EKOLOGIJA. 2006. Nr. 2. P. 34–43

Qualitative and quantitative parameters of phytocenoses in Lithuanian lakes of different trophic state

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A total of 446 lakes have been evaluated for the character of their overgrowing with macrophytes and the dependence of syntaxonomic and species diversity upon the trophic level of the lake. Eulittoral and littoral phytocenoses were found to belong to 7 vegetation classes and to include 81 lower syntaxa. The communities of *Phragmiti – Magnocaricetea elatae* (30), *Potamogetonetea pectinati* (26), *Charetea fragilis* (14) classes were more frequent, whereas the communities of *Littorelletea uniflorae* (4) class were very rare. Their distribution, growth peculiarities and species diversity varied in dependence on the trophic level of a lake.

The highest diversity of species and syntaxa was observed in oligomesotrophic and mesotrophic lakes. These lakes have the most favorable set of light climate, amount of biogenic substances, gas regime and other parameters for the development of macrophytes.

Though eutrophic lakes also exhibit a rather great diversity of syntaxa, only monodominant stands of 1–2 species often form in such lakes. The least species and syntaxa diversity was found in dystrophic lakes.

Key words: lakes, trophic level, macrophytes, phytocenoses, syntaxa

INTRODUCTION

Eutrophication of water bodies, or their enrichment with biogenous material, cause reversible and irreversible changes in the structure and productivity of all ecosystem components. The scope of water eutrophication significantly part depends upon the morphometric, hydrochemical and hydrobiological characteristics of a water body as well as on the nature of ecosystems surrounding the water body and the land use in the catchment area (Wetzel, 2001).

Most of Lithuanian lakes are functioning as sumps of outwash brought from the surroundings of the lake and the catchment basin. At the same time they are relatively closed systems as regards the outflow of biological substances, therefore, they are both the outcome of natural ecosystem succession and anthropogenic eutrophication.

Micro and macro vegetation, i.e. phytoplankton and macrophytes, are among the first to respond to an increase in biogenous matter (in particular, mineral and organic compounds of nitrogen and phosphorus). Shifting to a higher trophic level firstly causes quantitative changes (increase in productivity and biomass) and later qualitative alterations (vulgarization of species composition) in macrophyte communities.

Natural aging (succession) of lake ecosystems by turning from oligotrophic to mesotrophic and later to eutrophic and / or dystrophic status takes thousands of years, therefore, naturally eutrophic overgrown or quaggy lakes from the ecological point of view are very valuable habitats with peculiar complexes of phytocenoses. Effects of anthropogenic eutrophication can be observed already after some or dozens of years. Lake ecosystems that have a great load of biogenous matter turn from a lower to higher trophic status by leaps rather than gradually, thus the species of narrow ecological amplitude disappear and being replaced by monodominant stands of species of a wide ecological amplitude.

The purpose of the current research was to generalize data collected during *in-situ* investigations and literature references and to show the influence of the trophic level on the formation of lake macrophyte communities.

MATERIALS AND METHODS

The research was performed using the standard methods for macrophyte vegetation analysis (Katanskaja 1981; Wetzel, 2001). The main method reflecting the distribution of marcophyte species and communities depending upon the species biological peculiarities, growth character and attachment to habitats was the description of study squares in the selected lake eulittoral and littoral contours and profiles (transects) of vegetation. The size of the contour varied from 4 m^2 (monodominant communities) to 10 m^2 subject to the peculiarities of the community and its distribution in the littoral. Communities were evaluated for their quantitative and qualitative features.

Phytocenoses were classified applying the principles of vegetation research and classification of Zurich–Montpellier School (Braun-Blanquet, 1964), which is the basis for classification of vegetation in European countries (Podbielkowski, Tomaszewicz, 1996; Westhoff, Maarel, 1980; Pott, 1992; Dierssen, 1996) and Lithuania (Rašomavičius (ed.) 1998). All the species that formed phytocenoses and identified characteristic species (concentrated in one or several types of phytocenoses) corresponding with their optimal habitat for the classification were used. In order to identify characteristic species, the syntaxa digests of Lithuania (Balevičienė, 1991; Sinkevičienė, 1994) and neighboring countries (Pott, 1992; Dierssen, 1996; Podbielkowski et al., 1996) were used. The hierarchic system of syntaxa was compiled. The class was treated as the highest unit including the communities of similar ecological and physiognomical features. The class subordinates were orders, alliances and associations, which are the basic unit of classification. Only classes and associations are presented in the article because of the limited space. An association includes vegetation communities of a similar floristic composition, distributed in ecologically close habitats. These units of classification were used to describe the syntaxa of lake vegetation.

To evaluate the phytocenotic significance of communities, the following vegetation constancy classes were determined: V – 81–100%, IV – 61–80%, III – 41–60%, II – 21–40%, I – 11–20%, + – 1–10%. Only constancy classes V, IV and III show that a syntaxon is constant in a certain type lake.

