Chapter

Natural and Anthropogenic Impacts on the Macrophytes of Soft-Water Lakes of Estonia

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Abstract

Oligotrophic and semidystrophic lakes (water alkalinity <80 mg HCO_3^- L^{-1}; dichromate oxygen consumption <40 mg O L^{-1}) are the main habitats for rare macrophytes, especially isoetids. They are characteristic for the lakes with $HCO_3^- \leq$ 30 mg L^{-1}; the higher alkalinity and related higher trophy level support elodeids. Anthropogenic impact on these lakes in Estonia started with flax retting and water lowering and continued with sauna building, agricultural nutrients, and holiday activities. The present overview is based on the data of the last 50 years. Anthropogenic acidification of Estonian lakes is not known, but natural dystrophication due to the inflow of humic compounds is probable. Alkalization and eutrophication are closely related, amplifying each other, and water level modifies these processes. Eutrophication increases the occupation of shallow zone by emergent belts, suppression of isoetids by elodeids, and overshadowing by phytoplankton blooms in a deeper zone or host plants by macroalgae. Fast-growing eutraphents accelerate the accumulation of organic sediments, unfavorable for isoetids. Among floating-leaved plants hybridization between rare and common species as well as introgression takes place. It is almost impossible to reverse back ecosystems that formed and balanced over thousands of years and became unbalanced during a much shorter period. Easier would be to keep functioning ecosystems.

Keywords: oligotrophy, dystrophication, eutrophication, hydrophytes, competition

1. Introduction

The concept of oligotrophic state of the lakes has been applied relatively widely, mostly not concerning natural types of lakes. In literature, it has been used also for the lakes with mean or high content of the bicarbonate ion (HCO_3^-) in the water, if the content of main nutrients (C, N, P) is low. Light soft-water lakes are 'real' oligotrophic (OL) lakes, because in some cases, their clear water is comparable with distilled water. The next step of their development may be semidystrophic (SD) lakes, where moderate content of humic compounds from the forest or peatland stains water yellow or light brown [1]. Most of these two types, hereafter, named soft-water lakes (SWL—excluding acidotrophic and dystrophic lakes), are located in the boreal region of the northern hemisphere, but they occur also in warmer climates, for example, in Atlantic dyne areas of SW France, as well as in mountains. For the composition of macrophytes and other primary producers, the content of bicarbonate ions in the water plays a significant role, allowing the growth of HCO_3^- demanding macrophytes in SWL only close to inflows of mostly hard (with some exceptions) groundwater in the littoral. Long-term research in North Wisconsin revealed that, in seepage lakes, groundwater recharge formed 0–25% [2]. When the nutrient loading is accompanied by bank erosion or a decline in water level (an increase of the proportion of groundwater), HCO_3^- supply increases too.

Most characteristics of SWL are submerged mosses and isoetids that are small, slow-growing and adapted to the nutrient-poor environment. However, adaptation to the nutrient-poor habitat does not mean that these plants perish immediately after uncommon nutrient loading. Mostly they are suppressed during the following years, by fast-growing 'common' species, being able to colonize the habitat in changed conditions and producing larger amounts of organic remains leading to oxygen depletion. The other negative impact of higher trophy for submerged plants is mass-propagation of epiphytic and/or planktonic algae and a decline in light availability. In some taxa, for example, *Nuphar* and *Sparganium*, eutrophication supports introgression, while common species hybridizes with the specimens of rare species and again with the hybrids during the generations.

Estonian soft-water lakes are formed during the Late Glacial and Holocene in sandy areas on both alkaline (limestone) and acidic (sandstone) bedrock (**Figure 1**). Sandy areas were formed by glacier meltwaters or on coastal terraces of Baltic Sea [3], and during the Holocene sand in the slopes of the lake basins was washed through,

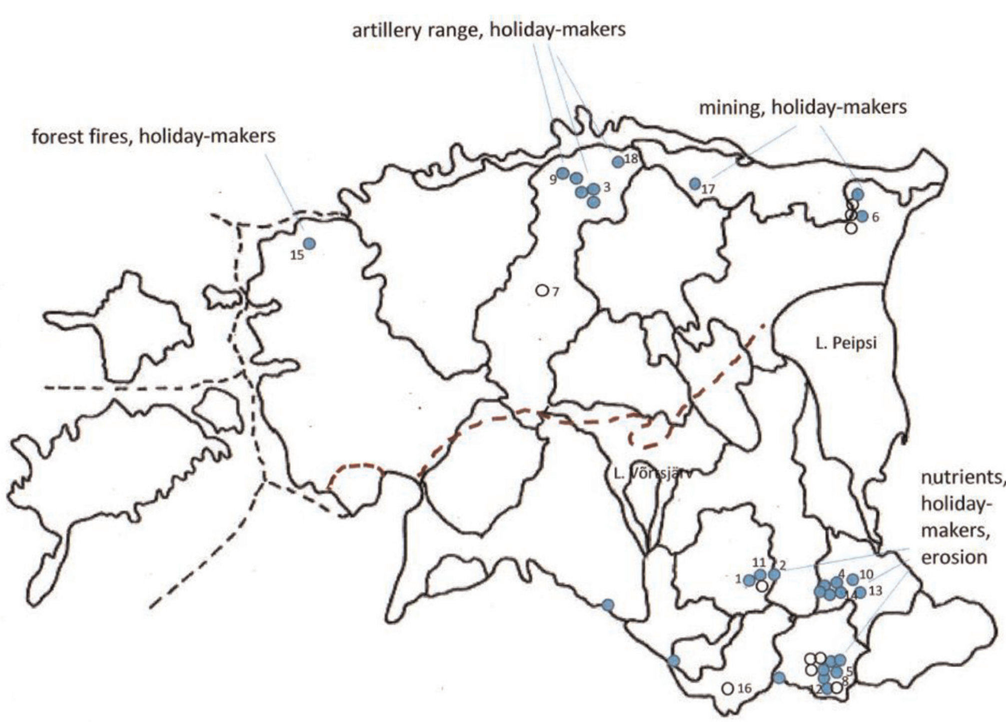

Figure 1.
Main anthropogenic impacts on the OL and SD lakes in different regions of Estonia and the occurrence of rare macrophytes: empty circles—found in 1971–2011; blue circles—persisted also in 2012–2022; brown dashed line—approximate border between Ordovician & Silurian limestones and Devonian sandstone. Black lines—geographical (landscape) districts. The numbers of lakes in ***Table 1****: 1, Hüüdre; 2, Ihamaru Palojärv; 3, Jussi Pikkjärv; 4, Karsna; 5, Kirikumäe; 6, Kurtna Valgejärv; 7, Matsimäe Pühajärv; 8, Mikeli; 9, Mähuste; 10, Nohipalu Valgjärv; 11, Piigandi; 12, Pullijärv; 13, Solda; 14, Tsolgo Pikkjärv; 15, Tänavjärv; 16, Ubajärv; 17, Uljaste; 18, Viitna Pikkjärv.*

