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ECOLOGY OF THE EULITTORAL ZONE OF LAKES

(Ekol. Pol. 20: 637-732). Environmental conditions and biological processes in the eulittoral - intermediate zone between lake and surrounding land were analysed. Investigations were carried out on 16 lakes (eutrophic, mesotrophic and dystrophic) of Masurian Lakeland in northern Poland. The range of eulittoral depending on the water level fluctuation and configuration of shore terrace, is to a considerable extent modified by the erosion and accumulation processes. Allochthonous matter (of lake and terrestrial origin) and autochthonous production are the sources of organic matter in the eulittoral. The decomposition rate of this kind of matter was analysed. The role of the eulittoral in the functioning of lake system was discussed.

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I. INTRODUCTION

Hydrobiological literature provides many suggestions for the division of the shore region of lakes, and several manuals present a collection of terms and comparisons of different classifications (Naumann 1931, Zernov 1949, Welch 1952, Hutchinson 1967 and others). The division of the shore region proposed in this paper (Fig. 1), is based on the classic Forel division (Lityński 1952) followed by many present-day limnologists.

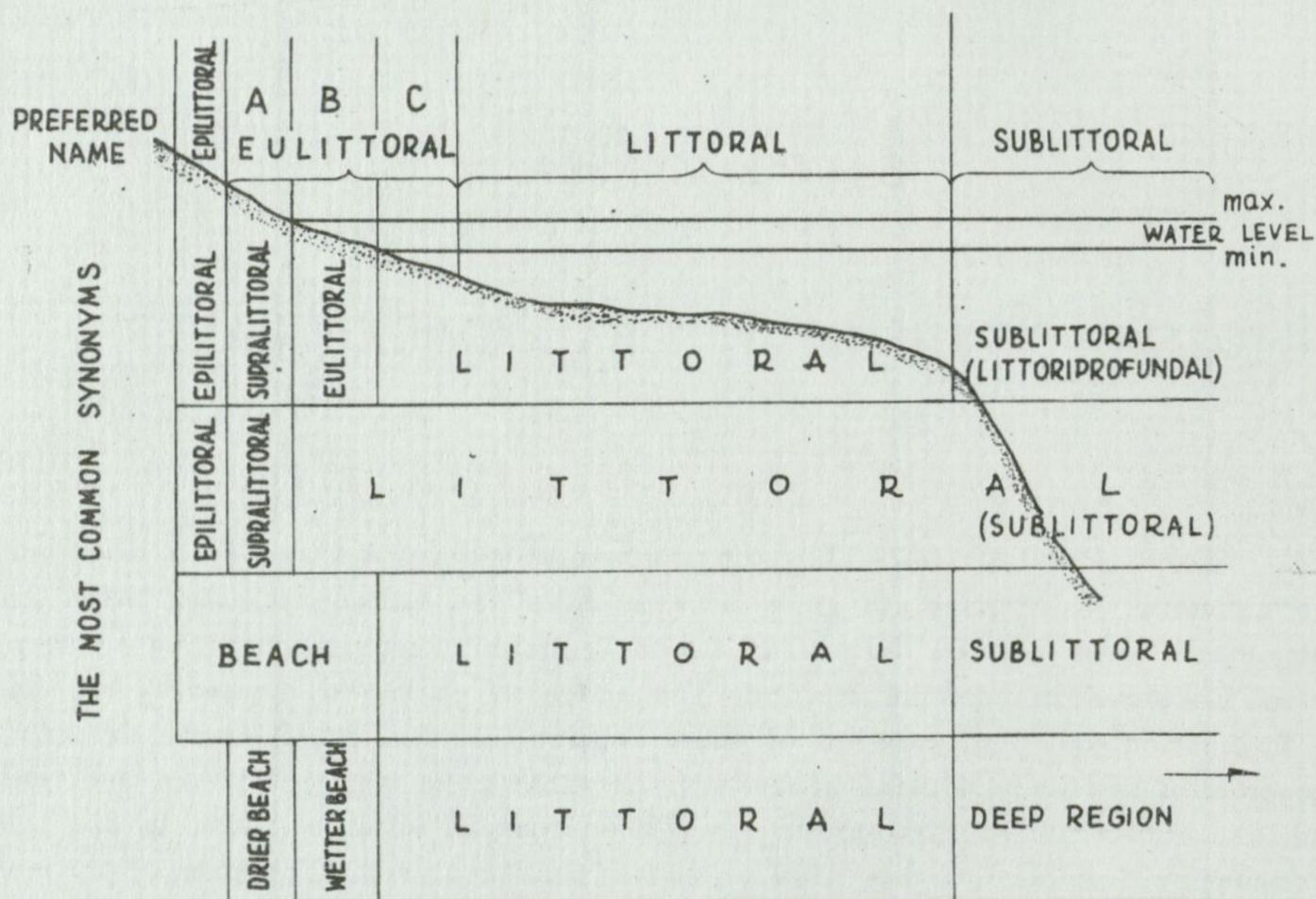


Fig. 1. Division of the shore region of lakes

The following zones can be distinguished in the shore region of lakes:

1. Epilittoral – part of land adjoining the water body, entirely above water level and never splashed by the waves;

2. Eulittoral – transitional zone between the land surrounding lake and littoral divided into:

A. Emergent part of eulittoral – entirely above water level, even at the highest water, periodically splashed by waves;

B. Flooded eulittoral – under the water at the highest water level. Its boundaries are determined by the highest and lowest seasonal water levels;

C. Submerged part of eulittoral – constantly submerged zone, even at the lowest water level, directly adjoining the previous one. At the lowest water level this zone is intermittently uncovered by the waves;

3. Littoral – constantly submerged shoal area with rooted vegetation. It consists of the abrasion and accumulation regions. The shoal slope is regarded as sublittoral.

Therefore, the eulittoral is the border zone between lake and surrounding land. It includes the area contained between the highest and lowest seasonal water levels and also the neighbouring areas, which are being splashed or exposed during wave action. The range of this zone is conditioned by fluctuations of water level and the formation of shore terrace.