Unpublished descriptions of phytocenoses made by Balevičius and Balevičienė as well as literature references (Minkevičius et al., 1957, 1958; Bagdonaitė, 1960, 1962; Galinis, 1962; Šarkinienė, 1961, 1963, 1968, 1977; Trainauskaitė, 1970, 1977; Sinkevičienė, 1994; Stepanavičienė, 1991; Strazdaitė et al., 1967; Balevičienė et al., 1981; Balevičienė, 1991; Balevičius, 1994, 1998, 2000, 2001) were used to evaluate the qualitative and quantitative parameters of lake phytocenoses. Evaluations of the structure of phytocenoses and their habitats were made in 446 Lithuanian lakes of a different trophic level.

Plant species were described using guides (Blindow et al., 1990; Frey et al., 1995; Gollerbach, Krasavina, 1983) and flora books (The Flora of the Lithuanian SSR, 1963; Hegi, 1981). The names of plant species are presented according to the species digests (Gudžinskas, 1999; Jankevičienė, 1998; Jukonienė, 2003).

The description of the trophic level was based on classical (Thieneman, 1925; Nauman, 1929) and slightly modified (Hutchinson, 1957; Carlson, 1977; Wetzel, 2001) assessments of trophic level.

RESULTS AND DISCUSSION

Distribution and growth peculiarities of macrophyte phytocenoses in lakes of different trophic level

Vegetation classes

Macrophyte phytocenoses of the lakes studied fall under 7 vegetation classes, which description is given below.

Cl. *Lemnetea minoris* de Bolos et Masclans 1955– small pleustophyte communities.

Characteristic species: *Lemna minor, Lemna trisulca, Spirodela polyrhiza*.

The class covers small pleustophyte communities of eutrophic and occasionally mesotrophic water bodies (Table 1).

These are the communities common in the boreal and temperate zone. Though the *Lemnaceae* family species that form communities are cosmopolitic, their distribution in northern latitudes does not reach further than southern Finland (60–63^0). The communities are formed by unanchored free-floating small plants-pleustophytes (*Lemna minor, L. trisulca*, *Spirodela polyrhiza*, *Hydrocharis morsus – ranae*), which can be observed in the shallow littoral in all vegetation belts of the lake. Under certain conditions, they can cover the entire surface of a water body.

In northern Europe (Dierssen, 1996), five associations of this class can be distinguished: *Lemnetum gibbae, Lemno–Spirodeletum polyrhizae, Lemnetum trisulcae, Ricciocarpetum natantis, Riccietum fluitantis,* which can be found in hypertrophic or eutrophic waters. These communities are distributed in Lithuania as well (Sinkevičienė, 1994; Balevičius, 2000). *Riccietum fluitantis* and *Ricciocarpetum natantis* communities are rare, their characteristic species *Ricciocarpos natans* is enlisted into the Red Data Book of Lithuania (Kundrotas, 2003).

These two-to-four-species communities are widespread in the eulittoral of the lakes, at a depth of 0.1–0.3 m, in eutrophic bays protected from direct wave activity, and sometimes they can entirely cover the surface of the lake.

Cl. *Charetea fragilis* Fukarek ex Krausch 1964–stoneworth algae communities.

Characteristic species: *Chara contraria, Chara fragilis, Chara vulgaris.*

The class covers benthos stoneworth algae (*Charophyta*) communities formed by macroalgae species of the *Characeae* family. Together with other species (*Ceratophyllum demersum, Drepanocladus sendtneri, Elodea canadensis, Fontinalis antipyretica*) *Characeae* form limneid belts, which could reach a depth of 8–10 m in oligomesotrophic clear water lakes. In eutrophic lakes with the dominance of phytoplankton, the distribution of limneids is limited by a low water transparency (0.8–2 m according to Secchi) during the vegetation period, therefore, in such lakes the greatest depth of the occurrence of limneid communities is 2–4 m.

Table 1. **Phytocenotic significance of macrophyte communities in the lakes of different trophic level**