reducing their nutrient content. General delimitation of SWL according to alkalinity of the epilimnetic layer in summer is <80 mg HCO_3^- L^{-1}. These lakes are divided into two groups: (A) alkalinity <30 mg; (B) 30–80 mg HCO_3^- L^{-1} [4]. The content of dissolved organic matter/humic compounds, expressed as chemical oxygen demand: dichromate oxygen consumption (COD) is mostly <35 mg O L^{-1}. The lakes with remarkably higher COD belong to dystrophic (> 40) and acidotrophic (> 80 mg) groups, [1, 4], not addressed below. Due to negligible buffer capacity, OL lakes are most sensitive to eutrophication, and nowadays in Estonia oligotrophic lakes of reference state are lost. On the basis of the data from the twentieth century, the book concerned on Estonian SWL in 1991 covered 121 lakes [4], but among them about 50 were already eutrophic. At the end of the twentieth century, an estimated number for the lakes close to OL was 20, and for SD lakes, 40 [1]. These two lake types are the main habitats for several rare hydrophytes and have been subject to the both, natural and mediated/immediated anthropogenic impacts. The aims of the present overview is to discuss already specified threats to SWL and to point out particular features of Estonian SWL. Hopefully, it helps to understand which changes may be irreversible and what is in our chancery to improve the situation.

2. Materials

First single descriptions of the vegetation of small, < 100 km^2 lakes, including soft-watered, date back to the beginning of the twentieth century, and some lake groups in East Estonia were studied already between two World Wars. The main part of investigations were carried out since the 1950s, and today most of the SWL have been studied repeatedly but not regularly. Macrophyte data are assembled into a special database and kept at the Chair of Hydrobiology and Fishery of Estonian University of Life Sciences. There, the data from 1960s to 1990s originate from the studies by Aime Mäemets (1930–1996); subsequently, SWL were studied by the author, L. Freiberg, Dr. K. Palmik-Das, G. Ratasepp, Dr. K. Karus, Dr. T. Feldmann and M. Lehtpuu. A more intense investigation of the macrophytes of SWL started in 2011 when the author studied 52 lakes for the compiling of protection plans for rare macrophytes. Later on, inventories of protected plants were carried out in 2012 (18 SWL), in 2018–2019 (26 SWL) and in 2021–2022 (20 SWL) by the author, Dr. K. Palmik-Das and MSc student E. Kara.

Passing the littoral of the whole lake by boat, composition and relative abundances of the macrophyte species (separately for all belts: emergent, floating-leaved, etc.) were estimated for a lake in a modified 1 ... 5 scales of Braun-Blanquet. Using the plant hook with marked rope (or stick), depth limits of macrophytes were measured on transects. Also, vegetation schemes were drawn in the field, using the signs of taxa. This method has been used since the 1950s and serves as the basis for the estimation of ecological quality classes for SWL [5]. At the inventories of protected macrophytes also an approximate number of their individuals was estimated, as well as GPS coordinates and distribution polygons were fixed. Additionally, vitality of plants, entailed taxa and other circumstances were studied.

The area of the 60 OL and SD lakes varies between 1 and 137 ha. However, the majority—38 lakes—belong to the group of <10 ha water bodies, overwhelmingly seepage lakes. Macrophyte data with different frequencies are available for all lakes. There are some deeper and some very small A-lakes without any submerged vegetation during the all recorded time, very probably due to flax retting, taking place (mainly) until the first half of the twentieth century. Preferred were SWL, and at least 15 SWL have 'flax' in their name. We do not know about their vegetation before flax retting.

As shown in **Figure 1**, during the last 50 years, rare macrophytes were found in 38 lakes [6], but in the last decade, they have not more occurred in nine lakes. In 29 lakes with the newest findings, vital populations of at least one species occurred in 16 lakes. The map in **Figure 1** does not include the lakes where during the studied period only very few vegetative (undetermined) narrow-leaved *Sparganium* plants were found.

Hydrochemical data of 18 SWL inhabited by rare plants are presented in **Table 1** and the list of characteristic vascular plants of SWL in **Table 2**. Among selected lakes annual hydrochemical monitoring of the lakes of Nohipalu Valgjärv, Uljaste and

Lake	Year	SD m	pH	HCO_3^- mg L^{-1}	COD mg O L^{-1}	P_{tot} mg P L^{-1}	N_{tot} mg N L^{-1}
Hüüdre (Sg)	1972	1.8	6.8	12.2	46	—	—
Hüüdre (**Sg***)	2021	0.5	9.0	13.1	65	0.057	1.600
Ihamaru Palojärv (**Il Sa**)	1964	3.3	6.0	0.01	33	—	—
Ihamaru Palojärv (**Il Sa**)	1981	3.5	6.4	4.27	41	—	—
Ihamaru Palojärv (Il)	2005	2.6	8.0	9.15	26	0.015	0.683
Jussi Pikkjärv (Sa N)	1990	2.0	7.0	3.0	29	0.030	0.300
Jussi Pikkjärv (Sa N)	2009	2.7	6.9	≤6.1	28	0.025	0.429
Jussi Pikkjärv (Sa N)	2021	3.3	6.5	5.30	23	0.013	0.530
Karsna (**Il Sg E**)	1981	4.0	7.1	30.5	54	—	—
Karsna (**Sg** Il Ma)	2012	1.7	6.2	12.2	44	0.028	1.000
Karsna (**Ma Sg*** Il)	2021	1.9	7.8	15.2	40	0.026	1.100
Kirikumäe (**L Il**)	1990	1.0	6.4	3.1	48	0.094	1.830
Kirikumäe (**L Il**)	2010	1.4	7.5	3.1	32	0.025	0.520
Kurtna Valgejärv (**L** Il)	1981	4.3	7.0	18.3	26	—	—
Kurtna Valgejärv (**L** Il)	2001	2.1	6.7	6.0	—	0.008	0.390
Kurtna Valgejärv (**L** Il, Sa)	2010	1.9	7.6	<6.1	42	0.015	0.420
Matsimäe Pühajärv (Sa)	1964	1.3	≤5	0	43	—	—
Matsimäe Pühajärv	2021	—	4.8	3.04	40	0.026	1.100
Mikeli (Sa)	1970	2.0	5	—	—	—	—
Mikeli	2021	—	4.9	≤1	80	0.047	0.760
Mähuste (**L Il N** Ie)	1969	5.3	6.7	0.6	10	—	—
Mähuste (**L Il N** S*)	1981	3.5	6.6	18	32	—	—
Mähuste (**L Il** N Sg)	2021	3.2	6.8	5.24	28	0.013	0.670
Nohipalu Valgjärv (**Il Sa** L)	1973	4.5	6.0	1.2	14	—	—
Nohipalu Valgjärv (**Il S*** L)	1991	3.8	6.9	6.1	12	0.016	—
Nohipalu Valgjärv (**Il** S*)	2012	4.5	6.3	3.05	23	0.013	0.690
Piigandi (Il S*)	1973	4.5	7.4	24.4	25	—	—
Piigandi (**Il** Sg N)	1991	3.8	7.2	42.7	12	0.011	0.530