In many hydrobiological papers in English the term eulittoral is used exclusively to determine the zone contained between the highest and lowest water level (Welch 1952, Hutchinson 1967 and others). In this paper the eulittoral includes also the neighbouring zones exposed to the action of waves as a distinct ecological zone. Such division of the littoral zone corresponds to Forel's classic division and divisions of the shore zone used in several German, French and Russian limnology handbooks.

The border zone between land and water has been little studied compared with typical terrestrial and aquatic habitats. Relatively speaking the marine eulittorals have been given the greatest attention. Many of these habitats have already received monographic treatment. Examples are the work of Lewis (1964) on the ecology of rocky shores and of Heydemann (1967) on the ecology of meadows in the zone of ebb and flow of marine tides.

As regards the inland waters there has been no general approach to the subject. Only sandy beaches periodically flooded with water have been elaborated in greater detail. Studies of this habitat were initiated by Zasuchin, Kabanov and Neizvestnova (1927), and were continued and advanced by Wiszniewski (papers published in the years 1932–1947). Other types of eulittoral have not been objects of hydrobiological investigations; scarce information about these habitats may be found in several papers on systematics and biology of different plant and animal groups and in limnological monographic investigations of various water bodies (Borner 1921 – St. Moritzer Lake, Berg 1938 – Lake Esrom, Entz and Sebestyen 1946 – Balaton, Ökland 1964 – Lake Borrevann and others).

This study concerns:

- the characteristics of the hydrological and physico-chemical conditions in the lake eulittoral;
- analysis of the regularity of the occurrence of communities of plants and animals;

- estimation of production and decomposition processes;
- analysis of the rôle of the eulittoral in the functioning of lake ecosystem.

II. SITES

16 lakes of the Masurian Lakeland were examined. Systematic quantitative research was conducted in 5 lakes: Flosek, Mikołajskie, Śniardwy, Tałtowisko and Warniak (Tab. I).

Hydrographical characteristics of these lakes are based on the following papers: Olszewski and Paschalski (1959), Szostak et al. (1961), Mikulski (1966), Szostak (1967), Jezierska (unpublished).

Mikołajskie Lake, examined in the years 1963–1970 was the main object of studies, and also lake Warniak was examined in the years 1967–1970. In these water bodies hydrological, physico-chemical and biological studies of various eulittoral types were conducted, taking into consideration their variation during the annual cycle.

To a smaller extent, studies were conducted on 11 lakes of Węgorzewo district (Tab. I). These lakes have been characterised by Bernatowicz (1960), Kondracki and Szostak (1960) and Patalas (1960a, b, c, d).

