LONG-TERM CHANGES IN THE FLORA AND VEGETATION OF LAKE MIKOŁAJSKIE (POLAND) AS A RESULT OF ITS EUTROPHICATION

BARBARA SOLIŃSKA-GÓRNICKA, EWA SYMONIDES

Department of Plant Ecology and Nature Protection, Warsaw University
Al. Ujazdowskie 4, 00-478 Warsaw, Poland

(Received: August 2, 2001. Accepted: October 10, 2001)

ABSTRACT

Changes in littoral flora as well as aquatic and swamp vegetation were analysed with increasing eutrophication of the mesotrophic Lake Mikołajskie. Over 30 years the habitat conditions of the lake deteriorated and the phytolittoral was reduced from a zone 6 metres wide to one of only 2 metres. In addition, the number of submerged macrophyte species decreased by 50% and the frequency of most of the remaining species declined severalfold. No new species were encountered. Species retreating from the lake littoral included all *Chara* species, *Potamogeton obtusifolius*, *P. natans* and *Hydrocharis morsus-ranae*. A significant lowering of the phytosociological diversity and species richness of aquatic and swamp communities was observed. By 1994, six of the 12 associations identified in 1964 and representing the submerged and floating-leaved vegetation (e.g. *Nitellopsidetum obtusae*, *Charetum asperae* and *Potamogetonetum compressi*) were no longer present. In turn, 6 swamp communities from among the original 14 identified in the lake were lacking (e.g. *Typhetum angustifoliae*, *Sagittario-Sparganietum emersi* and *Eleocharitetum palustris*). At the same time, two new aquatic and swamp communities appeared (*Ranunculetum circinati*, *Myriophylletum spicati*, *Caricetum acutiformis* and *Caricetum distichae*). In contrast there was an increase in the species richness of reedswamp communities due to an influx of marshland species. While the 1990s witnessed a distinct decrease in concentrations of nutrients in Lake Mikołajskie, the consequent increase in water transparency was not associated with an increase in the area of submerged macrophytes, or the species richness of aquatic vegetation.

KEY WORDS: submerged macrophytes, species diversity, aquatic plant communities, swamp communities, eutrophication.

INTRODUCTION

An increase in fertility in the Great Mazurian Lakes over the past 50 years has been attributed mainly to human-induced processes (e.g. tourism and recreation) and limited local government subsidies in response to them, as well as to the intensive use of artificial fertilisers which are eventually washed into lakes from agricultural land, as was indicated by Rybak (1972), Gliwicz et al. (1980), Hillbricht-Ilkowska (1989), Kufel and Kufel (1990). Like many others undergoing eutrophication, the mesotrophic lakes of the Mazurian Lake District have experienced a significant decline in the biomass and area of submerged macrophytes as a result of dense phytoplankton blooms and bad light conditions (cf Schiemer 1979; Ozimek and Kowalczewski 1984; Lachavanne 1985; Kowalczewski and Ozimek 1993). Contrasting results regarding the response of emergent plants to eutrophication are available. While Löffler (1979) and Guanatilaka (1985) indicated that a high biomass of *Phragmites australis* paralleled increasing eutrophication in Lake Neusiedler, Best et al. (1984), Schröder (1987) and Ostendorp et. al. (2001) found that this species had taken on a more restricted distribution among the swamps of some highly-eutrophicated lakes. As the changes occurring in plant communities with the progressive eutrophication of mesotrophic lakes were not dealt with in the aforementioned papers, it remains uncertain, whether the numbers of phytosociological types of vegetation, as well as the species richness of aquatic communities and swamps, are increasing, declining or remaining relatively constant, regardless of the changes in the floristic composition of vegetation.

The aim of the present paper was thus to determine the nature and scale of the changes in the flora and communities of the mesotrophic Lake Mikołajskie that were due to the long-term process of eutrophication. The starting point for the assessment of these changes was provided by the authors' unpublished data obtained in the years 1961-1963 and concerning the distribution of submerged and floating-leaved macrophytes and the phytosociological differentiation of both aquatic and swamp vegetation, as well as the significant changes observed in submerged plant biomass and distribution in Lake Mikołajskie between 1971-1990 (Ozimek and Kowalczewski 1984; Kowalczewski and Ozimek 1993).

The second survey carried out on the vegetation of Lake Mikołajskie after about 30 years aimed at testing the following hypotheses: (1) that the increase in the nutrient concentration of a mesotrophic lake does not lead to the impoverishment of the flora and a lower diversity of communities in spite of the decrease in the frequency of particular populations of species and their more restricted occurrence; (2) that as the fertility of a lake increases, species associated with oligotrophic and mesotrophic habitats are replaced by eutrophic species, with the result that – as with oligotrophic lakes undergoing eutrophication – the species richness of aquatic communities and swamps remains the same or can even increase (e.g. Vöge 1992).

MATERIALS AND METHODS

Lake Mikołajskie belongs to a system of interconnected postglacial lakes, situated in the Region of the Great Mazurian Lakes. It covers 498 ha in area, is up to 25.9 m deep, and is mostly surrounded by moraine. In the early 1950s it was classified as mesotrophic with water transparency less than 3 m and recorded markedly low concentrations of phosphorus and nitrogen (Szczepański 1968). The littoral zone is narrow, something which can be ascribed to the steep slopes and specific morphometry of the lake. Therefore, the area available for aquatic and swamp vegetation is greatly restricted. A greater diversity of habitats and the zonation of plant communities is observed in the few bays and in the shallow south-eastern sector of the lake. The catchment area of Lake Mikołajskie is 11.9 km^2, with forests accounting for 45%, arable land for 33% and built-up areas for 22% (Fig. 1). The lake has been enriched, mainly as a result of the influx of sewage from the nearby town of Mikołajki, which is visited by about 10 000 tourists every summer, as well as to a lesser extent by artificial enrichment due to runoff from agricultural land (Hillbricht-Ilkowska 1989).

Samples of submerged macrophytes were taken with an Ekman grab from different depths around the periphery of the lake. A total of 542 and 1380 samples were collected in 1961 and 1993 respectively. In order to determine the effect of the water quality of the lake on the vegetation, 746 samples were taken in 1998 after lake conditions had improved due to limited fertiliser runoff from agricultural land during the previous ten years. The sampling sites were depicted on a bathymetric map.The frequency of samples with macrophytes as well as with particular species was determined for different depth classes during the three sampling periods.

In the years 1962-1963 and in 1994 relevés were recorded, 87 and 97 respectively, in the aquatic and swamp communities by means of the Braun-Blanquet method (Braun-Blanquet 1964). The relevés were analysed using the Tüxen-Ellenberg method (Ellenberg 1956), with plant