Lake	Year	SD m	pH	HCO_3^- mg L^{-1}	COD mg O L^{-1}	P_{tot} mg P L^{-1}	N_{tot} mg N L^{-1}
Piigandi (**Il**)	2012	3.1	8.2	48.8	—	0.015	0.500
Piigandi (**Il** S*)	2021	3.0	8.5	50.0	29	0.019	0.530
Pullijärv (**Ma** L, S*)	1973	2.9	8.0	24.0	28	—	—
Pullijärv (**Ma L** Sg Il)	1990	2.6	7.8	34.0	18	0.030	1.010
Pullijärv (**Ma L** E)	2010	2.8	8.6	42.7	30	0.017	0.690
Solda (**Sg** S*)	1974	1.1	8.4	38.4	40	—	—
Solda (Sa S*)	1981	0.8	10	67	50	—	—
Solda (Sg S*)	2021	0.7	7.4	29.9	120	0.052	1.700
Tsolgo Pikkjärv (E S*)	1961	1.7	7.0	13.4	36	—	—
Tsolgo Pikkjärv (**Ma** Sg)	2021	2.5	8.1	29.6	<15	0.025	0.880
Tänavjärv (**L**)	1976	—	7.1	12	32	—	—
Tänavjärv (**L** Il Sg S*)	1995	1.5	7.3	6.1	24	0.010	0.400
Tänavjärv (**L** S* Il)	2012	1.4	8.4	12.2	22	0.017	0.610
Tänavjärv (**L** S* Il)	2021	1.4	7.9	12.2	27	0.019	0.780
Ubajärv(**Sg** S* Ie)	1974	1.1	7.6	16.48	48	—	—
Ubajärv (**Sg**)	1978	—	6.2	12	56	—	—
Ubajärv (**Sg** S* Ie)	1983	0.6	6.5	6.1	59	—	—
Ubajärv	2021	0.4	6.7	9.1	50	0.073	1.100
Uljaste (**L** Il)	1981	1.5	6.8	15.25	28	—	—
Uljaste (**L Il**)	2000	1.8	7.4	12	34	0.030	0.560
Uljaste (**L** Il)	2012	2.4	7.6	9.15	35	0.022	0.360
Viitna Pikkjärv (**L Il Sa**)	1972	3.3	6.5	5.49	10	—	—
Viitna Pikkjärv (**L Il Sa**)	1992	4.1	6.0	3.0	13	0.016	0.644
Viitna Pikkjärv (**L Il** Sa)	2012	3.6	8.5	12.2	26	0.016	0.610

Abbreviations in brackets: L, Lobelia*; E,* Elatine*; Ie, Il,* Isoëtes*; Sa, Sg,* Sparganium*; Ma, Msi,* Myriophyllum*; N,* Nuphar. ***Bold****, taxa with abundance 3–5; S*, hybrid or vegetative. Latin species names are shown in* ***Table 2****.*

Table 1.
Hydrochemical data of surface layer in midsummer in SWL inhabited by populations of protected vascular plants.

Species name	Category/Red List status	Comments
Isoëtes echinospora Durieu, spiny-spored quillwort	I/RE	Extinct
Isoëtes lacustris L., lake quillwort	II/EN	In the last decade in 12 SWL
Lobelia dortmanna L., water lobelia	II/EN	Vital in 7 SWL, most damaged by holiday-makers
Sparganium angustifolium Michx., narrowleaf bur-reed	II/EN	9 (small) pure, 10 mixed/hybrid populations

Species name	Category/Red List status	Comments
S. gramineum Georgi	II/CR	1 perished pure, 14 mixed/hybrid populations
Myriophyllum alterniflorum DC, alternate water-milfoil	II/EN	In 7 SWL, including 3 very large populations
Elatine hydropiper L., eight-stamened waterwort	II/EN	In SWL rarely, main population in large L. Peipsi
Juncus bulbosus L., bulbous rush	NT	In one SWL
Potamogeton alpinus Balb., reddish pondweed	NT	In eutrophied SWL and in other lake types and rivers
Potamogeton obtusifolius Mert. & W.D.J. Koch, blunt-leaved pondweed	NT	In eutrophied SWL and other lake types
Potamogeton gramineus L., various-leaved pondweed	—	In B- and other lakes where shallow free littoral exists
Potamogeton rutilus Wolfg., Shetland pondweed	EN	In B-lakes; occurs also in other lakes with shallow free littoral

RE, regionally extinct; EN, endangered; NT, near threatened; CR, critically endangered.

Table 2.
Submerged and amphibious macrophytes of OL and SD lakes of Estonia and their actual protection status.*

Viitna Pikkjärv has been carried out since 1994, but in **Table 1** are presented 3 years from different periods, for comparison on the larger scale. A more profound comparison of their hydrochemical data with macrophyte composition deserves special analysis. Older data on hydrochemistry, until 1996, derived from a special database of the Centre for Limnology at Estonian University of Life Sciences. Latter data are compiled from the open monitoring reports by my colleagues. Data on the phosphorus and nitrogen for the studied lakes are available since the 1990s when contemporary, more reliable analyze methods were applied. For the lakes of Matsimäe Pühajärv (**Figure 2**) and Mikeli hydrochemical data are extremely poor, but they were included due to extreme conditions for observable taxa. In 2021, water samples from 14 lakes, which had the scarcest data, were chemically analyzed (project 18,745 of Estonian Environment Investment Centre). Quagmires of SWL of South-East Estonia were studied in 2013 [7] and the latest study of water mosses took place in 2014 [8]. In 2021 MSc student E. Kara and the author carried out a botanical study in 18 lakes with *Sparganium angustifolium* Michx. and/or *S. gramineum* Georgi, and (in cooperation with Tallinn University) a study of sediments in four lakes. E. Kara carried out germination experiment with *Sparganium* seeds from sediments [9].

Littorella uniflora (L.) Asch. (I category) is found only in brackish pools on the western coast of Saaremaa Island; *Subularia aquatica* L. is very probably extinct.