III. METHODS

1) Hydrographical studies. For the general hydrographical characteristics of the lakes and their direct drainage basin data from the National Institute for Hydrology and Meteorology were used. Independent measurements at chosen stations were made. Changes of water level, duration and thickness of ice cover, phenomena of shore erosion and accumulation, intensity of wave action and currents, were determined. Regular bathymetrical measurements were made at all stations. An analysis of wave action was based on point measurements of direction, height and wave velocity (measurements with a vertical marking pole). Wave action intensity was also estimated on the basis of an analysis of wind direction and velocity.

To determine the water flow in the eulittoral fluorescein solution, detectable in very small concentrations, was used. The method was as follows: 1) The flow rate and direction of currents – a drop of fluorescein solution was added to the water in eulittoral and its propagation was observed, measuring the time with a stopwatch; 2) Water filtration through various barriers differentiating the habitat (detritus or plant heaps and the like) – fluorescein was added to isolated part of eulittoral and then its appearance and distribution in the neighbouring habitats was observed.

Limnological characteristics of Masurian lakes studied
A – lakes intensively studied, *B* – lakes studied to a smaller extent

Tab. I

Lake	Surface area (ha)	Depth (m)		Development of shore line	Area of littoral in percentage of total lake surface*	Limnological type	
		mean	maximum				
<i>A</i>	Flosek	4	3.0	8.0	1.1	~ 9	dystrophic
	Mikołajskie	460	11.0	27.8	1.7	19	eutrophic
	Śniardwy	10970	5.9	23.4	2.2	34	eutrophic
	Tałowisko	327	14.0	39.5	1.8	29	b-mesotrophic
	Warniak	38	1.2	3.7	1.1	~100	eutrophic
<i>B</i>	Czarna Kuta	25	1.3	3.6	1.5	10	eutrophic
	Czarna Woda	1	2.2	4.0	1.1	~10	dystrophic
	Głęboka Kuta	18	7.6	21.5	1.1	30	eutrophic
	Gołdopiwo	860	12.6	26.9	1.4	8	b-mesotrophic
	Krzywa Kuta	123	4.0	25.0	2.5	36	eutrophic
	Pozezdrze	124	2.2	4.0	1.3	30	eutrophic
	Przyleśne	26	1.0	1.5	1.3	100	eutrophic
	Smolak	5	2.4	5.1	1.5	~ 7	dystrophic
	Święcajty	814	10.5	28.0	1.7	8	b-mesotrophic
	Wilkus	94	1.7	5.6	2.0	42	eutrophic
	Żabinki	41	10.6	42.5	1.0	8	eutrophic

*The area of littoral in dystrophic lakes (Flosek, Czarna Woda and Smolak) is difficult to determine. The area, where macrophytes are found as well as periphyton (in this environment overgrowing mainly the tree branches submerged in water) is recognised as the littoral zone.

2) Physico-chemical studies of water and sediments. For light measurements a selenium cell registering within the range 420–730 nm, maximal sensitivity at 550 nm, was used. The apparatus could be used for underwater and above water measurements in 4 ranges: 100, 1000, 10000 and 100000 lux. Each measurement consisted of 10 readings at 1 min intervals.

The temperature was determined using mercury thermometer, maximum and minimum, and thermistor thermometers.

Samples of sediments were taken in all types of eu littoral using a metal cylinder, 10 cm² in cross-section. Also, in the emergent eu littoral, samples were taken uncovering successive layers of a surface of 200 cm² delimited by a plastic frame. In the submerged eu littoral a Lastočka sampler with a cross-section of 10 cm² and a plastic cylinder 500 cm² in cross-section were used. In sediments the proportions of detritus of allochthonous and autochthonous origin were analysed as well as the content of water and organic matter, and the calorific value. Hydration of samples was determined by comparing the sample weight immediately after sampling and after drying at 105°C to constant weight. Organic matter content in dry weight was estimated by ashing in electric furnace for 5 hr at 550°C. Time and temperature of ashing were chosen according to the methodical research on this subject by Rybak (1969). The calorific value was determined on the basis of direct measurements with a Polish adiabatic calorimeter type KL 3.

Samples for chemical analyses of water were taken from the depth above 20 cm with a 1-litre Patalas sampler. For sampling water at small depths (up to 20 cm) and in winter, from under the ice, modification of Vereščagin's (1927) apparatus was used (Fig. 2).

