, some of them not recorded or possibly really lacking earlier.

An increase in species diversity after some elevation of the trophic level has been noted also in case of the macrovegetation of Estonian small lakes (Mäemets, 1985). The dry matter production of submergent species (Table 4) reached its peak values in L. Peipsi in 1966–67, surpassing even the respective parameters of more southern regions and attracting researchers' attention as a sign of unfavourable changes in the whole ecosystem (Raspopov, 1985). Lake Peipsi *s.s.* was more than earlier occupied by submerged vegetation (mainly elodeids) and reeds were increasingly expanding.

Table 4. Productivity of some macrophyte associations (dry weight g m^{-2}) after Nedospasova (1974) and Sudnitsõna (1990)

Association (incomplete names unchanged)	L. Pihkva		L. Peipsi *s.s.*	
	1970	1988	1970	1988
Phragmites	130	880	20	789
Phragmites–Schoenoplectus	370	636	240	761
Potamogeton perfoliatus	690	168	680	104
Potamogeton pectinatus	–	18	20	37
Stratiotes aloides	820	273	780	158
Elodea canadensis	1402	204	–	126

– Not recorded.

Around 1980 a trend towards impoverishment of submergent vegetation was already established in the southern part of the lake. *Potamogeton panormitanus* had disappeared and *Subularia*, *Potamogeton rutilus*, and *P. filiformis* occurred very rarely. The amount of filamentous algae had increased and most of the shoreline was bordered with reeds. Investigations carried out in 1988–89 (Sudnitsõna, 1990) showed that the area under emergent vegetation, particularly reed, as well its production, had considerably increased, while the production of submergent vegetation had decreased. The growth depth for submerged plants was restricted to 1.5–2 m, in rare cases up to 2.5 m. Both the diversity of plant communities and differences between lakes Peipsi *s.s.*, Lämmijärv, and Pihkva had decreased (Sudnitsõna, 1990).

In recent years the trend of vegetation towards impoverishment has become more pronounced. Open water free of reeds can be found only along the shore stretches that are most unfavourable for plants and in harbours. The above-mentioned *Potamogeton* species have either disappeared or become very rare, while *Subularia* has probably become extinct. The reasons are loss of habitats due to expanding reeds and lower water transparency. Besides submerged species, also several amphibious species and plants growing in the flooded coastal zone, such as *Alisma gramineum*, *Eleocharis acicularis*, *Ranunculus reptans* etc., are suppressed. Abundance of nutrients and existence of sheltered habitats between reeds have been most favourable for the distribution of small floating plants tolerant of the shade of reeds. The present state of the macroflora of L. Peipsi is still unclear with regard to many (less common) species, because since 1980 the Russian part of the shore has been studied mainly with the aim of finding out the most widespread communities and their production.

Specific features of the macroflora of Lake Peipsi

Estonia is a border of the distribution area for a large number of plant species, among which the majority are growing on the northern or northeastern boundary of their area. Several coastal species occur on their southeastern border in Estonia (Kukk, 1999). Some plant species of L. Peipsi whose eastern boundary of the area passes the lake have been rarely found (*Peplis portula*) or have not been recorded in recent decades (*Montia lamprosperma*). Among the species occurring on the shore of L. Peipsi *Rumex maritimus*, *Alisma gramineum*, *Cyperus fuscus*, and very rare *Potamogeton trichoides* are growing on their northern boundary in Estonia; *Oenanthe aquatica*, *Sium latifolium*, *Hottonia palustris*, *Potamogeton crispus*, and *Symphytum officinale* reach their northern border in the Baltic Sea region (Jalas & Suominen, 1972–1999). *Scolochloa festucacea* and *Rorippa amphibia* are most widely spread in eastern and north-eastern Europe and in eastern Estonia.