3. Vegetation of soft-water lakes of Estonia

The emergent vegetation belt of SWL is usually narrow or absent. If the reed belt (*Phragmites australis* (Cav.) Trin. ex Steud.) exists, it is fragmentary and sparse in the lakes of good status. The main sedges are tufted sedge *Carex elata* Bell. ex All., bottle

Figure 2.
Pine bog dominates on the banks of L. Matsimäe Pühajärv (author's photo).

sedge *C. rostrata* Stokes and slender sedge *C. lasiocarpa* Ehrh. In SD lakes peaty banks or quacking bogs in the water border yield a considerable chemical influence, increasing the content of humic compounds and decreasing the pH of water. These stretches are without isoetids, obviously not able to grow on organic-rich, oxygen-demanding loose sediments [see also 10, 11]. Isoetids grow only at sandy banks and depend on the proportion of peaty and sandy stretches (**Figure 3**). Among nymphaeids, the most frequent is broad-leaved pondweed *Potamogeton natans* L., but also amphibious bistort *Persicaria amphibia* (L.) Gray, water lilies *Nymphaea* spp. (mostly hybrids), *Nuphar lutea* (L.) Sm. and *Nuphar pumila* (Timm) DC. are not rare. Among *Sparganium* (bur-reed) occurrence of species depends on the water alkalinity, as shown in **Figure 4**, made based on the data from the 1970s to 1980s for 24 SWL [12]. Also, the composition of submerged vascular species reflects water alkalinity: SWL with typical isoetid vegetation [excluding *Littorella*—see also 13] and without elodeids containing ≤30 mg HCO_3^- L^{-1}, that is, they are A-lakes. To draw a limit for COD is more complicated. In most of the isoetid-lakes, summer COD value remains <35 mg O L^{-1}, but in some SD lakes and some years, it has been higher (**Table 1**). We can suppose that at long-lasting enrichment of A-lakes with humic substances (at COD values ≥40 mg O L^{-1}), the isoetids decline, especially *Isoëtes*, inhabiting also deeper zone >1 m. However, data in **Table 1** do not support that supposition in all cases. Very probably, high COD data of some lakes (e.g. Karsna) reflect organic pollution from settlement too. At remarkable dystrophication, few plants of *S. angustifolium* may persist in some lakes during the decades, on a single sandy place. They are very vulnerable, also because there are commonly swimming places.

Figure 3.
Lake quillwort and narrowleaf bur-reed grow near the higher, sandy banks, avoiding pine-bog water border (L. Jussi Linajärv, author's photo).

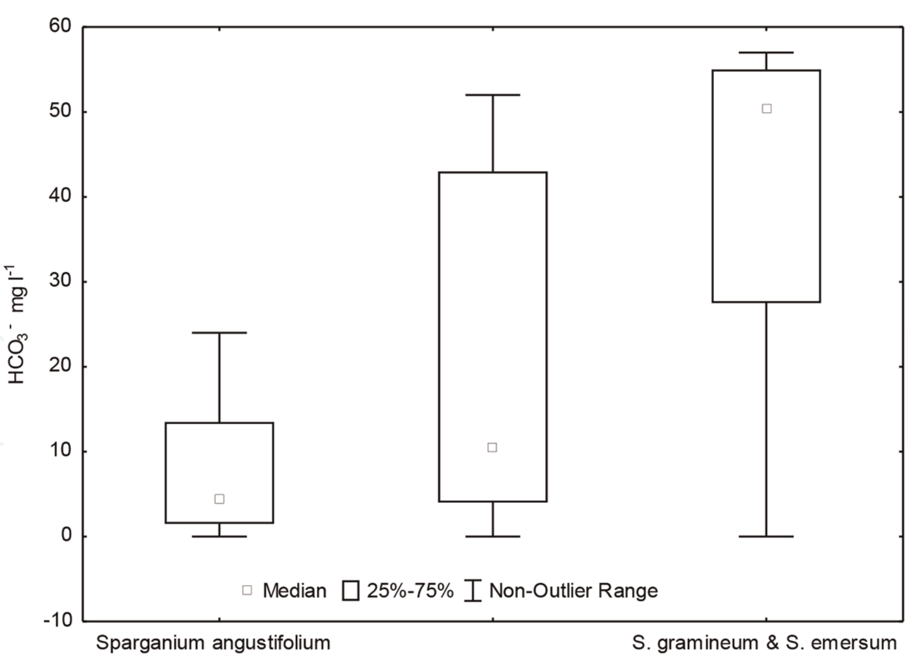

Figure 4.
Water alkalinity and Sparganium *species in 24 lakes (compiled by Dr. R. Laugaste).*

The species of submerged and amphibious vascular plants presented in **Table 2** are growing mainly in lakes in good ecological status. In the case of eutrophication, the submerged vegetation in A-lakes may disappear [6], but B-lakes may be settled by

Indicator	Unit	High	Good	Moderate	Poor	Bad
pH		5.5–7	>7–7.5	>7.5–8	>8–8.5	>8.5
Ptot	mg/l	<0.01	0.01–0.02	>0.02–0.04	>0.04–0.06	>0.06
Ntot	mg/l	<0.2	0.2–0.5	>0.5–0.8	>0.8–1.1	>1.1
SD	m	>5	3–5	2–<3	1–<2	<1

Table 3.
The limits of the values for the estimation of the ecological status of OL and SD lakes according to abiotic indicators [15].

eutraphents: fan-leaved crowfoot *Ranunculus circinatus* Sibth., Canadian pondweed *Elodea canadensis* Michx., Siberian water-milfoil *Myriophyllum sibiricum* Komar., flat-stalked pondweed *Potamogeton friesii* Rupr. etc., inhabiting zone of 1–3 m depth. These secondary taxa are not presented in **Table 2**. Emergent and floating-leaved belts increase too. Lake Piigandi (see **Table 1**) has changed from A-lake to a B-lake due to erosion of steep slopes and conjoint eutrophication, inhabiting now *Ranunculus* and *M. sibiricum*. Some elodeids, such as *Potamogeton gramineus* or *P. rutilus*, need shallow free littoral, and in B-lakes of good status, this habitat is relatively common. In the last 35 years, at least 23 species of submerged mosses have been found in SWL [8, 14], including calciphilous *Drepanocladus sendtneri* (H. Müll.) Warnst. Nowadays, submerged mosses inhabit depth zone 1–11 m [8], and their occurrence is not so clearly related to water alkalinity as to scanty availability of the main nutrients: C (mainly CO_2), N and P. Low nutrient content of the habitat is appropriate, because the metabolism of water mosses may be extremely sparing: the author has been 'cultivating' *Rhynchostegium riparioides* (Hedw.) Card. for 8 years, in a 1 l glass vessel, adding tap or rainwater and rarely removing decaying plant remains. Among charophytes *Chara virgata* Kützing and *Nitella flexilis* (L.) are not rare in B-lakes.

The main abiotic indicators of the water quality and their values for the estimation of the ecological status of OL and SD lakes, established by Estonian Ministry of Environment according to EU Framework Directive [15] are presented in **Table 3**.