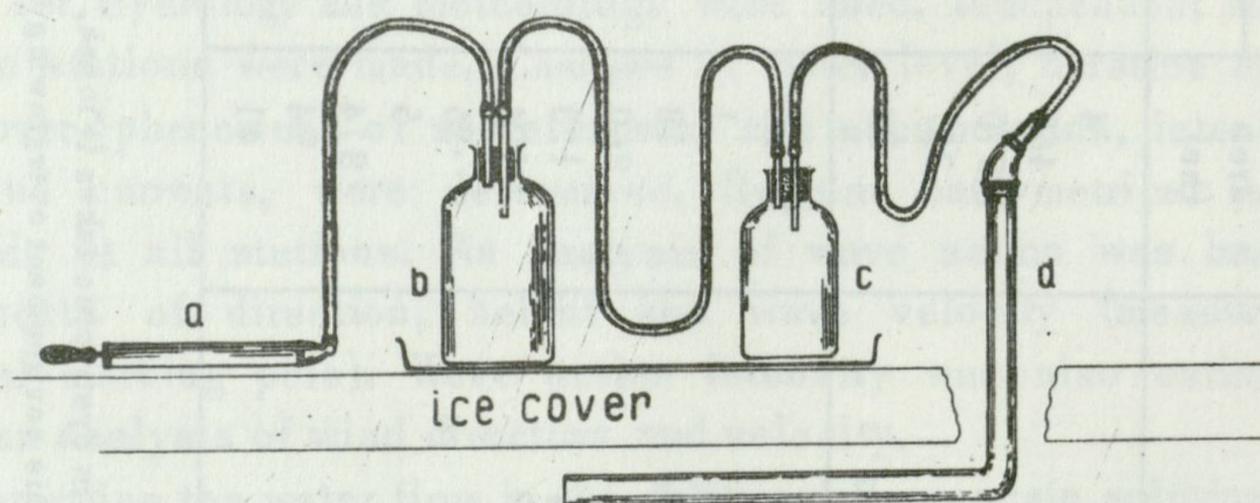


Fig. 2. Apparatus for sampling water from small depths and from under ice
a — suction pump, b, c — oxygen bottles, d — plastic tube, diameter 1 cm, with a screen at the end

Samples of interstitial water in the emergent part of eu littoral were taken according to the method described by Wiszniewski (1934) — careful water suction using a pipette supported on bolting-cloth placed on the top of sediments.

Chemical composition of water was analysed using the classic methods (Werešćagin 1932, with some modification by Just and Hermanowicz 1964 and Standard Methods (1960):

– dissolved oxygen (Winkler's method) – analysis of the entire contents of calibrated bottles, pH (electrometrically), conductance (electric conductometer); in $\mu\text{S } 20^\circ\text{C}$;

– calcium, sodium and potassium (flame photometer);

– phosphates, total iron, nitrates, nitrites, ammonia (colorometrically);

– total hardness (versenate method), magnesium (calculations on the basis of analyses of total hardness and calcium);

– organic nitrogen (Kjeldahl's method), oxygen demand (permanganate in acid medium);

– colour (in platinum-cobalt scale), chlorides (Mohr's method).

The analyses were made in the Hydrochemical Laboratory of the Hydrobiological Station of the Institute of Ecology, Polish Academy of Sciences at Miłkołajki.

3) Biological studies. Plant communities and primary production. The species composition and biomass of macrophytes were determined, and in the case of helophytes also their numbers. Quantitative samples of plants were taken in profiles from the shore deep into the lake. Each sample was the macrophytes from 0.25 m^2 . Fresh and dry weight were determined as well as the organic matter content and calorific value of the plants. Net primary production of macrophytes was estimated on the basis of maximal biomass taking into account biomass losses before the period of the maximum biomass due to wave action and grazing of fauna. These calculations were based on an analysis of the amount of plants accumulating on shores as a result of wave action, and on an estimation of the reduction of plant mass by grazing and mining by fauna (Soszka, Urban unpublished data). In the case of algae the biomass and primary production were measured. The species was determined only for the dominant forms. The gross primary production of algae was measured using the oxygen method of dark and light bottles. Calibrated bottles of a capacity about 150 ml were used. Samples were exposed in the lake for 24 hr. For net primary production calculation of respiration intensity of algae in relation to the rate of gross production was taken into account. This required literature data (Ščerbakov 1953, Elster 1963, Thomas 1963), and measurements conducted during mass monospecific appearances when it is possible to isolate the producers from the entire community. Plankton samples for photosynthesis analyses were taken with the appropriate apparatus as used for sampling water for chemical analyses (described above). In case of attached (periphytic) algae the photosynthesis of material separated from the substrate was determined. It was established previously, that the isolation of periphyton from the substrate

does not cause essential changes in primary production rate (Pieczyńska unpublished data).