Syntaxa	Trophic level	**Oligome-sotrophic**	**Mesotro-phic**	**Eutrophic**	**Dystrophic**
	Number of lakes (446 in total)	34	182	168	62
	Average number of species	90	78	73	43
	Total number of syntaxa	56	78	72	40
	Number of constant syntaxa	4	16	29	3
	Average number of syntaxa in the lake	26	41	14	7
		Constancy classes			
***Cl. Lemnetea minoris* de Bolós et Masch. 1955**					
Ass. *Lemnetum trisulcae* Knapp et Stoff 1962		+	I	II	+
Ass. *Lemnetum gibbae* Bennema et all. 1943 em. Miyawaki et J. Tx. 1960			+	II	
Ass. *Lemno - Spirodeletum polyrhyzae* W. Koch 1954 ex R. Tx. et A. Schwabe-Braun 1972			I	II	
Ass. *Ricciocarpetum natantis* Segal 1963 em. R. Tx. 1974			+	+	
Ass. *Riccietum fluitantis* Slavnić 1956 em. R. Tx. 1974			+	I	
Cl. *Charetea fragilis* Fukarek ex Krausch 1964					
Ass. *Charetum contrariae* Corrillion 1957		II	III	III	I
Ass. *Charetum fragilis* Fijalkowski 1960		+	II	III	I
Ass. *Nitellopsidetum obtusae* (Sauer 1937) Dąmbska 1961		I	II	II	I
Ass. *Charetum jubatae* Krausch 1964		II	I	II	+
Ass. *Charetum rudis* Dąmbska 1966		III	III	II	+
Ass. *Charetum tomentosae* (Sauer 1937) Corrillion 1957		III	IV	II	+
Ass. *Charetum asperae* Corrillion 1957		III	IV	+	
Chara delicatula community		I	I	I	
Ass. *Charetum hispidae* Corrillion 1957		+	I	+	
Ass. *Nitelletum flexilis* Corrillion 1957		+	+	+	
Ass. *Nitelletum opacae* Corrillion 1957		+	+	+	
Ass. *Nitelletum syncarpae* Corrillion 1957		+	+	I	
Ass. *Nitelletum mucronatae* Tomaszewicz 1979			+	I	
Lychnothamnus barbatus community*		+	+		
Cl. *Fontinaletea antipyreticae* Hub. 1957					
Ass. *Fontinaletum antipyreticae* Kaiser 1936		I	III	I	+
***Cl. Potamogetonetea pectinati* R. Tx. et Prsg.1942 corr. Oberd. 1979**					
Ass. *Elodeetum canadensis* (Pign. 1953) Passarge 1964		+	II	IV	+
Ass. *Myriophylletum spicati* Soó 1927		I	I	III	+
Ass. *Najadetum marinae* Fukarek 1961		+	I	+	+
Ass. *Nupharetum luteae* (W. Koch 1926) Hueck 1931		I	III	V	II
Ass. *Nymphaeetum candidae* Miljan 1958		+	+	III	+
Ass. *Potamogetonetum lucentis* Hueck 1931		II	III	II	+
Ass. *Potamogetonetum pectinati* Carstensen 1955		I	II	III	+
Ass. *Potamogetonetum perfoliati* W. Koch. 1926 em. Passarge 1964		II	III	III	+
Ass. *Ranunculetum circinati* Sauer 1937		I	II	IV	+
Ass. *Potamogetonetum natantis* Soó 1927		II	III	IV	+
Ass. *Ceratophylletum demersi* Hild 1956		+	I	III	
Ass. *Potamogetonetum compressi* Tomaszewicz 1979		I	I	III	
Ass. *Potamogetonetum mucronati* Tomaszewicz 1979		+	I	II	
Ass. *Potamogetonetum praelongi* Sauer 1937		I	I	I	
Potamogeton alpinus community		+	I	+	
Potamogeton crispus community		+	II	+	
Ass. *Polygonetum natantis* Soó 1927		I	III	I	
Ass. *Stratiotetum aloidis* Nowinski 1930		I	III	III	

Table 1 (continued)

Ass. *Myriophylletum verticillati* Soó 1927		+	IV	+
Ass. *Nupharetum pumilae* Oberd. 1957 ex. Th. Müller et Görs 1960 *		+	I	+
Ass. *Nupharo - Nymphaeetum albae* Tomaszewicz 1977	II	I		
Ass. *Potamogetonetum filiformis* W. Koch. 1926	+	+		
Ass. *Hydrylletum verticillati* Tomaszewicz, 1979 *		I	I	
Ass. *Lemno - Utricularietum vulgaris* Soó 1947		+	III	
Ass. *Nymphoidetum peltatae* (Allorge 1922) Bellot 1951 *		+	+	
Ass. *Zannichellietum palustris* (Braun 1911) Koch 1926 *		+	+	
Cl. *Littorelletea uniflorae* Br.-Bl. et R. Tx. 1943 ex Westh. et all. 1946				
Eleocharis acicularis community	IV	II		
Ass. *Isoëtetum lacustris* Szankowski et Klosowski 1996 *		+		
Ass. *Lobelietum dortmannae* (Osv. 1923) R. Tx. ap Dierss. 1972 *	+	+		
Ass. *Myriophylletum alterniflori* Westhoff 1944 *	+			
Cl. *Utricularietea intermedio – minoris* Pietsch. 1964				
Ass. *Sparganio minimi – Utricularietum* (Schaaf 1925) R. Tx. 1937		+	+	I
Ass. *Scorpidio – Utricularietum intermediae* (Ilschner 1959) Müller et Görs 1960				+
Cl. *Phragmiti – Magnocaricetea elatae* Klika ap. Klika et Novak 1941				
Ass. *Acoretum calami* (Schulz 1941) Knapp et Stoffers 1962	+	III	V	+
Ass. *Equisetetum limosi* Steffen 1931	II	III	IV	III
Ass. *Glycerietum maximae* Hueck 1931	+	I	III	+
Ass. *Caricetum gracilis* Almquist 1929	I	I	III	+
Ass. *Caricetum rostratae* Rübel 1912	+	III	IV	+
Ass. *Cicuto-Caricetum pseudocyperi* Boer et Siss. in Boer 1942	+	II	III	+
Ass. *Phragmitetum australis* (Gams 1927) Schmale 1939	I	III	IV	+
Ass. *Thelypterido-Phragmitetum australis* Kuiper 1957	+	+	III	IV
Ass. *Typhetum angustifoliae* (All. 1922) Soó 1927	I	II	III	+
Ass. *Scirpetum lacustris* (All. 1922) Chouard 1924	II	II	III	+
Eleocharis palustris community	II	IV	II	+
Ass. *Caricetum vesicariae* Br.-Bl. et Denis 1926	+	+	+	
Ass. *Caricetum ripariae* Soó 1928	+	I	II	
Ass. *Glycerietum notatae* Kulczynski 1928	+	+	+	
Ass. *Hippuridetum vulgaris* Rübel 1912	+	+	II	
Ass. *Phalaridetum arundinaceae* Libbert 1931	+	+	+	
Leersia oryzoides community	+	+		
Ass. *Scirpetum tabernaemontani* Passarge 1964	+	+		
Ass. *Caricetum elatae* W. Koch 1926		II	II	II
Ass. *Caricetum appropinguatae* Soó 1938		II	II	+
Ass. *Typhetum latifoliae* Soó 1927		II	IV	I
Menyanthes trifoliata community		I	III	IV
Ass. *Caricetum paniculatae* Wangerin 1916 ex Rochov 1951		+	II	
Ass. *Iretum pseudacori* Eggler 1933		+	III	
Ass. *Caricetum acutiformis* Sauer 1937		+	+	
Ass. *Oenantho – Rorippetum* Lohm. 1950		+	II	
Ass. *Sagittario-Sparganietum emersi* R. Tx. 1953		+	II	
Ass. *Scolochloetum festucaceae* Rejewski 1977 *		+	I	
Ass. *Sparganietum erecti* (Roll 1938) Phill 1973			IV	I
Ass. *Cladietum marisci* Allorge 1922 ex Zobrist 1935 *			+	II