4. Stressors and their synergies

As follows, the main natural and anthropogenic stressors and their interactions in SWL will be observed. Most of them are specified by Murphy [10] and Smolders et al. [16], and some are specific to Estonia.

4.1 Acidification, dystrophication and mixotrophication

Acidification in Estonian SWL, if proceeding at all, is natural, not anthropogenic, as in air-polluted Scandinavian lakes on the acidic rock. It may be caused by peaty or/and pine-forested banks and catchment. Substantially it could be dystrophication—natural development direction from OL lakes to SD lakes and further to dystrophic state [1]. Studying the quagmires of SWL in South-East Estonia [7], we found that pH in the water of quagmire societies at seven SD lakes varied largely: 3.34–7.32. In some cases, the pH in the water of moss beds differed remarkably near the same lake, for example, 3.39–6.52. The average pH was lowest in the societies of *Sphagnum fallax*

Figure 5.
Lake Ubajärv and its surroundings (clip from the map of Estonian land board). Extensive quagmire at the lake ends is probably enhanced by melioration drains (blue lines).

(3.6), *Sphagnum magellanicum* agg. & *S. fuscum* (3.7), *S. centrale* (3.8) and *S. flexuosum* (3.9) [7]. Widening of *Sphagnum* quagmires has impoverished submerged vegetation near the water border, in some SWLs, it had persisted communities of Bryales in the deeper zone. Regardless of the acidic quagmire, water pH in the surface layer of all seven lakes was ≥6.

For most of the lakes presented in **Table 1**, the data of COD do not support dystrophication hypothesis. Only in L. Ubajärv, surrounded by extensive forest and mire areas (**Figure 5**), a gradual increase in COD and decrease in water transparency and HCO_3^- has taken place from 1974 to 2021. *Isoëtes echinospora*, earlier occurring sporadically in the northern part, has disappeared during the last 20 years. However, this dystrophication may be enhanced by humans, by earlier melioration, in **Figure 5**, are visible the drains. High value of COD may be caused also by organic pollution from the settlement, and probably also by simultaneous input of organic matter from humic substances and settlement, resulting in enormous values, as in L. Solda (**Table 1**). If the anthropogenic inflow of nutrients overcomes associative capacity of humic substances of the lake to retain nutrients, the lake become mixotrophic: increases the amount of the nutrients in the water, phytoplankton abundance and decomposition of humic substances [1]. These processes are closely related and intensify each other.

4.2 Alkalization, eutrophication, lowering of water level

Water pH of the eutrophied SWL is a highly capricious indicator and depends on the intensity of photosynthesis, therefore, on the season and time of day. Well-pronounced was photosynthetic increase of pH (=9) in water of L. Hüüdre in 2021 (**Table 1**). Water parameters corresponded to ‘poor’ or ‘bad’ ecological status

(**Tables 1** and **3**), and a strong phytoplankton bloom decreased SD to 0.5 m. Submerged vegetation was absent, among floating-leaved plants *Sparganium gramineum* and some common species occurred. Temporary photosynthetic alkalization is among the stressors acting in unbalanced SWL. In **Table 1** become evident, that most high pH values are joint with higher nutrient contents. In the period of the highest nutrient loading (1981 in **Table 1**) L. Solda was measured with the highest pH value: 10. Alkalization during the intensification of photosynthesis is described in the isoetid-lake Uljaste (**Figure 6**), in 1993, where pH raised >9.5 and started fish kill. The reason for fish kill was a complex of phenomena: high water temperature, a wide range of oxygen content fluctuation during a short period, very high pH, water bloom caused by toxin-producing cyanobacteria and ammonia toxification [17].

As mentioned above, elodeids (including potamids) appear in SWL with the increase in trophic level. Eutrophication may be caused by direct nutrient loading but also by increased alkalinity. Water enrichment with minerals in SWL may take place even by adding unwashed sand in a swimming place. Carbonates may come from eroded steep slopes (L. Piigandi; **Table 1**), but in Scandinavia, they were added mainly by liming. According to a profound study by Lucassen et al. [18] on Norwegian carbon-limited Isoëteto-Lobelietum SWL, liming decreased redox potential and increased availability of HCO_3^-, CO_2, NH_4^+, PO_4^{3-} and Fe^{2+} in sediment pore water. In Sweden, the occurrence of several acid-sensitive plants, *Myriophyllum alterniflorum* among them, increased in many limed lakes [19]. Interestingly, Lucassen et al. [18] concluded that *Sparganium angustifolium* is more dependent on the quality of sediment and its pore water than on the nutrients in the water since this bur-reed appeared in the limed plots. According to these authors, it is able to take up CO_2 by roots. Our study of the sediments (0–20 cm) of L. Jussi Pikkjärv, located on the

Figure 6.
Lake quillwort in littoral of L. Uljaste, endangered by opening of new mines (author's photo).

limestone bedrock in North Estonia, revealed that $CaCO_3$ content in dry weight under the stands of *S. angustifolium* formed 0.5–2.7%; organic matter 48–96% [20]. We can suppose that nutrient resource for the fast development of long leaves of *S. angustifolium* is indeed supported by sediment because all trophy parameters of the water were among the lowest of SWL studied in 2021: HCO_3^- 5.3 mg L^{-1}; COD 23 mg L^{-1}; dissolved organic carbon 9.8 mg C L^{-1}; P_{tot} 0.013 mg L^{-1}; N_{tot} 0.54 mg L^{-1}; pH 6.5. In the lake occurred dwarf water lily *Nuphar pumila*; in the shallower part *Isoëtes lacustris*, but abundant was also *Potamogeton natans* L., inhabiting eutrophic-hypertrophic lakes as well. We can conclude that water parameters are not always reflecting the sediment properties of different macrophytes.

Anthropogenic liming in Estonia has been mostly unintended. Some SWL and peat bogs of Northeast Estonia were limed by the oil-shale ash from thermal power stations [21]. In the same region, the drinking water supply lowered the water level of some SWL 3–4 m in the 1970s, resulting in loss of isoetids and growth of pine trees in former littoral. Remarkably, in this period charophytes appeared in the SWL of this region, again disappearing after the raising of the water level. However, changed littoral with remains of trees was no anymore suitable for isoetids. Lowering of the water level combines several effects: alkalization due to increased impact of groundwater (**Table 1**, L. Kurtna Valgejärv in 1981), increased nutrient concentrations, new habitats for emergent belt, promoted by increasing trophy, and advantage of eutraphents among hydrophytes. Nowadays new mines threaten the SWL of Northeast Estonia.

Due to rarity of SWL, limnological studies are concerned mainly with direct nutrient loading, frequently resulting in the mass propagation of phytoplankton or large filamentous algae as suppressors or competitors. All these chemical and biological factors are unfavorable also for SWL, their ecosystem become unbalanced. As seen above, the relations of alkalization and trophy level are more complex than presumed, and water level may modify their impact.