Biomass and primary production of algae were referred to surface unit of lake, water volume, substrate surface (in the instance of attached algae) and algal biomass (in instances of mass appearances, when the determination of the biomass of producers was possible). In the latter case the algae separated from other community components, were weighed on an analytical balance. The size of substrate, from which the attached algae were separated, was estimated by linear measurements and comparisons with simple geometric solids. In all habitats the amount of substrate available for colonization was determined. This problem has been discussed in a paper by Pieczyńska (1968).

Animal communities. Species composition, density and biomass of macroinvertebrates and microfauna were measured. Quantitative samples for macroinvertebrates were taken in the same manner as sediment samples. This material was preserved with formalin. Microfauna samples were taken with a glass tube 0.9 cm^2 in cross-section. Fresh samples were analysed. Samples were sorted without sieving. In the case of macroinvertebrates the biomass of particular groups of organisms was determined on an analytical balance.

4) Decomposition. The intensity of decomposition processes in the eulittoral was examined by measuring the weight loss of various kinds of material placed in nylon bags and exposed in natural conditions. In the case of macrophytes and parts of terrestrial plants falling to the water, weighed portions were placed in nylon mesh bags measuring $35 \times 25\text{ cm}$. The mesh sizes were 0.25 , 4.0 and 20.0 mm^2 . Bags with plants were distributed in various eulittoral habitats and left for 1 to 60 days, most frequently for 10 days. The plants were weighed before being placed in bags to determine their fresh weight, parallel plants were collected from the same habitat to analyse their water content. After the exposure the dry weight of the plant remains in the bags was determined.

Decomposition rate of algae was examined on the basis of losses of material exposed in nylon mesh bags measuring $10 \times 10\text{ cm}$ and mesh size 0.25 mm^2 .

The decomposition intensity in the eulittoral was also estimated on the basis of an analysis of oxygen consumption by detritus. Weighed amounts of detritus were placed in bottles with well oxygenated water and exposed for 10 hr. in the darkness at 20°C , then the oxygen content in bottle was determined by Winkler's method.

5) Accumulated material of lake and terrestrial origin. Material of terrestrial origin. For quantitative estimation of litter fall, containers 60 cm high and 30 cm^2 in cross-section (Fig. 3) were placed at different distances from the shore line (in the direction of water and land). Series of 20 con-

tainers were placed at several stations in the lake, having different vegetation cover and exposure to wind. Containers were emptied every 5 days. The composition of the falling material (leaves, seeds, bark, branches, flowers), dry weight, organic matter content and calorific value, were determined.