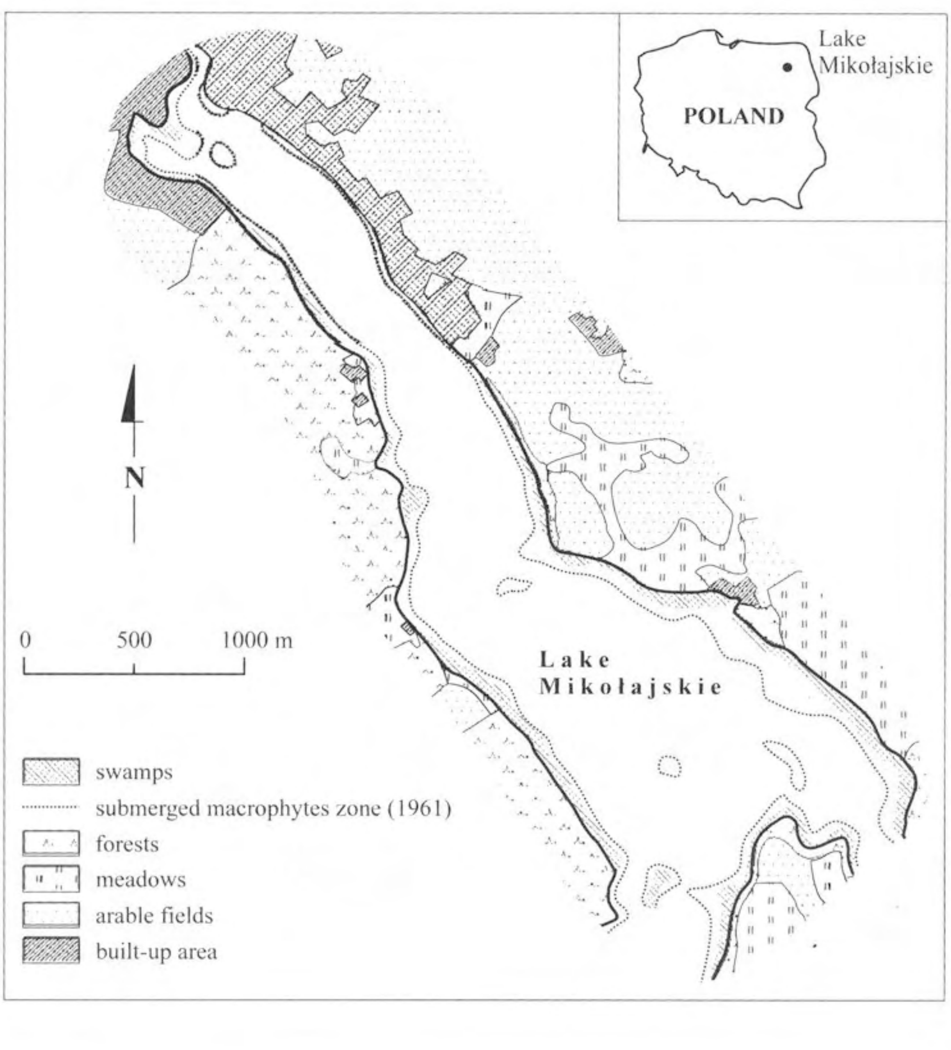

Fig. 1. Map of Lake Mikołajskie.

communities determined according to the generally applied methods described in syntaxonomical papers (Tomaszewicz 1973, 1974, 1977). Lists of the species and communities identified during the two sampling periods were compared with respect to diversity and species composition.

RESULTS

The flora of the littoral zone and the distribution of submerged macrophytes

In 1961 the submerged vegetation comprised 21 species, which occurred quite abundantly throughout the littoral area with the exception of the sectors adjacent to settlements. The highest frequencies of submerged macrophytes (over 90%) were those recorded at water depths of 1-3 m. However, dispersed stands of some species also occurred at 5-6 m (Fig. 2). The samples mainly contained vascular plants, although there was a high incidence of stoneworts (represented by four species of *Chara* and *Nitellopsis*) as well as of the moss *Fontinalis antipyretica* (Table 1).

TABLE 1. Frequency of the different submerged macrophytes in the total number of samples.

Year	1961	1993	1998
Total number of samples (100%)	542	1380	746
Stoneworts (Charophyceae)	38.0	2.5	1.5
Musci (Bryophyta)	34.7	1.3	1.7
Vascular plants	63.3	47.7	45.3

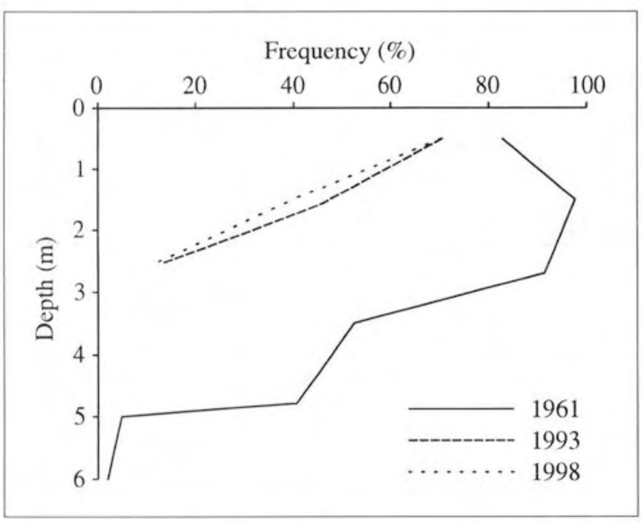

Fig. 2. Depth-range and frequency of submerged macrophytes.

The frequency of occurrence of the macrophyte species identified in the study varied from 0.1 – 44.5% (Fig. 3). Among the vascular plants, it was *Batrachium circinatum*, *Elodea canadensis* and *Ceratophyllum demersum* that were the most common species. A relatively high incidence of *Potamogeton perfoliatus* and *Potamogeton obtusifolius* was also noted. Stoneworts were represented mainly by *Nitellopsis obtusa* and *Chara vulgaris*. The moss *F. antipyretica* occurred with a higher frequency than any other submerged plant species even in the deepest parts of the phytolittoral.

The area occupied by submerged aquatic macrophytes declined over the 30 year period. In addition there was a considerable decrease in the frequency of most species, which were confined to the shallow waters of the littoral zone. Sporadic occurrence of aquatic plants was reported at water depths of 2-3 m, whereas no species were encountered in the samples taken from depths beyond 3 m. There was a sharp decline in the frequency of most species, particularly of stoneworts and mosses. Among the four representatives of the genus *Chara*, three species were not found in the samples taken in 1993. In turn, the frequency of *N. obtusa* was only at one-tenth of its earlier level. After the passage of about 30 years it was the frequencies and area of *F. antipyretica* that were most markedly lower. Frequencies around the same level were noted for *Potamogeton pectinatus* and *P. perfoliatus*, while *Myriophyllum spicatum* was the only species to occur more frequently following the increase in the fertility of the lake (Fig. 3 and 4).

The investigations carried out five years later confirmed a trend towards lower richness of flora in the lake littoral. At the same time, the species experiencing a decline in frequency were *E. canadensis*, *C. demersum*, *P. pectinatus*, *M. spicatum* and *N. obtusa*. Stands of *P. obtusifolius*, *Sagittaria sagittifolia* and *Chara aspera* probably disappeared altogether. *P. perfoliatus* and *Potamogeton lucens* occurred in samples much more frequently than in 1993. A slight increase in the frequency and area of *F. antipyretica* was recorded as well. A comparative analysis of the floristic lists made in the years 1961-1998 suggested that about 50% of the species identified had disappeared completely. At the same time, submerged macrophytes had become restricted to a littoral zone 2 metres wide. Occurring sporadically at water depths of 2-3 m were *F. antipyretica*, *P. perfoliatus*, *P. lucens* and *M. spicatum* (Fig. 3).

Aquatic plant communities

In 1963, 12 communities of aquatic vegetation were distinguished in the littoral zone of the lake: two associations belonging to the alliance *Charion fragilis*, six from the alliance *Potamogetonion* and four from the alliance *Nymphaeion*. In 1994 the number of associations was lower by 1/3 than 30 years earlier. About 50% per cent of the associations could no longer be identified, while two new ones were described (Table 2). Furthermore the numbers of species in the particular communities were also lower (Fig. 5)

It appears that the "charophyte meadows", which were abundant in the south eastern part of the lake and covered the deepest regions of the littoral zone in the 1960s, disappeared completely over the 30-year period. Only one charophycean species, namely *N. obtusa*, was found growing in the lake and it was associated with species of the class *Potamogetonetea*. In 1994 the *Potamogetonetum compressi*, *Ceratophylletum demersi* and *Elodeetum canadensis* communities were not encountered in the lake. The sporadic occurrence of *Potamogetonetum compressi* patches was recorded in the 1960s. The stands occurred exclusively at the depth of 1.5-2 m. The dominant pondweed, *Potamogeton compressus*, was also found in other communities of *Potamogetonion*. The species dominating in the other two communities, which were frequent in the 1960s, and occurring in close association with other communities of the classes *Charetea* and *Potamogetonetea* were intermixed with other species of submerged vegeta-