* Communities enlisted into the Red Data Book of Lithuania.

These communities are common in brackish and fresh hard water lakes of different trophic level (oligotrophic and mesotrophic, occasionally eutrophic) with neutral or alkaline reaction (Trainauskaitė, 1970). According to literature references (Dierssen, 1996; Pott, 1992; Tomaszewicz, 1979; Podbielkowski et al., 1996; Dąmbska, 1964; Sinkevičienė, 1994; Balevičius, 2001), the communities of the class are subordinated into two orders: *Nitelletalia flexilis* (having 1 alliance) and *Charetalia hispidae* (having 1 alliance).

The class does not have many diagnostic species. In Lithuania, the communities of this class are characterized by 6–8 species. From 25 species of the *Characeae* family growing in Lithuaniam water bodies, merely 14 form communities in the lakes.

12 associations and 2 rankle communities belonging to *Charetea fragilis* were inventoried in the lakes studied.

The communities reach their ecological optimum and the highest species diversity in calcareous oligomesotrophic and mesotrophic lakes, yet they are rare in eutrophic and hardly met in dystrophic lakes (Table 1). Four species of the class (*Nitella flexilis, N. mucronata, N. syncarpa* and *Lychnothamnus barbatus*) are enlisted into the List of the Red Data Book of Lithuania (Kundrotas, 2003), and *Lychnothamnus barbatus* community enters the Red Data Book of Lithuania (Balevičius, 2000).

Cl. *Potamogetonetea pectinati* R. Tx. et Prsg. 1942 corr. Oberd. 1979–rooted and floating-leaved macrophyte communities.

Characteristic species: *Batrachium circinatum, Elodea canadensis, Myriophyllum spicatum, Persicaria amphibia var. natans, Potamogeton lucens, Potamogeton natans, Potamogeton pectinatus, Potamogeton perfoliatus.*

The class includes hydrophyte communities formed by rooted, floating–leaved or submerged plant species (*Potamogeton* sp*., Nuphar* sp*., Nymphaea* sp*.*). The communities are common in the boreal and temperate zones of Eurasia and North America. They grow in lakes and rivers of different trophic level (oligomesotrophic, mesotrophic, eutrophic, less frequent-dystrophic) and different type of overgrowth (Pott, 1992; Dierssen, 1996; Strand, 1999). Lithuanian phytocenologists describe three alliances: *Nymphaeon albae, Hydrocharition morsus – ranae, Potamogetonion pectinati* (Minkevičius et al., 1958; Bagdonaitė, 1962; Šarkinienė, 1963; Sinkevičienė, 1994; Balevičienė, 1991; Balevičius, 1994, 1998, 2001).

These communities form potameid and nympheid belts in the littoral zone of lakes at a depth of 1.5–3.5 m. Most frequent were *Potamogeton* species (*Potamogeton lucens, P. perfoliatus, P. natans*) as well as *Nuphar lutea, Persicaria amphibia, Myriophyllum spicatum*, which formed solitary stands or belts of different width in nearly all mesotrophic and eutrophic lakes, however their diversity was low in dystrophic lakes. The phytocenoses were assigned to 26 syntaxa: 23 associations and 3 rankless communities.

The communities of this class reach their highest constancy (III–IV) in eutrophic (12) and mesotrophic (6) lakes (Table 1). *Myriophylletum spicati, Myriophylletum verticillati, Nupharetum luteae, Ceratophylletum demersi, Elodeetum canadensis* communities often determine the entire overgrowth of shallower eutrophic lakes, but their role is considerably lower in oligomesotrophic and dystrophic lakes.

Cl. *Littorelletea uniflorae* Br.–Bl. et R. Tx. 1943 ex Westhoff et al. 1946-communities of small hydrophytes.