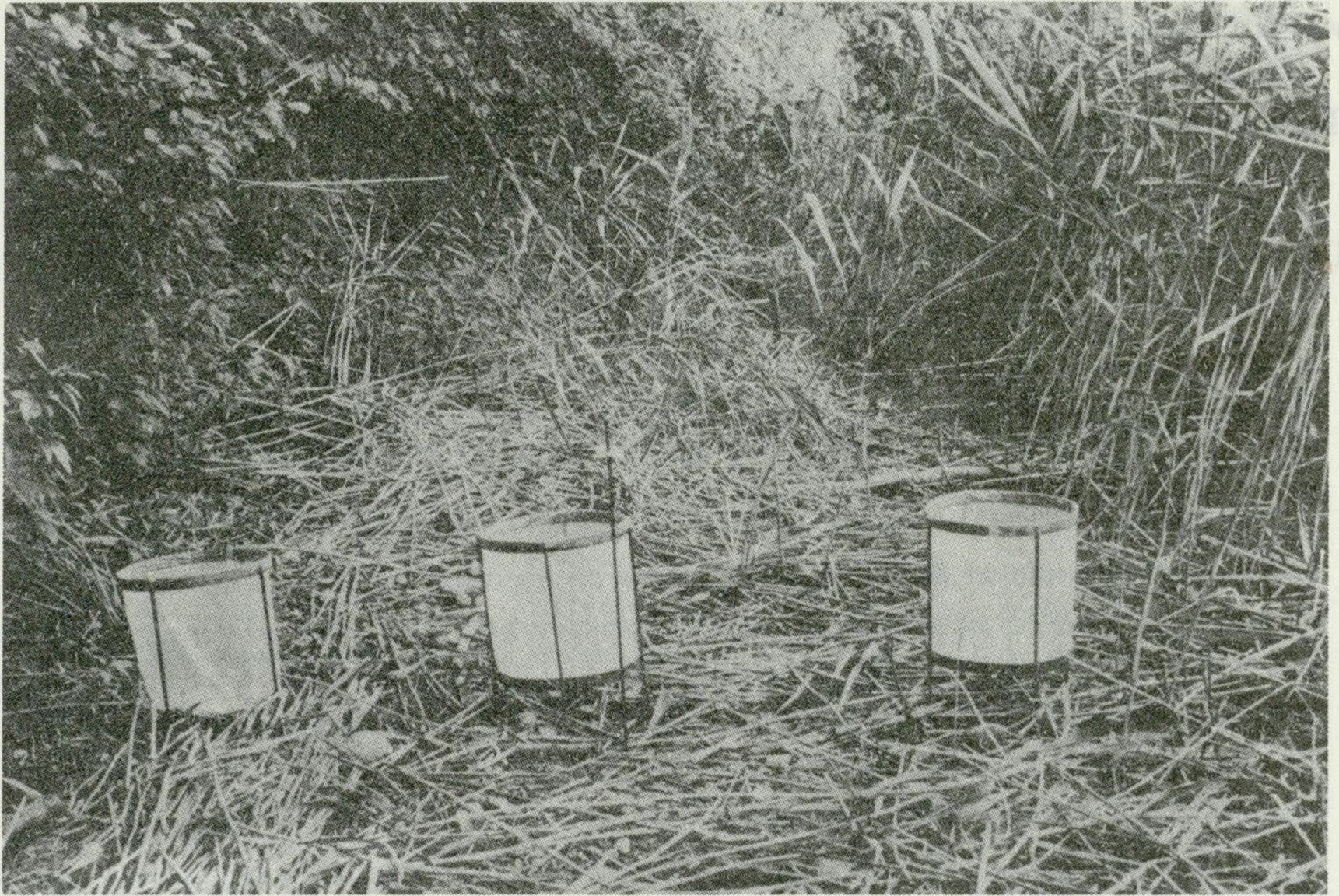


Fig. 3. Containers for collecting leaf litter

The soil eroded due to wave action was determined. The amount of soil eroded from part of the shore line 0.5 m long in 24 hr. was treated as one sample. On the shore, on the border of land and water, plastic boards were driven horizontally to the depth of 30 cm from the soil surface. Some sites were isolated from wave action by means of plastic covered metal frame, 0.7x0.5 m, others were left exposed. Soil losses above the boards at the exposed sites were compared with the protected sites. Other kinds of material of terrestrial origin (municipal sewage, material flowing in from the drainage basin) were calculated using data from the National Institute for Hydrology and Meteorology and the Department of Water Economics and Air Protection of the District Council at Mrągowo.

Material of lake origin. All kinds of material accumulating on the shores were quantitatively analysed (macrophytes, planktonic and periphytic organisms, macroinvertebrates, detritus of various origin). Each time the material was

collected from an area 15 m long and 2 m wide, 1 m from the shore line in the direction of land and water, except that material accumulating on the shore line itself was sampled separately. In the case of macrophytes fragments of plants floating on water up to 5 m from the shore line, were also sampled. In the laboratory the material was sorted, identified and weighed, and dry weight, organic matter content and calorific value were determined.

Together with this research several field experiments were conducted. They will be discussed in the following chapters.