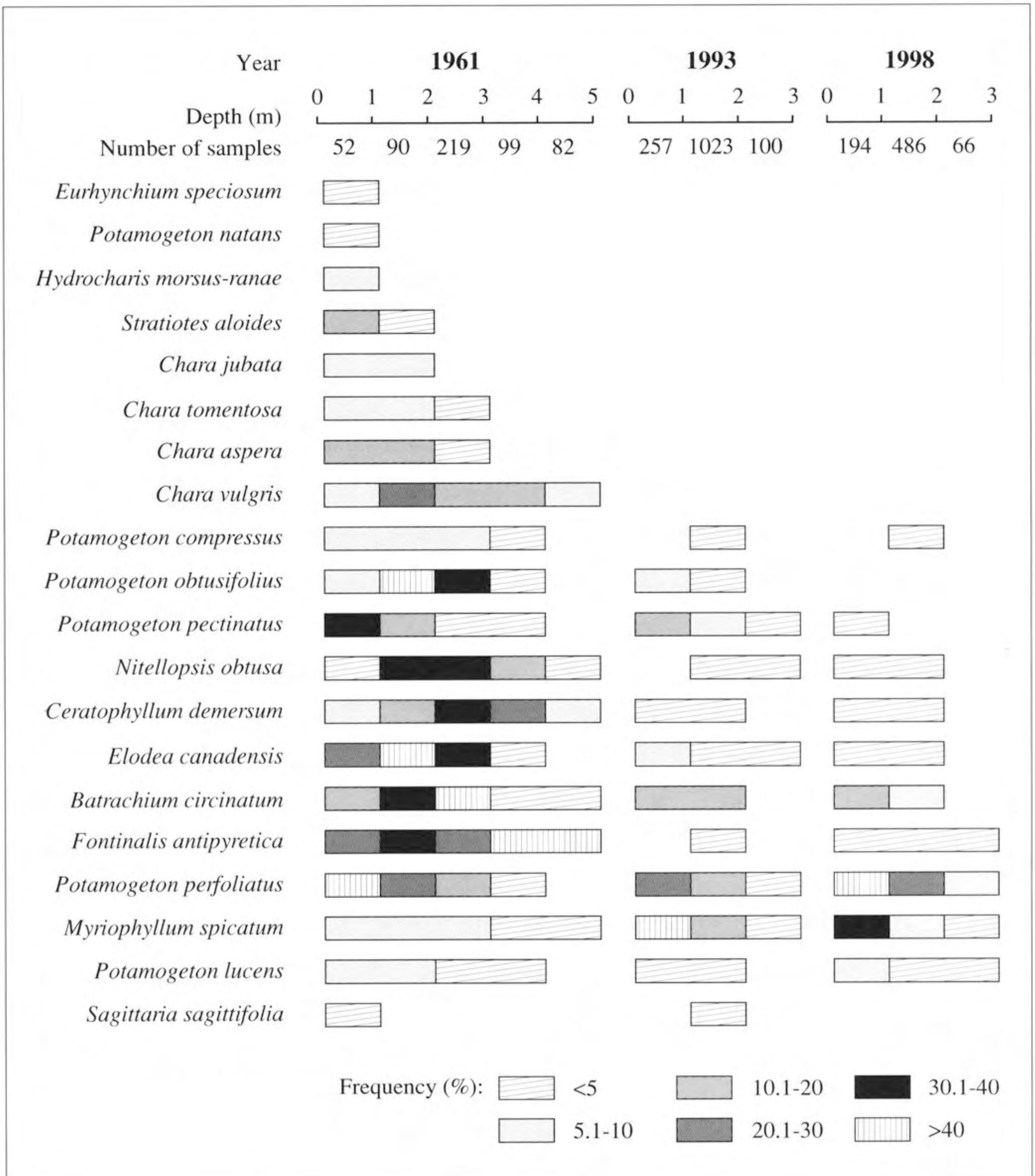

Fig. 3. Depth-range and frequency of submerged macrophyte species.

tion. Among the associations of *Nymphaeion*, the patches of *Hydrocharetum morsus-ranae*, which occurred as a single small stand in 1963, were the only communities whose complete disappearance from the lake over the 30-year period can be inferred.

Only six associations (three belonging to the alliance *Potamogetonion* and three from the alliance *Nymphaieon*) were identified during both sampling periods (Table 2). Patches with pondweeds, which occurred in the depth range 0.2-3.0 m dominated in the lake littoral: *Potamogetonetum lucentis* in 1963 and *Potamogetonetum perfoliati* in 1994. The patches of the aforementioned communities occurred in the shallow bays devoid of swamp vegetation, beside the reed-belt and on rises at some distance from the lake shore. The community of *Nupharo-Nymphaeetum* subass. with *Nuphar luteum* dominated in the relatively shallow bays of the lake (depth of 1 m) and were still extending their range.

The phytocoenoses of *Myriophylletum spicati* and *Ranunculetum circinati*, which dominated in the littoral in 1994, produced large stands at 0.5-2.0 m in the quiet bays of Lake Mikołajskie. The two communities had not been

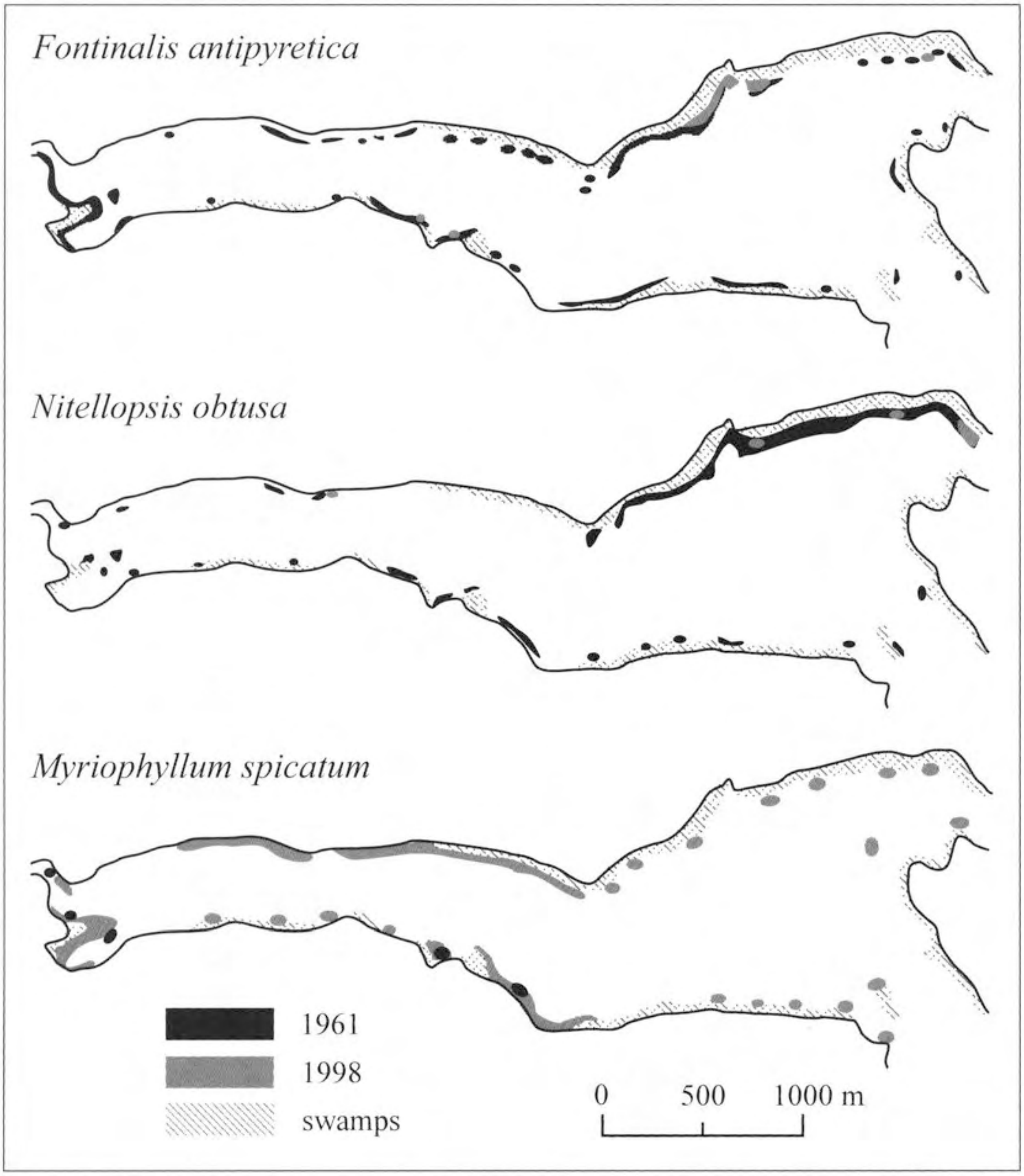

Fig. 4. Distribution of selected macrophyte species.

encountered in the 1960s and the characteristic species of these associations were found in other communities of *Potamogetonetea*.