4.3 Competition

For submerged hydrophytes worsening of the light conditions due to decreased water transparency by phytoplankton blooms or thick epiphyton may be decisive. Our experiment with seeds of *S. angustifolium* and *S. gramineum* [9, 20] revealed that there exist unrecognized threats. Besides low germination percentage (varying in sediment samples 2–17%), all seedlings declined under the thick cover of green filamentous algae (*Oedogonium* sp.), despite repeated removal of algal bunches under stereomicroscope during several months. Very probably, algae used decaying seedlings also as a nutrient resource. Supposedly the algae derived from the mud samples that originated from the studied lakes. It can be supposed that also in natural conditions seedlings may perish, but this process on the lake bottom is not observable by a field investigation. In the course of 10 macrophyte investigations of L. Piigandi (in 1953–2022), vegetative plants of *S. gramineum* with floating leaves were found four times and fertile once. In 2 years, only seedlings were found and three times bur-reeds were absent. Perishing of seedlings in L. Piigandi is very probable also under the masses of elodeids that increase their abundance at increased alkalinity. In L. Mähuste thick loose algal mat has been covering the beds of *Isoëtes lacustris* in the depth of 1–2 m in the last years. It is not possible to ascertain the presence of *Isoëtes echinospora*, earlier growing mixed with *I. lacustris*. The duration of this algal mat during the vegetation period is not studied, probably there are periods of lesser abundance. However, photosynthesis of isoetids is hindered under the algal mat. Near the distribution area of isoetids is a holiday place, in use since the Soviet time. According to information from local people, even military tanks were sometimes washed in the lake.

Species growing deeper are more dependent on water transparency, thus, plants with fine-divided leaves, enabling larger surfaces for photosynthesis, are in advantage. It is notable, that the appearance of alternate water milfoil in 14 lakes in South-East Estonia coincided with intense eutrophication and erosion from 1960s to 1980s. During the last 20 years, this species has disappeared from 11, remained in three and inhabits four new lakes. In the lakes where milfoil recently has the highest abundance, the ecological status according to all indicators (**Table 3**) was 'moderate' or 'poor' in the last years. In the lakes filled by *M. alterniflorum*, it displaces other rare species: *Isoëtes lacustris*, *Sparganium gramineum* and *Lobelia dortmanna*. In L. Pullijärv, alternate water-milfoil was found in 1968 and occurs as a dominant until now (**Figure 7**). In 2012 L. Tsolgo Pikkjärv was inhabited by a large single pure population of *S. gramineum*, but water-milfoil, by itself under the cover of algal mass, had destroyed the population of bur-reed in 2021 (**Figure 8**). In the particular lake, our germination experiment [9] ascertained viable seeds of *Sparganium* in the sediments, and the samples contained also spores of *Isoëtes lacustris* and seeds of *Elatine*, growing in the lake before the loading from the pigsty on the bank had its effect. Now their growth zone is covered by an emergent belt. For disturbed SWL *M. alterniflorum* can be considered as eutraphent, despite its rarity. Also, *Myriophyllum sibiricum* Komar., rapidly spreading in very different lakes, has been found in 10 SWL during the last decade.

Applied law does not allow the eradication of one rare species in favor of the other of the same category even in a small part of the lake. In the author's opinion, we must consider the global distribution areas and the level of extinction risk in such cases. The area of *M. alterniflorum* includes North America and Eurasia, but *S. gramineum* is

Figure 7.
In L. Pullijärv water lobelia inhabits depth zone to 1 m. deeper on, to 4 m, grows alternate water-milfoil (author's photo).

Figure 8.
Stands of Sparganium gramineum *in L. Tsolgo Pikkjärv in 2012 (above) and the same area occupied by* Myriophyllum alterniflorum *and algae in 2021 (below; author's photos).*

distributed in North Europe and in Siberia, occurring rarely everywhere. In this context, the attempt to save *S. gramineum* is urgently needed. Of course, we cannot be sure that we have adequate information about survival for suppressing species in all parts of its distribution area. Making a decision may sometimes be complicated due to rapid changes also for species that were more common previously.

The studies by Bertrin [22] in the littoral of the lakes of Southwest France (Lacanau, Casaux-Sanguinet, Perentis-Biskarrosse) found that isoetids tolerate mechanical stress by wind and waves relatively well, and our data affirm this conclusion. In the presence of invasive species *Lagarosiphon major* and *Egeria densa* in the lakes studied by Bertrin and co-authors, isoetids persisted better in the areas of higher wind stress. In Estonia water lobelia, inhabiting zone up to 1 m grows under the wave stress in open littoral or in the narrow, sparse and low reed belt. In general, increase and densification of emergent belt is unfavorable for isoetids; also the tuft sedge may reach 1 m water depth and between the tufts organic sediments accumulate.

4.4 Holiday-makers

After the end of flax retting period 50 years ago, many saunas have been built on the banks of SWL, mostly without water purification. Several smaller SWL have lost their typical vegetation. Nowadays, when the mobility of people has increased, the risk of invasive species introduction or diseases affecting the native biota, has sharply increased.

Unfortunately, the most sensitive OL lakes are under the greatest pressure of holiday-makers, because their banks are sandy within the whole perimeter (**Figure 9**). Especially beloved are larger shallow areas, attracting swimmers. In the 1 m zone plants are trampled out and into pieces—all places of frequent swimming are without isoetids. The same result is reported also from France [22]. Besides destruction of plant beds, rich assortment of chemicals is used for washing, UV-protection, warding off insects, etc.; added are the nutrients by swimmers themselves. The shores of OL lakes are very vulnerable to treading due to poor and thin soil layers and also erosion from sandy banks with scarce vegetation increases remarkably. In SD lakes, the survival of isoetids depends on the proportion of sandy and peaty stretches and the number of holidaymakers. Eutrophied B-lakes are under less pressure because masses of elodeids and wider emergent belts make them less attractive.

5. Conclusions

To the protected hydrophyte taxa of Estonian SWL belong isoetids *Isoëtes lacustris*, *Isoetes echinospora* and *L. dortmanna*; floating-leaved *S. angustifolium* and *S. gramineum*, amphibious *Elatine hydropiper* and elodeid *M. alterniflorum*. Isoetids are characteristic for A-lakes: water alkalinity <30 mg HCO_3^- L^{-1}. Elodeids occur mainly in B—lakes: 30–80 HCO_3^- L^{-1}, and their role increases by eutrophication. The relationship between alkalization and eutrophication is complicated because alkalization enhances nutrient enrichment and eutrophication supports the rise of alkalinity, including higher pH in peak hours of photosynthesis. The potential of sediments for nutrient supply of isoetids and *Sparganium* does not be reflected in water parameters (**Figure 10**).