A specific feature of L. Peipsi is the occurrence of species typical of the seashore, such as *Potamogeton pectinatus*, *P. pusillus*, *P. filiformis*, *Zannichellia palustris*, *Eleocharis uniglumis*, and *Bolboschoenus maritimus* (Nedospasova, 1974). Compared with L. Peipsi a conspicuous feature of large lakes of the northwestern part of the Russian Platform (Raspopov, 1985, Table 2) is total absence of *Zannichellia* and *Eleocharis uniglumis* and low occurrence of Characeae (Table 2). According to the data of Maristo (1941) and Rintanen (1996) for 113 lakes, some above-mentioned seashore species appeared in Finnish small lakes in the period from the late 1930s to the early 1980s, though in small numbers: *Potamogeton pusillus* (three findings), *P. pectinatus* (one finding), *Zannichellia palustris* (one finding), and in addition even *Najas marina* (two findings), which does not occur in L. Peipsi. Although in case of both L. Peipsi and Finnish lakes it cannot be excluded that some of these species had remained undetermined during earlier research (Maristo, 1941; Tuvikene, 1966), it is more likely that the appearance of "marine" species or their more frequent occurrence is related to higher trophy.

Lakes Peipsi, Võrtsjärv, Ladoga, and Onega as well as the other lakes of northwestern Russia presented in Table 2 share 19 macrophyte species: *Potamogeton gramineus*, *P. perfoliatus*, *P. lucens*, *Lemna trisulca*, *Nuphar lutea*, *Polygonum amphibium*, *Sparganium emersum*, *Equisetum fluviatile*, *Caltha palustris*, *Sium latifolium*, *Rorippa amphibia*, *Alisma plantago-aquatica*, *Sagittaria sagittifolia*, *Butomus umbellatus*, *Eleocharis palustris*, *Schoenoplectus lacustris*, *Carex acuta*, *Phalaris arundinacea*, and *Sparganium erectum* (coll.). Of other common species *Lysimachia vulgaris*, *Eleocharis acicularis*, *Phragmites australis*, and *Glyceria maxima* have not been recorded only in one lake, while *Myriophyllum spicatum*, *Stratiotes aloides*, *Potamogeton pusillus*, *P. pectinatus*, *Nymphaea candida*, *Ranunculus reptans*, *Myosotis scorpioides*, and *Lysimachia thyrsiflora* have not been found in two lakes. Comparing this list with data for Estonian small lakes, the following species can be regarded as typical of large lakes besides the above-mentioned seashore species: *Potamogeton gramineus*, *Ranunculus reptans*, *Eleocharis acicularis*, and *Sium latifolium*. It is interesting to note that *Phragmites* is totally lacking in large shallow L. Ilmen (1180 km^2, mean depth 3 m), which appears to be eutrophic considering the abundance of elodeids and some other features. This peculiarity as well as the paucity of other Poaceae was observed by Raspopov (1985). *Phragmites* is absent also from some hypereutrophic Estonian small lakes. The cause of the suppression of this cosmopolitan species would be worth studying.

Lake Peipsi lacks several species characteristic of the oligotrophic lakes of Fennoscandia and lakes Ladoga and Onega, located in the peripheral part of the Baltic shield. Lake Onega is the most soft-watered among the large lakes under discussion (total amount of ions only 34 mg L^{-1}) (Raspopov, 1985). These lacking species are *Lobelia dortmanna* L., *Isoëtes lacustris* L., *Myriophyllum alterniflorum* DC., *Sparganium angustifolium* Michx., *S. gramineum* Georgi, *Littorella uniflora* (L.) Aschers, and some others typical of oligotrophic waters. For these species the mineral content in the water of L. Peipsi is evidently too high. Also several species characteristic of oligo-mesotrophic lakes have occurred or occur presently in L. Peipsi (e.g. by Maristo, 1941; Mäemets, 1985; Palmer, 1992), but probably not so much due to the chemical properties of water as to high water transparency, the sandy littoral, and a small amount of competitors. Such species are *Subularia aquatica*, *Elatine hydropiper*, *Ranunculus reptans*, *Eleocharis acicularis*, and *Isoëtes echinospora* Durieu. These species are known to tolerate water salinity as high as 3.5‰, while *S. aquatica* can grow even at higher salinity (Svenonius, 1925 cited in Samuelsson, 1934; Grapengiesser, 1926, 1934; Arwidsson, 1931; Lohammar, pers. comm.). Disappearance of these species or decrease in their frequency are primarily related to water blooms or decrease in water transparency due to other causes but also the overgrowing of the littoral or its being covered with a mud layer. *Fontinalis antipyretica*, which is an oligo-mesotrophic species in the opinion of British and Finnish researchers (Palmer, 1992; Karttunen & Toivonen, 1995), occurs in Estonia more often in eutrophic waters and its habitats in L. Peipsi have shifted gradually northwards in the course of eutrophication. In most cases it has been a typical variety but in 1997–99 *Fontinalis antipyretica* var. *gracilis* (Lindb.) Schimp., occurring commonly in flowing waters (Kalda & Haab, 1994), was found (as outcast remains on water border) on a long stretch in the vicinity of the northern shore of L. Peipsi *s.s.* and in some other sites. However, neither *Riccia fluitans* L. nor *Ricciocarpus natans* (L.) Corda, both occurring in L. Ladoga and in eutrophied Finnish lakes (Raspopov, 1985; Toivonen, 1985; Karttunen & Toivonen; 1995), had been registered in L. Peipsi until 1999 when H. Mäemets found a few specimens of *R. natans*. A species characteristic namely of L. Peipsi and found mainly in the vicinity of this lake is *Alisma gramineum.* Its abundance here was moderate in 1970–80, but by now its frequency has decreased significantly as a result of the invasion of reeds. Among rarer species the occurrence of *Cyperus fuscus* and *Scirpus radicans* should be mentioned; recent data on *Bidens radiata* are lacking.