Swamp communities

In 1962 a total of 13 vegetation types of swamps were distinguished: nine associations from the alliance *Phragmition*, among which *Phragmitetum communis* communities dominated at 0-2 m, and four associations belonging to the alliance *Magnicaricion* (Table 3). The patches representing the latter alliance occurred mainly on flat shores on the south-eastern margins of the lake adjoining extensive pastures.

A lower diversity and 20% greater species richness of reed-swamp communities of the alliance *Phragmition* is implied by comparisons across the 30-year period. Phytocoenoses of the associations *Typhetum angustifoliae*, *Saggitatio-Sparganietum*, *Eleocharetum palustris* and *Equisetum limosi* had disappeared, and their dominant species were scattered and associated with other communities. Submerged macrophyte species retreating from the patches representing the other associations were: *F. antipyretica*, *P. lucens*, *P. pectinatus* and *E. canadensis*. The aforementioned species appear to have given way to a number of swamp species of the alliance *Magnocaricion*, namely: *Phalaris arundinacea*, *Carex gracilis*, *Lysimachia thyrsiflora* and *Iris pseudoacorus*, as well as to *Solanum dulcamara* and *Symphytum officinale*. A rare species of grass *Scolochloa festucacea* was found growing among the reed-swamp vegetation as well. At present the *Glycerietum maximae* communities occur with a higher frequency than in the 1960s, particularly in the close vicinity of the town of Mikołajki. The patches of *Scirpetum lacustris*, *Acoretum calami* and *Phragmitetum communis* have also extended their range, but to a lesser extent.

Significant changes in the sedge communities of the alliance *Magnocaricion* occurred over the 30 year period. However the number of associations identified throughout the whole study remained the same. The communities associated with mesotrophic waters, such as *Caricetum elatae* and *Caricetum rostratae* disappeared altogether while two new associations, i.g. *Caricetum acutiformis* and *Caricetum distichae* were encountered. Moreover the area of communities characteristic of eutrophic habitats, e.g.

TABLE 2. Diversity of aquatic communities.

Year	1963												1994							
No of community table	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Class	*Charetea*		*Potamogetonetea*																	
Alliance	*Charion*		*Potamogetonion*						*Nymphaeion*				*Potamogetonion*					*Nymphaeion*		
No of relevés per table	4	1	1	2	6	8	11	1	1	1	5	1	15	6	2	6	8	2	7	2
***Charetea* – character species**																				
Nitellopsis obtusa	4			1	2	2	2			1			7	2	1	4		1		
Chara vulgaris	2	1	1		2	1	3			1	1									
Chara aspera	2	1			3	1	2	1												
Chara tomentosa	1	1			2	1	1				1									
Chara jubata	1	1			2		2													
***Potamogetonetea* and *Potamogetonion* – character species**																				
Potamogeton compressus			1	1	1	1														
Ceratophyllum demersum	1			2	3	1	1		1	1	1		4	4	1	3		2	2	
Elodea canadensis	4	1	1	2	6	3	7			1	3		1			2		2	1	
Potamogeton perfoliatus			1	1	2	8	7	1			2	1	15	2	2	2	4			2
Potamogeton lucens						3	11	1			1		5	6		1				2
Potamogeton pectinatus					2	3		1		1		1	8	2	2	2	5	1	6	
Batrachium circinatum				1	5	2	7				1	1	6	2	1	6	4		4	
Myriophyllum spicatum			1		3		1				1			1	1	2	8		3	1
Utricularia vulgaris				1	2				1											
***Nympahaeion* – character species**																				
Stratiotes aloides					1				1	1										
Hydrocharis morsus-ranae									1											
Potamogeton obtusifolius					4	1	1			1	3		1		1	2		2	1	
Nuphar lutea			1								5								7	
Polygonum amphibium f. natans												1							1	2
Other species																				
Fontinalis antipyretica	2	1		1	5	1	4	1		1	1		3	4		4	1	1	1	
Lemna trisulca	2		1	2	5	1	3		1	1			4	1		2			1	
Phragmites australis											1		6			1			3	1
Lemna minor									1										1	
Sagittaria sagittifolia											1						1			

List of associations:

1 – *Nitellopsidetum obtusae* (Sauer 1937) Dąmbska 1961; 2 – *Charetum asperae* Corillion 1957; 3 – *Potamogetonetum compressi* Tomaszewicz 1979; 4 – *Ceratophylletum demersi* Hild 1965; 5 – *Elodeetum canadensis* (Pign. 1953) Pass. 1964; 6, 13 – *Potamogetonetum perfoliati* W. Koch 1926 em. Pass. 1964; 7, 14 – *Potamogetonetum lucentis* Hueck 1931; 8, 15 – *Potamogetonetum pectinati* Carstensen 1955; 9 – *Hydrocharitetum morsus-ranae* Langendonck 1935; 10, 18 – *Potamogetonetum obtusifolii* (Carstensen 1954) Segal 1965; 11, 19 – *Nupharo-Nymphaeetum albae* Tomaszewicz 1977; 12, 20 – *Polygonetum natantis* Soó 1927; 16 – *Ranunculetum circinati* (Bennema et Westh. 1933) Segal 1965; 17 – *Myriophylletum spicati* Soó 1927.

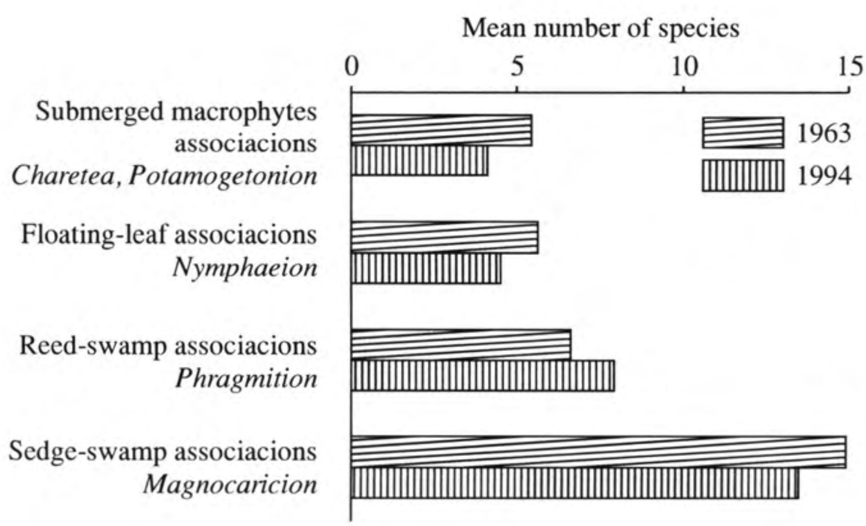

Fig. 5. Species richness of aquatic and swamp associations.

TABLE 3. Diversity of swamp communities.