Anthropogenic acidification of Estonian lakes is not known, but natural dystrophication due to the inflow of humic compounds is probable. In most SWL

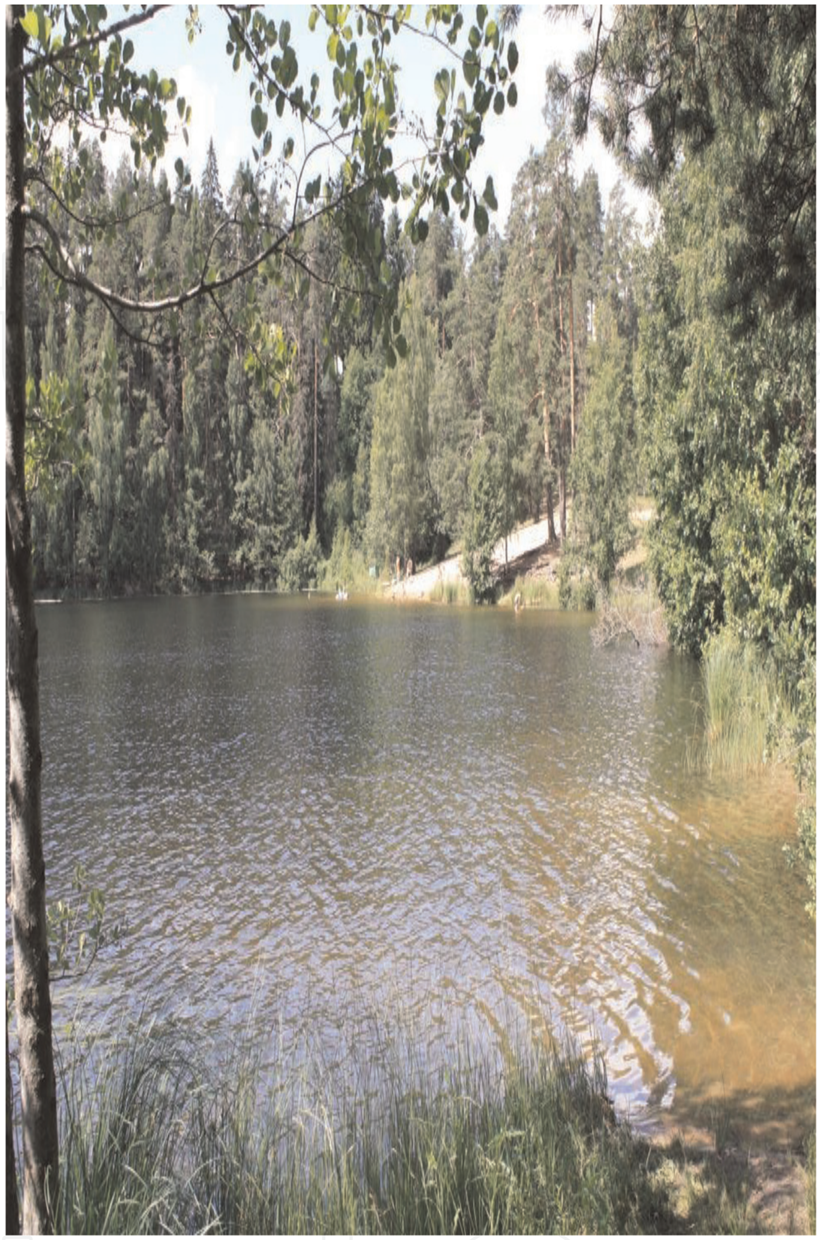

Figure 9.
All banks of L. Viitna Pikkjärv are sandy, so entrances of swimmers are apparent in many places—isoetids are lost (author's photo).

eutrophication and alkalization have counterbalanced the dystrophication, but in some lakes with unsettled catchment disappearance of isoetids and *Sparganium* obviously has been caused by this process. Water parameters are not always reflecting the sediment properties for different macrophytes.

Competition between primary producers takes place as an occupation of littoral habitats by widening emergent belts, suppression by elodeids and overshadowing by phytoplankton blooms or macroalgae. Filamentous algae may exterminate slow-growing plants already in seedling stage. Fast-growing eutraphents produce more biomass and the accumulation of organic matter decreases oxygen content of littoral sediments.

Nowadays, the mobility of people has increased, and the risk of invasive species or diseases has sharply increased. The most sensitive OL lakes are under the greatest

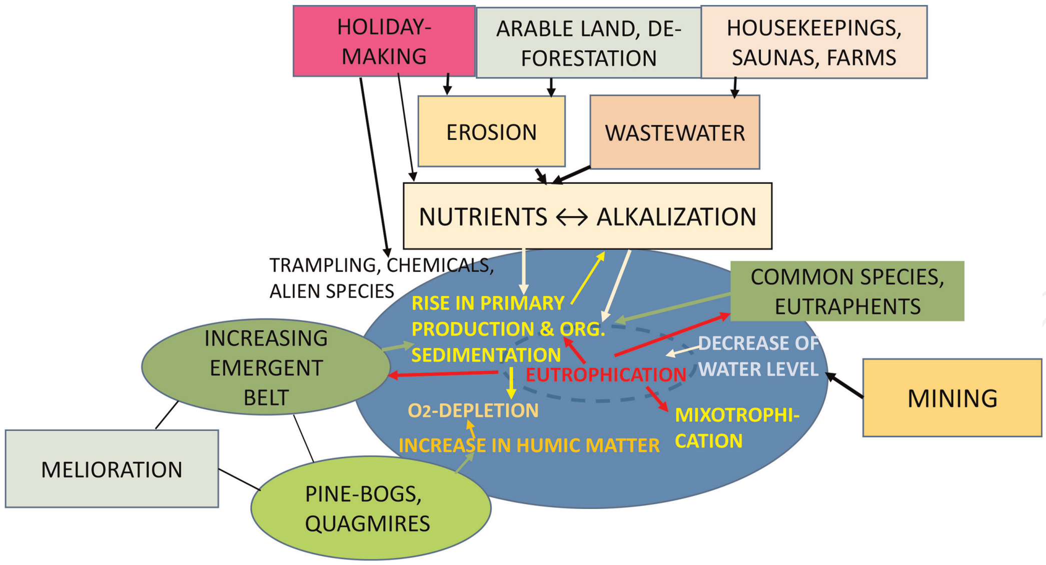

Figure 10.
Scheme of impacts on the soft-water lakes. Very probably, available knowledge is not adequate to depict all possible relationships and interferences.

pressure of holiday-makers, trampling in isoetid zone, causing erosion from lake banks and using chemicals.

Investigations of SWL during the decades have raised the necessity for better organization of the work. Under EU Water Framework Directive carried out monitoring of ecological status mainly on larger, > 10 ha lakes. In future, it is highly recommendable to join hydrochemical and biological monitoring with inventories of rare macrophytes and expand the selection to the smaller SWL. Also, the databases must be joined on behalf of better protection.