Characteristic species: *Eleocharis acicularis, Isoëtes lacustris, Lobelia dortmanna.*

The class includes the communities of small macrophytes growing in the shallow littoral of oligotrophic and mesotrophic inland water bodies. The communities are common in boreotemperate Europe and North America, showing attachment to oceanic regions. Communities of this class are very rare in Lithuania. They are more frequent in so-called Lobelia-lakes in the countries further north than Lithuania. Three alliances of the class were identified in boreal Europe (Dierssen, 1996), whereas only two (*Littorelion uniflorae* W. Koch 1926 and *Eleocharition acicularis* Pietsch 1967) in temperate Europe (Matuszkiewicz, 2002). In the lakes studied, two associations of both alliances and one rankless community *Eleocharis acicularis* were found.

Two communities of the class are enlisted into the Red Data Book of Lithuania: *Isoëto-Lobelietum* (Balevičienė, 2000) and *Myriophyllum alterniflorum* community (Bagdonaitė, 1960; Sinkevičienė, 2000).

Cl. *Phragmiti – Magnocaricetea elatae* Klika ap. Klika et Novak 1941–tall helophyte communities.

Characteristic species: *Acorus calamus, Equisetum fluviatile, Glyceria notata, Lycopus europaeus, Lysimachia vulgaris, Phragmites australis, Schoenoplectus lacustris, Scutellaria galericulata, Typha latifolia.*

The class includes swampy, fenny, lacustrine and riverine helophyte communities common to eulittoral and littoral zones of standing and flowing water bodies, wet relief depressions, meadow pools, etc. (Bagdonaitė, 1960; Balevičienė, 1991; Sinkevičienė, 1994; Matulevičiūtė, 1998; Balevičius, 2001). These communities include the *Poaceae* and *Cyperaceae* species tolerating surplus humidity and great water level fluctuations. Small helophytes (*Alisma plantago-aquatica, Eleocharis palustris, Equisetum fluviatile*), which grow at a depth of 0–0.4 m, do not cover large areas in the eulittoral and littoral of lakes and do not form continuous belts. Tall helophytes (*Phragmites australis, Schoenoplectus lacustris, Typha angustifolia, T. latifolia*) grow at a depth of 0.1–2.5 m and form stands or belts of different width in nearly all the lakes.

Communities of the class *Phragmiti-Magnocaricetea elatae* cover 27 associations and 3 rankless communities in the lakes studied. These communities reach their ecological optima in the swampy eulittoral of mesotrophc and eutrophic lakes. The communities of 11 associations were found in the lakes of all trophic levels, however, only five of them (*Acoretum calami, Caricetum rostratae, Equisetetum limosi, Phragmitetum australis, Scirpetum lacustris*) were constant. The communities of *Cladietum marisci* and *Scolochloetum festucaceae* associations are enlisted into the Red Data Book of Lithuania (Sinkevičienė, 2000).

Cl. *Fontinaletea antipyreticae* Hub. 1957– water–moss communities.

Characteristic species: *Fontinalis antipyretica*

Fontinaletea communities are common in middle Europe. According to the system of Hubschmann (1957), the class covers three orders. Only one community, *Fontinaletum antipyreticae*, belongs to the order *Fontinaletalia antipyretica* Hub. 1957, was found in Lithuanian lakes. *Fontinalis antipyretica* is predominant, whereas other species grow sporadically. These communities are more frequent in mesotrophic lakes however sporadically they might be encountered in all types of lakes.

Cl. *Utricularietea intermedio-minoris* Pietsch. 1964 – communities of insectivorous macrophytes.

Characteristic species: *Sparganium minimum, Utricularia intermedia, Utricularia vulgaris.*

The communities are distributed in the boreal and temperate Eurasia and North America. In Lithuanian lakes these insufficiently investigated communities (Balevičienė, 1991) are distributed in shallow swampy eulittorals zones of eutrophic and dystrophic lakes. The phytocenotic significance and areas occupied by these communities is minor.

THE GROWING PECULIARITIES OF PHYTOCENOSES IN LAKES OF DIFFERENT TROPHIC LEVEL

The abundance and diversity of macrophyte communities as well as development and distribution of vegetation belts in the eulittoral and littoral of a lake depend upon several factors: morphometric peculiarities of the water body (size, depth, shore sinuosity, steepness of submerged slopes), optical features of water (transparency and color), water dynamic (wind fetch, waves, beat of waves), trophic level, chemical parameters of water (chemical composition, especially concentrations of phosphorus and nitrogen organic and inorganic compounds, pH, gas regime), water temperature, flow of the lake, shading of the eulittoral and littoral zone, economic activities in the surroundings of the lake and in the whole catchment area, etc. The formation of macrophyte belts and organogenic littoral is more rapid in the areas of the littoral with less intensive hydrodynamic processes (Šimanauskienė et al., 2004).

According to the peculiarities of macrophyte growth, five ecological groups can be distinguished in water bodies (Wetzel, 2001). The eulittoral and littoral are characterized by helophyte and hydrophyte (nympheids, potameids, limneids, pleustophytes) ecological groups, which form vegetation belts in the lakes surveyed. These ecological groups were found in all lakes studied despite the differences in their phytocenotic significance.