Year	1962													1994								
No of community table	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Class	*Phragmitetea*																					
Alliance	*Phragmition*									*Magnocaricion*				*Phragmition*					*Magnocaricion*			
No of relevés per table	2	1	3	2	3	3	13	8	1	4	1	1	1	5	1	7	11	4	3	2	4	3
***Phragmitetea* and *Phragmition* – character species**																						
Typha angustifolia	2				1					1												
Sagittaria sagittifolia		1	1				1	1														
Sparganium emersum		1								1												
Oenanthe aquatica		1					1															
Eleocharis palustris			3				1	1	1	1				1								
Alisma plantago-aquatica	1	1				1	2										2				1	
Equisetum fluviatile	1		1	2	2	2	7	2	1	4	1	1				2	2	2			1	1
Schoenoplectus lacustris		1	2		3		5	2	1	3				5				3				
Typha latifolia				1	2	3	4	2		1					1	4	1	1	1	2		
Phragmites australis	2	1		2	3	1	13	5	1	4	1	1		1	1	7	11	1	3	1	3	2
Glyceria maxima	1			1	2	1	4	8		2			1			4	11	2	1	1	2	
Acorus calamus					1		1		1	1						2	3	4	3	1	1	2
Rumex hydrolapathum							1	1		1	1	1					3	1			1	2
Sparganium erectum							2	2		2												
Rare species: *Butomus umbellatus* (table 10), *Glyceria fluitans* and *Scrophularia umbrosa* (table 13)																						
***Magnocaricion* – character species**																						
Galium palustre							1	1	1	1	1	1	1						2	1	1	3
Carex rostrata					2		3	1		4	1	1					1					1
Cicuta virosa	1					1	2	3		2	1		1			3						
Lysimachia thyrsiflora							1			1	1					1	5	1			1	1
Carex pseudocyperus							1			1	1	1	1					1				
Carex elata										1	1					1		1			1	1
Carex gracilis	1											1				2	2	1	3			
Phalaris arundinacea								1	1	1			1			3	6	1	2	2	2	3
Carex acutiformis												1				1	1				4	2
Scutellaria galericulata											1								1		1	2
Carex disticha																		1	1	1		3
Poa palustris													1							1		
Differential species																						
Potamogeton lucens			1		1	1	2	1		1				1								
Fontinalis antipyretica			1		1		6	2		1												
Potamogeton pectinatus			1	1		1	1											1				
Lemna minor					1	1							1			3	7	2	2	1	3	
Iris pseudacorus										1		1					10		2	2	3	3
Solanum dulcamara								1					1		1	2	6			1	3	
Lemna trisulca																1	4	2	1		1	1
Symphytum officinale																1	1	1	1		1	
Lysimachia vulgaris																		1	2	1	1	2
Salix cinerea b,c																1	1		1		1	
Utricularia vulgaris																	2	1	1			3
Stellaria uliginosa																		1	1	1		2
Other species																						
Hydrocharis morsus-ranae	1	1				1	1			1						2	8	1			3	1
Potamogeton perfoliatus				1	1	2		2						3				2				
Lycopus europaeus							1	2	1	1	1	1	1			2	2	2			3	
Polygonum amphibium			1				1	1		1	1	1		1				1				
Mentha aquatica							1	1	1							3	2	1		1	2	
Myosotis palustris							1	2	1	1		1							1	1		
Nuphar lutea				1			1	2						1		1						
Drepanocladus aduncus							1	1	1	1			1									
Lythrum salicaria								1			1							2	1			2
Bidens cernua						1		1					1								1	
Agrostis canina							1		1		1		1									
Caltha palustris									1							1					1	2
Elodea canadensis	1						1	1														
Bidens tripartita						1		2					1									
Cardamine pratensis						1							1					1				
Epilobium palustre							1	2					1									

TABLE 3. cont.

Year	1962													1994								
No of community table	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Class	*Phragmitetea*																					
Alliance	*Phragmition*									*Magnocaricion*				*Phragmition*					*Magnocaricion*			
No of relevés per table	2	1	3	2	3	3	13	8	1	4	1	1	1	5	1	7	11	4	3	2	4	3
Other species (*continued*)																						
Urtica dioica								1		1		1	1									
Carex elongata								1														1
Acrocladium cuspidatum									1		1											2
Calamagrostis neglecta											1								2			1
Scolochloa festucacea																2	1	1				
Cirsium arvense																			1	1		1
Equisetum palustre																			1	1		2

Rare species: *Potamogeton natans*, *Stratiotes aloides*, *Chara sp.* (table 2, 7), *Batrachium circinatum* (table 2, 14), *Rorippa x armoracioides* (table 7, 12), *Ranunculus sceleratus* (table 8, 13) *Epilobium hirsutum* (table 10, 13), *Stellaria palustris* (table 11, 22), *Poa trivialis* (table 13, 20), *Calystegia sepium* (table 16, 21), *Alnus glutinosa* b, c (table 17, 18), *Fraxinus excelsior* b, c (table 17, 21), *Salix purpurea* c (table 17, 22), *Calamagrostis canescens*, *Carex nigra* (table 18, 22)

List of associations:
1 – *Typhetum angustifoliae* (Allorge 1922) Soó 1927; 2 – *Sagittario-Sparganietum emersi* R. Tx. 1953; 3 – *Eleocharitetum palustris* Šennikow 1919; 4 – *Equisetetum limosi* Steffen 1931; 5, 14 – *Scirpetum lacustris* (Allorge 1922) Chouard 1924; 6, 15 – *Typhetum latifoliae* Soó 1927; 7, 16 – *Phragmitetum communis* (Gams 1927) Schmale 1939; 8, 17 – *Glycerietum maximae* Hueck 1931; 9, 18 – *Acoretum calami* Kobendza 1948; 10 – *Caricetum rostratae* Rübel 1912; 11 – *Caricetum elatae* Koch 1926; 12, 19 – *Caricetum gracilis* (Graebn. et Hueck 1931) R. Tx. 1937; 13, 20 – *Phalaridetum arundinaceae* (Koch 1926 n. n.) Libb. 1931; 21 – *Caricetum acutiformis* Sauer 1937; 22 – *Caricetum distichae* (Nowiński 1928) Jonas 1933.

Caricetum gracilis and *Phalaridetum arundinacea* was greater (Table 3). The above phytocoenoses covered only a small area of the lake littoral in 1962. The total number of species dominating in the sedge communities decreased by about 10% (Fig. 5).

Alderwood forests and scrub developing beside the lake were a rare element of the vegetation landscape of Lake Mikołajskie in the 1960s. Some fragments of riparian forests of the alliance *Alno-Padion* were encountered. The same two associations, notably *Salicetum pentandro-cinereae* and *Ribo nigri-Alnetum* were distinguished after 30 years, but at present the swamp communities are characterized by a higher contribution of *Salix cinerea*, *S. pentandra* and *Alnus glutinosa*.

DISCUSSION

Symptoms of deteriorating water quality in Lake Mikołajskie were observed in the 1960s. Since then the process of lake eutrophication has proceeded rapidly. The index of water clarity and oxygen deficiency decreased by 10 units per decade, something that was linked with the increase in the biomass, intensity and longevity of algal blooms and the growth of bottom-associated filamentous algae (Gliwicz and Kowalczewski 1981; Pieczyńska et al. 1988). Since the early 1970s the clarity of water has not exceeded 1 m and the concentration of nutrients has been similar to that of the highly-eutrophic waters of dimictic lakes (Hillbricht-Ilkowska 1989).

The progressive eutrophication of Lake Mikołajskie in the years 1963-1980 was associated with a tenfold decrease in macrophyte biomass. In addition, submerged macrophyte vegetation became confined to the shallow (less than 3 m deep) waters of the phytolittoral (Ozimek 1992; Kowalczewski and Ozimek, 1993). The results of this study indicate that the retreat of species from the deeper layers of the littoral zone was still in progress in spite of the improvement in the quality and transparency of water in the 1990s (Kufel and Kufel 1999). In 1993 the frequency of submerged macrophytes in the depth range 2-3 m was estimated at 10%. The submerged plant communities consisted of six species. Over the next five years the range of other species (*P. pectinatus*, *E. canadensis* and *N. obtusa*) became restricted to the shallower layers of the lake littoral. It was assumed that the decline in the number, frequency and biomass of species in the shallow waters receiving more light was attributable to the abundant growth of filamentous algae of the genera *Vaucheria* and *Cladophora* (Pieczyńska et al. 1988; Ozimek 1990).

It has long been recognized that the ongoing nutrient enrichment of lakes leads to changes in the colour of water and turbidity. In consequence, much more light in the range 200-365 nm is absorbed and the photic zone in the lake is reduced due to the presence of organic matter which is responsible for the scattering of the light (Frimmel 1994). The negative response of plants to bad light conditions, including the retreat of species due to overshadowing, has been observed in various types of lakes (Chambers and Kalff 1985; Chambers and Prepas 1988; Middelboe and Markager 1997; Sand-Jensen et al. 2000).