Some aspects of temporal changes of the macroflora

The long-time high nutrient content in the water of L. Peipsi favours mainly expansion of taller emergent plants (first of all reeds) but also lemnids and, to a lesser degree, nympheids and ceratophyllids growing in their vicinity. The growth areas of elodeids and particularly of isoetids are rapidly diminishing. Of amphibian species "heliophytes" (*Alisma gramineum*, *Ranunculus reptans*, etc.) are undergoing a decline. For these species as well as for other open shore species new habitats are appearing: man-made or man-affected areas, e.g. harbours, where the pollution load is lower, and some beaches with lower recreational pressure.

However, changes in the frequency of several species are difficult to explain. According to some researchers (Table 2), *Potamogeton lucens* was even among the dominants in the 1960s but became quite rare in 1970–80. In 1988–89 Sudnitsyna (1990) mentions it again as belonging to more common plant communities. It could be supposed that there exist certain cycles in the frequency of species, which are influenced by factors so far unknown. Raspopov (1985) found *Ceratophyllum demersum* to be abundant in lakes Ladoga and Latsha in the early 1960s, but later the importance of this species has been modest or insignificant. As causes of its abundance, he suggests involvement of some cyclicity, anthropogenic eutrophication, or the effect of warm summers. It can be also supposed that such profound and rapid changes reflect instability of the ecosystem, in case of which a change of some single environmental condition will bring about larger fluctuations compared with those occurring in a stable system. In L. Peipsi it was the vegetation itself that played the stabilizing role with respect to the biota of the lake as a whole during the last decades; however, changes that have taken place in the composition of the vegetation indicate instability. As the results of the observations in 1997, 1998, and 1999 show, the stands of macrophytes underwent rapid fluctuations due to different summers. Nevertheless, undoubtedly there exist complicated interrelationships. For example, a high water level favours the input of nutrients and humic substances but impedes the expansion of the vegetation. A negative correlation probably exists between the productivities of phytoplankton and macrophytes, which in their turn depend on temperature conditions, etc. To differentiate between long-term changes and fluctuations, it is necessary to investigate the macrovegetation more frequently, paying attention to the growth conditions of every year.

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PEIPSI JÄRVE SUURTAIMESTIKU TAKSONITE KOMMENTEERITUD NIMISTU

Helle MÄEMETS ja Aime MÄEMETS

Peipsi järve rannikult on aastail 1962–1998 uurijate poolt leitud 128 taksonit õis-, sõnajalg-, sammal- ja mändvetiktaimi. Artiklis on antud lühiülevaade nende kasvualadest ja esinemissagedusest eri perioodidel ning võrreldud makrofloora koosseisu Peipsis ja teistes Vene lavamaa loodeservas paiknevates suurtes järvedes, tuues välja 31 ühist liiki. Peipsis puuduvad tõelised oligotroofsete järvede liigid, kuid vee hea läbipaistvus ja liivane avatud litoraal võimaldasid kuni 1970. aastateni mitmete põhjataimede sagedast esinemist. Antropogeense eutrofeerumise tõttu, mis algul soodustas liigirikkust ja ohtrat veesisest taimestikku, on praeguseks peaaegu kogu rannik hõivatud roostike poolt ning tugevad vee õitsemised on tinginud läbipaistvuse vähenemise. Makrofloora vaesumine on ilmne.