Different classifications have been created to evaluate the trophic level of a lake and relationships between the trophic level and various components of the ecosystem. Thieneman (1925) and Nauman (1929) singled out three types of lakes according to the trophic level: oligotrophic, eutrophic and dystrophic. Further classifications (Hutchinson, 1957; Carlson, 1977; Wetzel, 2001) distinguished mesotrophic and transitional lake types such as oligomesotrophic and mesoeutrophic. In Lithuania, we do not have oligotrophic lakes incident to the boreal zone and highlands, however, at the beginning of the Holocene, with the receding of the glacier, most of the lakes were of this type (Kabailienė, 1990). Based on the above–mentioned classifications, Lithuanian lakes may be assigned to three types of lakes: mesotrophic, eutrophic and dystrophic, however, some large thermally deep Lithuanian lakes differ from typical mesotrophic lakes and have certain oligotrophic features. Conditionally, we classified such lakes as oligomesotrophic.

Classification of lakes according to the distribution of eulittoral and littoral phytocenoses was done as well. I. Šarkinienė (1977) grouped Lithuanian lakes according to the development of macrophyte vegetation and formation of belts into four types of overgrowth: fragmentary, belt-type-fragmentary, belt-type-continuous and quaggy, which partially correlate with oligomesotrophic, mesotrophic, eutrophic and dystrophic types, respectively.

Mesotrophic lakes (182). Based on the above-mentioned classifications, most of the study lakes (182) belong to the mesotrophic type and correspond to the belt-type-fragmentary overgrowth degree. By origin, most of these lakes are fluvioglacial, characterized by steep slopes, great depth and narrow littorals, most often with the sand, gravel or pebble bottom in the littoral zone. During intensive vegetation their water clarity reaches 2–4 m Secchi. Macrophyte habitats are usually characterized by a 5–15 m wide eulittoral and 5–25 m wide littoral, most often with the gravel, sand or freshwater limestone bottom, covered with silt in deeper areas. Shoreline indentations contain shallow bays, with helophyte (*Phragmitetum australis, Scirpetum lacustris, Caricetum rostratae*) belts, which are very common in the northern end of the lakes surveyed. The littoral is wider (15–30 m) and the silt layer on the bottom of macrophyte habitats is much thicker there.

Mesotrophic lakes are characterized by two or three hydrophyte belts: the belt of limneids is fragmentary, rarely nearly continuous. Potameid and nympheid phytocenoses usually do not form belts. In deeper (6–8 m) places, *Fontinalis antipyretica* and *Drepanocladus sendtneri,* occasionally – *Nitella opaca* stands can be met.

Lakes of this type were found to have the highest syntaxa variety (78), but only 16 of them being

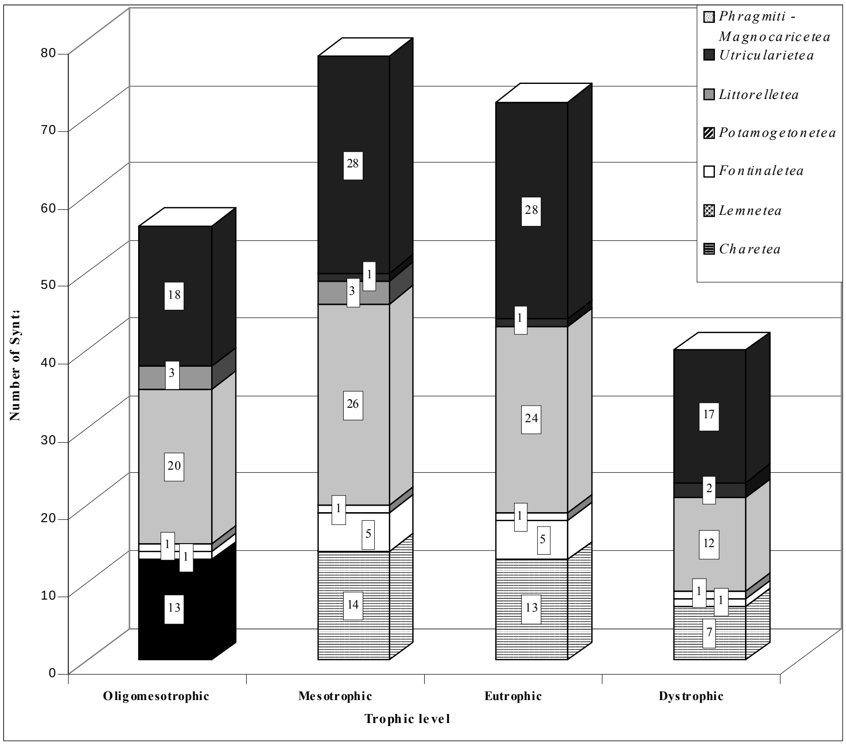

Figure. Distribution of syntaxa by vegetation classes in lakes of different trophic level

constant. More frequent are communities of the classes *Phragmiti-Magnocaricetea elatae* (28) and *Potamogetonetea pectinati* (26), *Charetea asperae* (14) (Figure). Most Lithuanian mesotrophic lakes are comparatively little overgrown with vegetation: macrophytes cover 15–20 (up to 30) % of the total area of lakes.