A great lowering in the frequency of stoneworts is apparent in Lake Mikołajskie, in association with the increasing fertility of waters and substrata. It is, however, difficult to explain why they have almost become locally extinct, since stoneworts tolerate a wide range of habitats and occur on both mineral and highly-organic substrata. Furthermore they can grow in deeper layers of a lake than vascular plants because of their low compensation point (Schwarz et al. 1996; Simons and Nat 1996; Schagerl and Pichler 2000). Nevertheless stoneworts are intolerant of adverse changes in light conditions (Hough et al. 1989; Blindow

1992a; Steinman et al. 1997). In the shallow waters of the littoral zone which receive more light, vascular plants join phytoplanktonic and epiphytic algae in being better able to compete with charophytes (Dijk and Vierssen 1991; Blindow 1992b, Berg et al. 1998).

During the life cycle of stoneworts it is the oospores which appear to be most vulnerable to poor light conditions. Vand der Berg (1999) indicated that the germination of *Ch. aspera* oospores under laboratory conditions did not exceed 15%. Under field conditions the percentage of germinating oospores may be even lower due to permanently or periodically reduced light conditions (Takatori and Imahori 1971; Stross 1989). Since the phenological period of oospore germination coincides with algal blooms, which are responsible for the substantial shading, it may be assumed that the reproduction of individuals is not possible because of lack of light. It is interesting to note that oospores buried at some considerable depth in the soil are also unable to germinate (Frankland et al. 1987).

The growth of stoneworts probably resembles that of other aquatic plants in also being limited by substances polluting the water and substrata (Wick et al. 1992; Vadstrup and Madsen 1995). Stoneworts use bicarbonate instead of free CO_2 in photosynthesis, which is more energy-demanding (Keeley 1998). The process of uptake of bicarbonate ions, which takes place in the plasmalemma, involves a series of enzyme- mediated reactions (Sültemeyer et al. 1993; McConnaughey 1998). Therefore photosynthesis can be disturbed or inhibited by substances which have a negative effect on the structure and functioning of the cell membrane as well as those binding Ca^{2+} ions in the water overlying the sediments and thus leading to the process of calcification (McConnaughey and Whelan 1997).

The frequency and area of occurrence of the moss *F. antipyretica* declined significantly in the years 1961-1993 in spite of the wide ecological tolerance of the species (Penuelas 1985; Karttunen and Toivonen 1995; Biehle et al. 1998). Under poor light conditions in eutrophic and polyhumic lakes individuals of this species are much longer and more frequently branched (Penuelas 1985). They can therefore absorb more light and take in more bicarbonate ions as a source of inorganic carbon. The fact that the individuals are highly plastic in their morphology increases their chances of survival in turbid, poorly-irradiated waters. Thus the moss can compete more successfully with aquatic vascular plants for light (Boston et al. 1989). Perhaps because of this the moss was not eliminated from the littoral zone and its frequency increased slightly in the years 1993-1998. This may also be attributable to the lower number of species forming the submerged macrophyte communities and therefore the weaker competition of vascular plants. Under similar conditions in rivers *F. antipyretica* is considered as being an invasive species (Englund et al. 1997). The populations of the moss can increase significantly provided that its rhizoids are firmly anchored in the substratum. The muddy bottom of the highly eutrophic Lake Mikołajskie is, therefore, unsuitable for the growth of the moss.

Some aquatic vascular plants, such as pondweeds *P. pectinatus, P. obtusifolius and P. perfoliatus*, as well as *M. spicatum* responded differently to the increase in the fertility of Lake Mikołajskie. In the 1980s the above species expanded rapidly in the lake littoral but after ten years or so some of them, particularly *P. obtusifolius* and *P. pectinatus*, started to retreat (Ozimek et al. 1986; Kowalczewski and Ozimek 1993). It appears that the species initially filled in the space abandoned by potentially stronger competitors which were more susceptible to the reduced light conditions. The deterioration of the water quality in the littoral area had a negative effect on the growth and reproduction of the species. Van Dijk et al. (1991) indicated that the biomass and number of tubers produced by *P. pectinatus* were reduced in low light conditions. It may therefore be assumed that *P. obtusifolius* shows the same response to the lack of light.

In the 1990s the submerged macrophyte communities consisted of only three species: *P. perfoliatus, M. spicatum* and *B. circinatum*, while only *P. pectinatus* tended to expand in the lake littoral. The above species tolerate high concentrations of electrolytes in the water and are thus often dominant in the polluted waters of eutrophic lakes (Rodwell 1995). Furthermore their leaves and stems are usually clustered above the water surface, so that the plant is well-adapted to the diminishing transparency of waters (Trebitz et al. 1993).

The survey suggested that the eutrophication of Lake Mikołajskie had led to a decline in the number and frequency of species that had dominated in the communities in the 1960s. Since no new species appeared, the species richness of the submerged and floating-leaved vegetation were significantly (respectively 25 and 20%) lower. In addition, a lower diversity of aquatic communities was reported. The phytocoenoses of 6 associations (including all communities of the class *Charetea*), which comprised 50% of those identified over the 30 years, had disappeared while two new vegetation types were encountered. The now-present communities of *Ranunculetum circinati* and *Myriophylletum spicati*, which were lacking in the 1960s, showed floristic similarities with those of the alliance *Nymphaeion* and were quite common in a wide depth range of the littoral zone in eutrophic lakes. They were usually associated with thin-layered organic bottoms (Tomaszewicz 1977). Although the patches of some communities were no longer present in the lake littoral, the area of *Potamogetonetum perfoliati* and *Nupharo-Nymphaeetum* increased considerably. It thus appears that the current findings do not support the hypotheses stated earlier in the paper. The increase in the fertility of Lake Mikołajskie apparently resulted in the impoverishment of the flora and in a decrease in the diversity and species richness of aquatic vegetation. It was demonstrated that the plant communites specific to the lake were gradually replaced by the eurytopic plant communities otherwise inhabiting old riverbeds and ponds.

A direct and indirect consequence of eutrophication of the lake water involved changes in the diversity of swamp vegetation over the 30-year period. Mesotrophic communities, such as *Caricetum rostratae* and *Caricetum elatae*, were eliminated from among the sedges, as in other lakes under similar conditions (Tomaszewicz 1977; Kłosowski 1990). By contrast, there was an increase in the area of communities characteristic of eutrophic lakes, like *Caricetum gracilis, Caricetum acutiformis* and *Phalaris arundinaceae*. Similarly, the *Glycerietum maximae* phytocoenoses associated with higher nutrient concentration mostly spread among the reed-swamp communities. This was attributed mainly to the high biomass production of *Glyceria maxima*, and to its wider range of tolerance of polluted waters (Sundblad 1990). The increase in the number of species in the communities of the alliance *Phragmition* was associated with a higher frequency of swamp species characteristic of the alliance *Magnocaricion*, and with encroachment of species of the class *Alnetea glutinosae*. The rapid accumulation of silt facilitates colonization by alder woodland, which takes the place of reed-swamps (Kłosowski and Tomaszewicz 1993). There is no doubt, however, that the development of alder and scrub exemplifies a stage in the successional changes of the lake to dry-land.

In recent years a distinct decrease in nutrient concentrations and an improvement in the transparency of water have been reported from Lake Mikołajskie (Kufel and Kufel 1999). The recolonization of the littoral zone by species which occurred earlier in the lake is therefore possible, especially where their propagules have persisted in sediments (Grillas et al. 1993; Bonis et al. 1995). Stoneworts play an important role in this process since they produce a large number of small propagules and can thereby recolonize habitats rapidly (Wade 1990; Grillas et al. 1993; Beltman and Allegrini 1997). The restoration of eutrophic lakes and reestablishment of submerged macrophytes has been indicated by various authors (e.g. Meijer et al. 1990; Simons et al. 1994). However, this process has been reported to proceed slowly, in spite of the improvement in habitat conditions (Lauridsen et al. 1994).

ACKNOWLEDGEMENTS

Our special thanks go to Mrs Irena Sawicka for her help and assistance during our stay at the Hydrobiological Station of PAS in Mikołajki.