IV. HYDROGRAPHICAL, PHYSICO-CHEMICAL AND BIOLOGICAL CHARACTERISTICS OF THE LAKE EULITTORAL

1. Range and differentiation of the eulittoral zone

The shore zone of water bodies is characterised by great variety. This variety in the case of discussed lakes was pointed out by Bernatowicz (1960), Kondracki and Szostak (1960), Bernatowicz and Pieczyńska (1965), Bernatowicz, Pieczyńska and Radziej (1968) and Bernatowicz (1969). Bernatowicz and Zachwieja (1966) distinguished 10 types of littoral on the basis of studies on microbathymetry, macrophytes, mechanical composition of sediments, and chemistry of water and bottom deposits in the littoral of the lakes of Masurian and Suwałki Lakelands. These littoral types formed a sequence from litholittoral and psammolittoral, most frequently found in oligotrophic, mesotrophic and large eutrophic lakes, to marsh phytolittoral typical of small, very shallow and muddy water bodies, and atrophic phytolittoral associated with small, mid-forest lakes. The authors point out that within one lake, several, even very different, types of littoral may occur.

The eulittoral is much more differentiated than littoral. This zone is characterised by a variable range depending on water level fluctuations and the configuration of the shore terrace and areas adjoining the lake. Frequently in one lake we may find sites with a very broad eulittoral, and others where this zone has a very small range.

In order to illustrate this variation the area contained between the shore line at the highest and lowest water level (flooded eulittoral) in four lakes was compared for 1967 (Tab. II). To determine the variation within the water body, the shore line of each was divided into 500 m sections, and within these areas the surface periodically flooding and drying up during one year was estimated. The calculations were made by drawing profiles according to maps and measurements of water level fluctuations, and on the basis of direct field measurements of the shifting the shore line of the water body. The material

compared in Table II points to a very great variation of the area occupied by the discussed zone not only between the compared lakes, but also within one water body. The range of this zone is the greatest and most variable in lake Śniardwy. In this water body, with extensive shore shallows, the shore line moves on the average 53 m during the discussed year, and maximum 296 m. But at the same time at some sites the shore line moves scarcely 1.9 m. The smallest range of the flooded eulittorals is observed in lake Warniak. This is largely due to the considerably smaller water level fluctuations. Also in this case the variation within the lake is considerable. In lakes Tałtowisko and Mikołajskie, despite the same amplitude of water level fluctuations as in lake Śniardwy, the movements of shore line during the year are much smaller, but considerable variations are observed in particular parts of each lake (Tab. II).

Korolec (1968) also points to a considerable variation of shore region in Mikołajskie Lake. She found that in places where the lake shores are low and flat the shore line moves about 100 m within a year. During the present studies of Mikołajskie Lake maximum annual movements of shore line attaining up to as much as 150 m were observed (in 1964).

The area contained between the shore line at the highest and lowest annual water level is only part of the eulittoral zone. Eulittoral also includes the neighbouring areas, splashed or exposed during wave action (emergent and submerged parts of eulittoral). These areas, difficult to estimate numerically on the scale of

The area of the zone contained between the highest and the lowest water levels in four Masurian lakes in 1967

Tab. II

Lakes	Yearly difference in water level (cm)	The distance between the shore lines for the highest and the lowest water levels (m)		The area between the shore lines for the highest and the lowest water levels	
		average	range of variations	ha	per cent of total lake surface
Mikołajskie	41	12	0.8-103	16	3.5
Śniardwy	41	53	1.9-296	441	4.0
Tałtowisko	41	15	1.1-71	17	5.2
Warniak	28	8	1.2-16	2	5.3

the entire lake, are on the average 10% of the previously discussed area of flooded eulittoral. When taking them into consideration as well it was found that the range of the eulittoral zone in 1967 in the lakes listed in Table II ranges from 4% (Mikołajskie Lake) to 6% of lake surface (lake Warniak).

Changes in the range of the eulittoral vary in different years, depending on water level fluctuations.