Oligomesotrophic lakes (34). Some mesotrophic lakes, especially those situated in forested areas and not suffering from a hard anthropogenic impact, have some features of oligotrophic lakes and their vegetation markedly differs from that of other lakes. Lakes of this type are large and deep, the average depth exceeding 12–15 m, water clarity during vegetation reaching 5–9 m Secchi, with calcareous water in most lakes and diatom algae dominating in phytoplankton throughout all the vegetation season (Kavaliauskienė, 1996). Submerged slopes of the lakes are steep, therefore, the littoral overgrown by macrophytes is narrow (5–12 m wide), the bottom is clean or silted sand or gravel, water transparency during intensive vegetation reaches 3–7 m Secchi, macrophytes form communities at a depth of 5–8 m, though solitary plants grow down to 7–11 m deep. Hydrophytes do not form any larger belts in such lakes. More frequent are phytocenoses of limneids (*Charetum tomentosae*), less frequent being those of nympheids (*Nupharetum luteae*) and potameids (*Potamogetonetum lucentis, Potamogetonetum perfoliati*). The area overgrown with macrophytes reaches up to 10–20% of the lake area. Minor fragments of helophyte communities (*Caricetum rostratae, Thelypterido-Phragmitetum australis, Phragmitetum australis, Scirpetum lacustris* communities) reaching merely several meters in width can occasionally be found at the ends of the lakes.

The diversity of species (90) and syntaxa (56) is rather high, however, the numbers of constantly growing species (18 per lake on average) and syntaxa (4) are not so high.

The highest syntaxa diversity in oligomesotrophic lakes was found in the classes *Potamogetonetea pectinati* (20 syntaxa), *Phragmiti-Magnocaricetea elatae* (18) and *Charetea fragilis* (15) (Fig 1.). However, most of these syntaxa are of minor constancy (classes I–II), or rare (+).

Eutrophic lakes (168). This type usually includes small, comparatively shallow (3–6 m mean depth) lakes with high quantities of allochtonous and/or autochtonous organic matter. Such lakes are often surrounded by agricultural lands, their coasts are low, sometimes quaggy; the bottom usually has a thick layer of sapropel or silt rich in biogenous material. Eutrophic lakes may be of two states: most of the organic substance in the lake may be formed either by phytoplankton (phytoplankton–dominated lakes) or by macrophytes (macrophyte–dominated lakes). In phytoplankton–dominated lakes, limneids are usually very scarce (their distribution is restricted by the low water transparency (0.5–1.5 m Secchi), so helophyte and nympheid phytocenoses are prevailing. In macrophyte–dominated lakes, water is much more transparent (2–4 m Secchi), phytocenoses cover 70–100% of the lake area. Nearly equally developed phytocenoses of emerged and submerged vegetation often overlap; some of them cover large areas obtaining the character of continuous stands.

Wet eulittorals are dominated by helophytes (*Thelypterido-Phragmitetum australis, Typhetum latifoliae, Equisetetum fluviatile*). Among hydrophytes, phytocenoses of nympheids (*Myriophylletum verticillati, Potamogetonetum natantis*), limneids (*Elodeetum canadensis, Ceratophylletum demersi*) and potameids (*Potamogetonetum perfoliati, Potamogeton crispus* community) are well expressed.

The lakes are characterized by lower diversity of species (73) and communities (72, of them 29 being constant). The communities are not rich in species, often monodominant, with the dominance of *Phragmiti-Magnocaricetea elatae* (28), *Potamogetonetea pectinati* (24), *Charetea fragilis* (13). Limneid communities of *Fontinaletea antipyreticae* are rather rarely met in eutrophic lakes, whereas the communities of *Littorelletea uniflorae* class have not been found at all.

Dystrophic lakes (62). This type includes shallow, often silted up, small lakes with waterlogged coasts turning into a quagmire. The ground is formed by silt or peaty sapropel, whereas water is of brownish or brown color because of solute humic substances. Though water clarity in dystrophic lakes is not low (2–3m Secchi), they hardly contain submerged vegetation (limneids). Nympheids (*Nuphar luteum*, rarer solitary plants of *Nymphaea candida*) and potameids (solitary *Potamogeton perfoliatus* or *Myriophyllum spicatum*) are also scarce. More abundant macrophyte vegetation usually concentrates in the bog surrounding the lake, where belts are formed by the communities of high helophytes (*Thelypterido-Phragmitetum australis Caricetum rostratae*, occasionally *Phragmitetum australis* or *Cladietum marisci* – the community enlisted into the Red Data Book of Lithuania.

Dystrophic lakes are the oldest lakes likely to turn to bogs. Their species (43) and syntaxa (40) diversity is low, with especially low numbers of constant syntaxa (3). More frequent are the communities of *Phragmiti–Magnocaricetea* (17) and *Potamogetonetea pectinati* (12) classes. Seven communities of the *Charetea fragilis* class have been inventoried, however, the communities of this class are very rare in dystrophic lakes and their constancy is low (+–I).

CONCLUSIONS

About 210 macrophyte species, the communities formed whereby are grouped into 81 syntaxa (73 associations and 8 rankles communities) belonging to 7 vegetation classes, have been inventoried in 446 lakes studied. The most widely spread were the communities of *Phragmiti–Magnocaricetea elatae* (30), *Potamogetonetea pectinati* (26), *Charetea fragilis* (14), *Lemnetea minoris* (5), *Fontinaletea antipyreticae* (1) classes; rarer were the communities of *Utricularietea intermedio-minoris* (2), and very rare were the communities of the *Littorelletea uniflorae* (4) class. Their distribution, growth peculiarities and species abundance varied in lakes of a different trophic level. Twenty nine syntaxa were found to be common to all trophic lakes, though their phytocenotic significance considerably depending on the trophic level of the lake.