LITERATURE CITED

BELTMAN B., ALLEGRINI C. 1997. Restoration of lost aquatic plant communities: new habitats for *Chara*. Neth. J. Aquat. Ecol. 30: 331-337.

BERG M.S. v.d., COOPS H., SIMONS J., de KEIZER A. 1998. Competition between *Chara aspera* and *Potamogeton pectinatus* as a function of temperature and light. Aquat. Bot. 60: 241-250.

BERG M.S. v.d., SCHEFFER M., Van NES E., COOPS H. 1999. Dynamics and stability of *Chara sp.* and *Potamogeton pectinatus* in shallow lake changing in eutrophication level. Hydrobiologia 409: 335-342.

BEST E. P., VRIES D. de, REINS A. 1984. The macrophytes in the Loosdrecht Lakes: A story of their decline in the course of eutrophication. Verh. int. Verein. Limnol. 22: 868- 875.

BIEHLE G., SPATZ C., SPECK T. 1998. Hydrodynamics and biomechanics of the submerged water moss *Fontinalis antipyretica* – a comparison of specimens from habitats with different flow velocities. Bot. Acta 111: 42-50.

BLINDOW I. 1992a. Decline of charophyte during eutrophication: comparison with angiosperms. Freshwat. Biol. 28: 9-14.

BLINDOW I. 1992b. Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. Freshwat. Biol. 28: 15-17.

BONIS A., LEPART J., GRILLAS P. 1995. Seed bank dynamics and coexistence of annual macrophytes in a temporary and variable habitat. Oikos 74: 81-92.

BOSTON H.L., ADAMS M.S., MADSEN J.D. 1989. Photosynthetic strategies and productivity in aquatic systems. Aquat. Bot. 34: 27-57.

BRAUN-BLANQUET J. 1964. Pflanzensoziologie. Grundzüge der Vegetationskunde. 3 Aufl. Springer, Viena, New York, pp. 865.

CHAMBERS P.A., KALFF J. 1985. Depth distribution and biomass of submerged aquatic macrophyte communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. 42: 701-709.

CHAMBERS P.A., PREAPAS E.E. 1988. Underwater spectral attenuation and its effect on the maximum depth of angiosperm colonization. Can. J. Fish. Aquat. Sci. 42: 1010-1017.

DIJK G.M. van, VAN VIERSSEN W. 1991. Survival of a *Potamogeton pectinatus* population under various light conditions in a shallow eutriphic lake (Lake Veluwe) in the Netherlands. Aquat. Bot. 39: 121-130.

ELLENBERG H. 1956. Aufgaben und Methoden der Vegetationskunde. Eugen Ulmer, Stuttgart, pp. 136.

ENGLUND G., JONSSON B.G., MALMQVIST B. 1997. Effect of flow regulation on bryophytes in north Swedish rivers. Biol. Conservation 79: 19-86.

FRANKLAND B., BARTLEY M.R., SPENCE D.H.N. 1987. Germination under water. In: Plant life in aquatic and amphibious habitats. Crawfor R.M.M. (ed.). Blackwell Scientific Publications, Oxford, pp. 167-177.

FRIMMEL F.H. 1994. Photochemical aspects related to humic substances. Environ. Int. 20: 373-386.

GLIWICZ Z.M., KOWALCZEWSKI A. 1981. Epilimnetic and hypolimnetic symptoms of eutrophication in Great Masurian Lakes, Poland. Freshwater Biol. 11, 425-433.

GLIWICZ Z.M., KOWALCZEWSKI A., OZIMEK T., PIECZYŃSKA E., PREJS A., PREJS K., RYBAK I. 1980. Ocena stopnia eutrofizacji Wielkich Jezior Mazurskich. Wydawnictwo Akcydensowe, Warszawa, pp. 103.

GRILLAS P., GARCIA-MURILLO P., GERZ-HANSEN O., MARBA N., MONTES C., DUARTE C.M., THAN HAM L., GROSSMANN A. 1993. Submerged macrophyte seed bank in a Mediterranean temporary marsh: abundance and reliationship with established vegetation. Oecologia 94: 1-6.

GUANTILAKA A. 1985. Nährstoffkreisläufe im Schilfgürtel des Neusiedler Sees. Auswirkungen des Grünschnittes. Wiss. Arb. Bgld. 72: 225-310.

HILLBRICHT-ILKOWSKA A. (ed.). 1989. Jeziora Mazurskiego Parku Krajobrazowego. Polska Akademia Nauk, Wrocław, Warszawa, pp. 168.

HILLBRICHT-ILKOWSKA A., SPODNIEWSKA I., WĘGLEŃSKA T. 1979. Changes in the phytoplankton zooplankton relationship connected with eutrophication of lakes. Symp. Biol. Hung. 19: 59-75.

HOUGH R.A., FORNWALL M. de., NEGELE B.J., THOMPSON R.L., PUTT D.A. 1989. Plant community dynamics in a chain of lakes: principal factors in the decline of rooted macrophytes with eutrophication. Hydrobiologia 173: 199-217.

KARTTUNEN K., TOIVONEN H. 1995. Ecology of aquatic bryophyte assemblages in 54 small Finnish lakes and their changes in 30 years. Ann. Bot. Fennici 32: 75-90.

KEELEY J.E. 1998. CAM photosynthesis in submerged aquatic plants. Bot. Rev. 64: 121-175.

KŁOSOWSKI S. 1990. Litoralvegetation stehenzer Gewässer-Ökologie, Dynamik und Bioindikationswert. Polish Bot. Stud. 1: 149-184.

KŁOSOWSKI S., TOMASZEWICZ H. 1993. Analysis of distribution, structure and habitat conditions of riparian vegetation in the river-lake system of the upper Szeszupa (Suwałki Landscape-park – north-estern Poland). Ekol. pol. 41: 123-156.

KOWALCZEWSKI A., OZIMEK T. 1993. Further long-term changes in the submerged macrophyte vegetation of the eutrophic Lake Mikolajskie (North Poland). Aquat. Bot. 46: 341-345.

KUFEL I., KUFEL L. 1990. Chemical characteristics of lake waters in the Great Masurian Lakes System. Monitoring of the Great Masurian Lakes, Hydrobiological Station Mikołajki, Progress report 1988-1989: 27-31.

KUFEL I., KUFEL L. 1993. Abiotic environment of the Great Masurian Lakes in 1991. Monitoring of the Great Masurian Lakes, Hydrobiological Station Mikołajki, Progress report 1990-1991: 12-15.

KUFEL I., KUFEL L. 1999. Spatial and temporal variability of chlorophyll and nutrients in the Great Masurian Lakes. Monitoring of the Great Masurian Lakes, Hydrobiological Station Mikołajki, Progress report 1996-1997: 10-13.

LACHAVANNE J.B. 1985. The influence of accelerated eutrophication on the macrophytes of Swiss lakes: Abundance and distribution. Verh. int. Verein. Limnol. 22: 2950-2955.

LAURIDSEN T.L., JEPPESEN E., SONDERGAARD M. 1994. Colonization and succession of submerged macrophytes in shallow lake Vaeng during the first five years following fish manipulation. Hydrobiologia 275/276: 233-242.

LÖFFLER H. (ed.). 1979. Neusiedlersee: The limnology of a shallow lake in central Europe. Monogr. Biol. 37: pp. 543.

McCONNAUGHEY T.A. 1998. Acid secretion, calcification, and photosynthetic carbon concentrating mechanisms. Can. J. Bot. 76: 1119-1126.

McCONNAUGHEY T.A., WHELAN J.F. 1997. Calcification generates protons for nutrient and bicarbonate uptake. Earth Sci. Rev. 42: 95-117.

MEIJER M.L., JEPPSEN E., VAN DONK E., MOSS B. 1994. Long term responses to fish stock reduction in small shallow lakes – interpretation of five-year results of four biomanipulation cases in the Netherlands and Denmark. Hydrobiologia 276: 457-466.

MIDDELBOE A.L., MARKAGER S. 1997. Depth limits and minimum light requirements of freshwater macrophytes. Freshwat. Biol. 37: 553-568.