In the case of competition between two rare species and the need to save suffering species, it is recommendable to consider the global distribution areas and compare the level of extinction risk of the species.

In principle, it is almost impossible to reverse back the changes in lake ecosystems that formed and balanced over thousands of years and became unbalanced during a much shorter period of anthropogenic intervention. The processes depicted here are complex and interactive, and it would be much easier to keep functioning ecosystems. Theoretically, it would be possible to remove eutraphents, redundant masses of organic sediments and to stop any anthropogenic input. Though the removal of sediments may cause loss of the seed bank, and then the plants must be re-settled from the existing populations if they are locally available. However, our experiment with seeds revealed that there exist unpredictable difficulties.

Main part (about 90%) of SWL with the rare macrophytes are officially protected in Estonia as lakes of type 3110 according to the EU Habitat Directive (*Natura* 2000), and mostly they belong to the larger protected landscape areas. Regrettably, *Natura*-protection is not sufficient for the water bodies, because larger or lesser part of their catchment remains unprotected. Also protection zone 10 m according to the Estonian Water Law is considered mainly by official institutions, private owners are not interested to know and follow the laws and control about their activities is weak. Logging of timber at water border is frequent.

In practice, the protection get tangled already in the first steps—on the level of political authorities, partially due to continuing under-evaluation of the importance of declining habitats and their species. As long as incompetence in ecology is not seen as a shortage for a career, the decisions are based on the populism or business interests. On the other hand, nature protection is shamed by unqualified implantation, by mechanically following of deficient enactments, without clarification and (friendly) discussion with people. The role of scientists in nature protection, theoretically extremely important, could be eliminated by ignoring their advices. The most common practice is using of resources for protection plans (made by scientists) without the accomplishment of recommended activities.

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Abbreviations

SWL	soft-water lake(s)
COD	dichromate oxygen consumption
P_{tot}	total phosphorus
N_{tot}	total nitrogen
OL	oligotrophic
SD	semidystrophic
SD	Secchi depth = water transparency

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References

[1] Ott I, Kõiv T. Estonian Small Lakes: Special Features and Changes. Tallinn; 1999. p. 128

[2] Webster KE, Bowser CJ, Anderson MP. Understanding the Lake-groundwater system: Just follow the water. In: Magnuson J, Kratz TK, Benson BJ, editors. Long-Term Dynamics of Lakes in the Landscape. Oxford: University Press; 2006. p. 400

[3] Arold I. Eesti maastikud. Tartu: Tartu Ülikooli Kirjastus; 2005. p. 453

[4] Mäemets A, Mäemets A. General characteristics of the lakes. In: Timm T, editor. State of the Estonian Soft-Water Lakes (in Russian, Summary in English). Tartu; 1991. pp. 9-38

[5] Poikane S, editor. Water Framework Directive Intercalibration Technical Report. Institute for Environment and Sustainability; 2009. p. 174

[6] Mäemets A. Macrophytes. In: Timm T, editor. State of the Estonian Soft-Water Lakes (in Russian, Summary in English). Tartu; 1991. pp. 80-122

[7] Paal J, Pärnsalu P-R, Mäemets H. Quagmires around southern and southeastern Estonian lakes. Mires and Peat. 2019;**24**:1-25. DOI: 10.19189/MaP.2019.OMB.StA.1766

[8] Uibopuu I. Eesti pehmeveeliste järvede sammaltaimed [thesis]. Tartu: Tartu University; 2015

[9] Kara E. Seed-Bank of Protected Floating-Leaved Bur-Reeds in Four Soft-Water Lakes in Estonia and Its Implications for Conservation [thesis]. Tartu: Estonian University of Life Sciences; 2022

[10] Murphy KJ. Plant communities and plant diversity in softwater lakes of northern Europe. Aquatic Botany. 2002; **73**(4):287-324. DOI: 10.1016/S0304-3770(02)00028-1

[11] Sand-Jensen K, Borum J, Binzer T. Oxygen stress and reduced growth of Lobelia dortmanna in sandy lake sediments subject to organic enrichment. Freshwater Biology. 2005;**50**:1034-1048. DOI: 10.1111/j.1365-2427.2005.01382.x

[12] Mäemets H. *Sparganium* in Soft-water Lakes of Estonia. 2015. DOI: . Available from: https://www.researchgate.net/publication/281319200_Sparganium_in_soft-water_lakes_of_Estonia

[13] Roll H. Isoetes, Lobelia und Litorella in kalkarmem und kalkreichem Wasser (Ein Beitrag zur Ökologie des Isoeteto-Lobelietum Koch). Beihefte zum Bot. Centralbl. 1939;**Bd. LIX**:345-358

[14] Haab H. Ida-Eesti viieteistkümne toitainevaese ja pehmeveelise järve veesammalde ökoloogia ja levik [thesis]. Tartu: Tartu University; 1987

[15] Order Document of Estonian Minister of Environment 21.04.2020. Pinnaveekogumite nimekiri, pinnaveekogumite ja territoriaalmere seisundiklasside määramise kord, pinnaveekogumite ökoloogiliste seisundiklasside kvaliteedinäitajate väärtused ja pinnaveekogumiga hõlmamata veekogude kvaliteedinäitajate väärtused

[16] Smolders AJP, Lucassen ECHET, Roelofs JGM. The isoetid environment: Biochemistry and threats. Aquatic Botany. 2002;**73**(4):325-350. DOI: 10.1016.S0304-3770(02)00029-3

[17] Ott I. What killed the fish in it? The state of a lake is reflected by its water. Estonian Nature. 1994:53-54

[18] Lucassen ECHET, Spierenburg P, Fraaije RGA, Smolders AJP, Roelofs JGM. Alkalinity generation and sediment CO2 uptake influence establishment of *Sparganium angustifolium* in softwater lakes. Freshwater Biology. 2009;**54**:2300-2314. DOI: 10.1111/j.1365-2427.2009.02264.x

[19] Brandrud TE. Effects of liming on aquatic macrophytes, with emphasis on Scandinavia. Aquatic Botany. 2002;**73**: 395-404. DOI: 10.1016/S0304-3770(02) 00032-3

[20] Mäemets H, Kara E. Lamedalehise ja ujuva jõgitakja seisund Eestis ning soovitusi olukorra parandamiseks. Report for Estonian Environmental Board. 2022

[21] Karofeld E. On technogenic changes in the vegetation and functioning of the bogs of the Kurtna Kames Field. In: Abstracts of the Republican IV Conference in Ecology. Tartu; 1988. pp. 62-64

[22] Bertrin V. Écologie et déterminisme physique des peuplements de macrophytes dans les lacs naturels peu profonds [thesis]. Bordeaux: L'Université de Bordeaux; 2018