The highest species (78) and syntaxa (78) diversity was observed in mesotrophic lakes. Mesotrophic lakes give home for many communities, including phytocenoses of the *Littorelletea uniflorae* class, which are rare and under protection in Lithuania. We may state that mesotrophic lakes, which are typical of the temperate climate zone, create the ratio between the light climate, amount of biogenic substances, gas regime, etc., which is the most favorable for the growth of macrophytes.

In oligomesotrophic lakes, the overgrowing with macrophytes and their syntaxonomic diversity (56 syntaxa) are lower, however, species diversity in such lakes is the highest (90). These lakes are characterized by the abundance of *Potamogetonetea pectinati* (20), *Phragmiti-Magnocaricetea elatae* (18), *Charetea fragilis* (13) communities exhibiting a low constancy (±2). Considerable water transparency and a relatively small amount of biogenic substances provide optimal conditions for the specialized deepwater limneid species of a narrower ecological amplitude.

The lowest phytocenotic significance of syntaxa was observed in dystrophic lakes: merely 3 helophyte communities of 40 syntaxa were constant. Fragments of some other communities were found only in 3–4 dystrophic lakes under investigation.

Eutrophic lakes were a strong second according to the number of syntaxa inventoried. Eutrophic lakes held 75 species and 75 syntaxa with the prevalence of the *Phragmiti-Magnocaricetea elatae* (28), *Potamogetonetea pectinati* (24), *Charetea fragilis* (14) class phytocenoses, which often occupied large areas of the eulittoral and littoral and formed the main part of the annual biomass in the lake ecosystem. However, macrophyte phytocenoses in eutrophic lakes were relatively poor – most communities being formed of 1–3 dominating species. The amount of biogenic substances in eutrophic lakes was highly favorable for the development of most macrophyte species of wide ecological amplitude. However, due to the low water clarity such lakes are not suitable for deepwater species of narrow ecological amplitude.

Dystrophic lakes were least favorable for the development of macrophytes. Most of biogenic substances in these oldest and bogging lakes were in the form of the humic substances that were not used by macrophytes, which to a significant degree conditioned the low species (43) and syntaxa (40) diversity. The eulittoral of dystrophic lakes held more halophyte communities of the *Phragmiti-Magnocaricetea elatae* (28) class, whereas in the shallow littoral (0.5–0.8 m) the fragments of *Potamogetonetea pectinati* (12) and *Charetea fragilis* (7) communities could be found. Deepwater macrophyte vegetation was very scarce, with only solitary plants or their small stands.

Lake overgrowth degree and the diversity of species and communities are closely related to the trophic level. Oligomesotrophic and mesotrophic lakes are relatively large, deep and rather young; they have a great variety of habitats and, subsequently, species (up to 70–120) and communities (up to 20–40). With the increase of eutrophication, the eulittoral and littoral of the lake are getting overgrown by monodominant macrophyte stands, so the species of a narrow ecological amplitude use to be eliminated from the communities. Therefore eutrophic lakes are not favorable for the development of a high macrophyte species (62–64) and communities (7–12) diversity.

From the viewpoint of the preservation of genetic pool and biological diversity, the most valuable are oligomesotrophic and mesotrophic lakes which have about 20 macrophyte species and 7 communities enlisted into the Red Data Book of Lithuania (2000).

Received 20 December 2005
Accepted 2 February 2006

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FITOCENOZIŲ KOKYBINIAI IR KIEKYBINIAI RODIKLIAI ĮVAIRAUS TROFIŠKUMO LIETUVOS EŽERUOSE

S a n t r a u k a
Įvertinta 446 ežerų užžėlimo makrofitais pobūdis, sintaksonominės bei rūšinės sudėties priklausomybė nuo ežerų trofinio lygio. Nustatyta, kad ežerų litoralės ir eulitoralės fitocenozės patenka į 7 augalijos klases ir apima 81 žemesnį sintaksoną. Plačiau paplitusios *Phragmiti–Magnocaricetea elatae* (30), *Potamogetonetea pectinati* (26), *Charetea fragilis* (14), labai retos *Littorelletea uniflorae* (4) klasės bendrijos. Jų paplitimas, augimo pobūdis bei rūšių gausumas įvairuoja priklausomai nuo ežero trofiškumo.

Didžiausia rūšių ir sintaksonų įvairovė stebima oligomezotrofiniuose ir mezotrofiniuose ežeruose. Šiuose ežeruose susiformuoja palankiausias makrofitų augimui šviesos, klimato, biogeninių medžiagų kiekio, dujų režimo ir kitų parametrų santykis.

Nors eutrofiniuose ežeruose sintaksonų įvairovė taip pat nemaža, tačiau čia dažnai formuojasi 1–2 rūšių monodominantiniai sąžalynai. Mažiausia rūšių ir sintaksonų įvairovė nustatyta distrofiniuose ežeruose.