OSTENDORP W., TIEDGE E., HILLE S. 2001. Effect of eutrophication on culm architecture of lakeshore *Phragmites* reeds. Aquat. Bot. 69: 177-193.

OZIMEK T. 1990. Aspects of the ecology of a filamentous alga in a eutrophicated lake. Hydrobiologia 191: 23-27.

OZIMEK T. 1992. Submerged macrophytes and their relationship with algae in eutrophic and hypertrophic lakes. Wiad. Ekol. 38: 13-34.

OZIMEK T., KOWALCZEWSKI A. 1984. Long-term changes of the submerged macrophytes in eutrophic lake Mikolajskie (North Poland). Aquat. Bot. 19: 1-11.

OZIMEK T., PREJS A., PREJS K. 1976. Biomass and growth rate of *Potamogeton pectinatus* L. in lakes of different trophic state. Ekol. pol. 34: 125-131.

PENUELAS J. 1985. HCO_3^- as a source for aquatic bryophytes *Fontinalis antipyretica* and *Fissidens*. J. Exp. Bot. 36: 441-448.

PIECZYŃSKA E., OZIMEK T., RYBAK I. 1988. Long-term changes in littoral habitats and communities in Lake Mikołajskie (Poland). Int. Rev. Ges. Hydrobiol. 73: 361-378.

RODWELL J.S. (ed.). 1995. British plant communities. Vol. 4. Aquatic communities, swamps and tall-herb fens. Cambridge University Press, pp. 283.

RYBAK I. 1972. Spatial and time changes of some environmental factors in the pelagial of Mikołajskie Lake. Ekol. pol. 20: 541-546.

SAND-JENSEN K., RIIS T., VESTERGAARD O., LARSEN S.E. 2000. Macrophyte decline in Danish lakes and streams over the past 100 years. J. Ecol. 88: 1030-1040.

SCHAGERL M., PICHLER C. 2000. Pigment composition of freshwater charophyceae. Aquat. Bot. 67: 117-129.

SCHIEMER F. 1979. Submerged macrophytes in the open lake. Distribution pattern, production and lonf-term changes. In: Neusiedlersee: The limnology of a shallow lake in central Europe. Löffler H. (ed.). Monogr. Biol. 37: 235-250.

SCHRÖDER R. 1987. Das Schilfstreben am Bodensee-Untersee. Beobachtungen, Untersuchungen und Gegenmassnahmen. Arch. Hydrobiol. Suppl. 76: 53-99.

SCHWARZ A.M., HAWES I., HOWARD-WILIAMS C. 1996. The role of phytosynthesis/light relationships in determining lower depth limits of *Characeae* in South Island, New Zealand lakes. Fresfwat. Biol. 35: 69-80.

SIMONS J., NAT E. 1996. Past and present distribution of stoneworts (*Characeae*) in the Netherlands. Hydrobiologia 340: 127-135.

SIMONS J., OHM M., DAALDER R., BOERS P., RIP W. 1994. Restoration of Botshol (The Netherlands) by reduction of external nutrient load: recovery of a characean community, dominated by *Chara connivens*. Hydrobiologia 275/276: 243-253.

STEINMAN A.D., MEEKER R.H., RODUSKY A.J., DAVIS W.P., HWANG S.J. 1997. Ecological properties of charophytes in a large subtropical lake. J. No. Am. Menthol. Soc. 16: 781-793.

STROSS R.G. 1989. The temporal window of germination in oospores of *Chara* (*Charophyceae*) following primary dormancy in the laboratory. New Phytol. 113: 491-495.

SŰLTEMEYER D., SCHMIDT C., FOCK H.P. 1993. Carbonic anhydrase in higher plants and aquatic microorganisms. Physiol. Pl. 88: 179-190.

SUNDBLAD K. 1990. The effects of cutting frequency on natural *Glyceria maxima* stands. Aquat. Bot. 37: 27-38.

SZCZEPAŃSKI A. 1968. Scattering of light and visibility in water of different types of lakes. Pol. Arch. Hydrobiol. 15: 51-76.

TAKATORI S., IMAHORI K. 1971. Light reaction in the control of oospore germination of *Chara delicatula*. Phycologia 10: 221-228.

TOMASZEWICZ H. 1973. The position of *Scirpo-Phragmitetum* W. Koch 1926 in systematics. Acta Soc. Bot. Pol. 42: 379-390.

TOMASZEWICZ H. 1974. Syntaxonomic position of *Hydrocharitetum morsus-ranae* van Langendonck 1935. Acta Soc. Bot. Pol. 43: 377-380.

TOMASZEWICZ H. 1977. Proposal of new syntaxonomic classification of *Myriophyllo-Nympharetum* W. Koch 1926 phytocenoses and their distribution in Poland. Acta Soc. Bot. Pol. 46: 423-436.

TREBITZ A.S., NICHOLS S.A., CARPENTER S.R., LATHROP R.C. 1993. Patterns of vegetation change in Lake Wingra following a *Myriophyllum spicatum* decline. Aquat. Bot. 46: 325-340.

VADSTRUP M., MADSEN T.M. 1995. Growth limitation of submerged aquatic macrophytes by inorganic carbon. Freshwat. Biol. 34: 411-419.

VÖGE M. 1992. Tauchuntersuchungen an der submersen Vegetation in 13 Seen Deutschlands unter besonderen Berücksichtigung der Isoetiden-vegetation. Limnologica 22: 82-96.

WADE P.M. 1990. The colonization of disturbed freshwater habitats by *Characeae*. Folia Geobot. Phytotax. 25: 275-278.

WIJCK C. van., De GROOT C.-J., GRILLAS P. 1992. The effect of anaerobic sediment on the growth of *Potamogeton pectinatus* L.: the role of organic matter, sulphide and ferrous iron. Aquat. Bot. 44: 31-49.

WIELOLETNIE ZMIANY FLORY I ROŚLINNOŚCI JEZIORA MIKOŁAJSKIEGO JAKO SKUTEK JEGO EUTROFIZACJI

STRESZCZENIE

Zanalizowano zmiany we florze litoralu oraz roślinności wodnej i szuwarowej mezotroficznego Jeziora Mikołajskiego w efekcie jego 30-letniej eutrofizacji. Stwierdzono, że strefa fitolitoralu została zredukowana z 6 do zaledwie 2 m, liczba zanurzonych gatunków makrofitów zmniejszyła się o 50% (przy czym nie pojawił się ani jeden nowy), a frekwencja większości tych, które przetrwały, spadła kilkakrotnie. Z litoralu wycofały się wszystkie gatunki z rodzaju *Chara*, *Potamogeton obtusifolius*, *P. natans*, *Hydrocharis morsus-ranae*, a dominujący na początku lat 60. mech *Fontinalis antipyretica* zachował się tylko na nielicznych stanowiskach. Istotnie zmniejszyło się także zróżnicowanie roślinności wodnej i szuwarowej, zanikło bowiem aż 12 spośród 26. zidentyfikowanych wcześniej zespołów (w tym m.in. *Nitellopsidetum obtusae*, *Charetum asperae*, *Eleocharitetum palustris* i *Typhetum angustifoliaei*), natomiast wykształciły się zaledwie 4 nowe typy zbiorowisk. Z wyjątkiem szuwaru trzcinowego zmalało bogactwo gatunkowe zbiorowisk.

W latach 90. stężenie substancji zanieczyszczających jezioro obniżyło się i wzrosła przeźroczystość wody, co jednak nie spowodowało wzrostu bogactwa florystycznego i zasięgu podwodnych łąk. Co więcej, w latach 1994--1998 z litoralu wycofał się *Potamogeton obtusifolius*, spadła frekwencja kilku innych gatunków i jedynie *P. perfoliatus* istotnie zwiększył swój areał. Nie oznacza to, że rekolonizacja litoralu przez makrofity nie nastąpi w warunkach dalszego spadku trofii jeziora, proces ten prawdopodobnie będzie jednak bardzo powolny (por. Meier i in. 1990; Lauridsen i in. 1994; Simons i in. 1994).

SŁOWA KLUCZOWE: podwodne makrofity, różnorodność gatunkowa, zbiorowiska roślin wodnych, zbiorowiska szuwarowe, eutrofizacja.