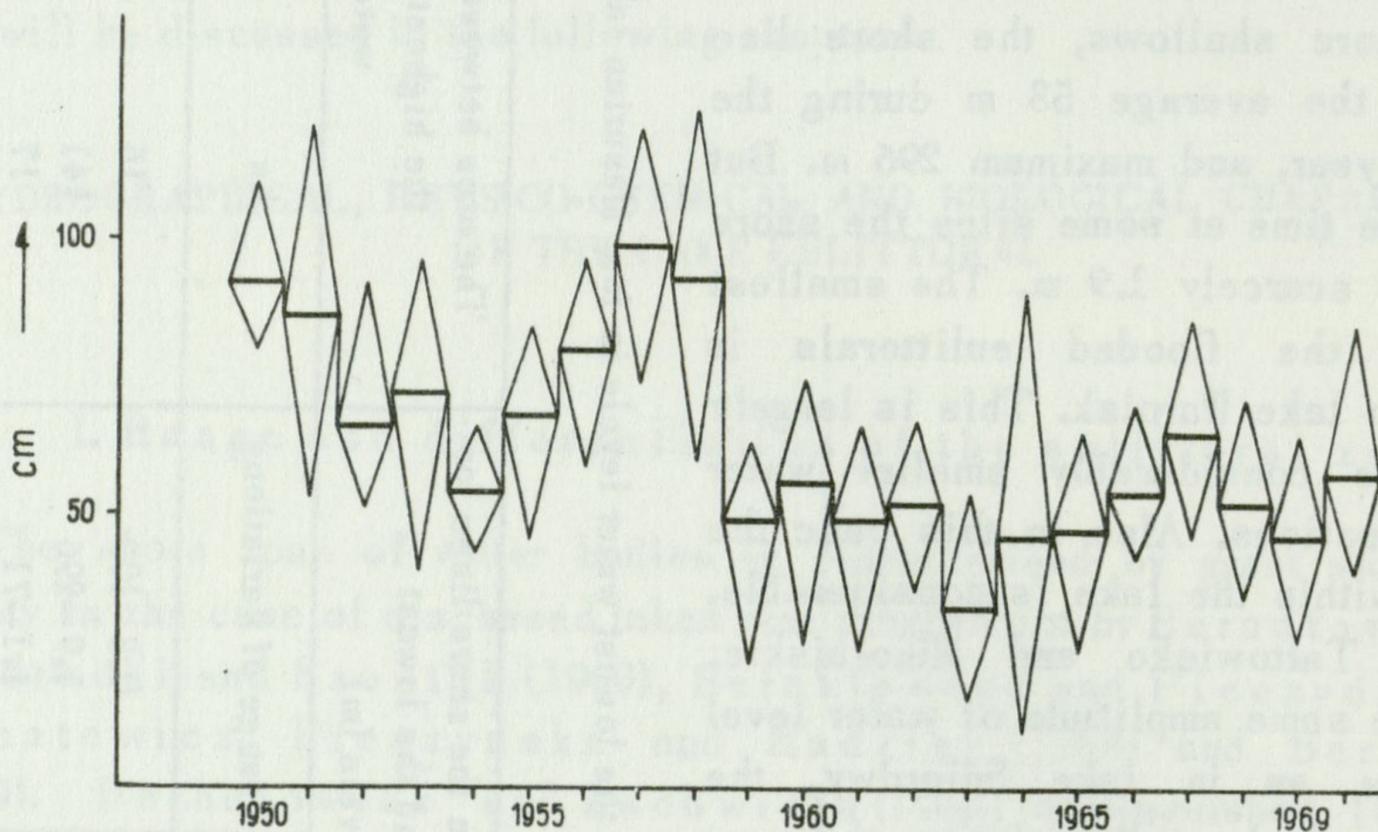


Fig. 4. Changes of water level in Mikołajskie Lake in 1950–1970, annual averages and range of variations

(Prepared using data from the National Institute for Hydrology and Meteorology)

Taking into account the water level fluctuations, various types of lakes may be distinguished. According to Mikulski (1965) the amplitude of water level fluctuations in Poland, in water bodies without the direct interference of man, has an average for several years within the 30–50 cm. Considerable part of lakes analysed in present study is characterised by considerably greater changes of water level. Lakes Tałtowisko, Mikołajskie and Śniardwy, belonging to the complex of Great Masurian Lakes, are a group of flow lakes joined together and partly regulated by a system of channels and locks. Great Masurian Lakes have very irregular water levels. Mikulski (1966) points to obvious periods of regression and violent rise of water level in these lakes in the last century. During the last twenty years the water level in these lakes has been gradually decreasing. The data of the National Institute for Hydrology and Meteorology allowed comparison of the mean annual and maximum and minimum water levels in Mikołajskie Lake in the years 1950–1970 (Fig. 4). These data illustrate also the water level fluctuations in lakes Tałtowisko and Śniardwy connected with Mikołajskie Lake. In the compared period the absolute difference

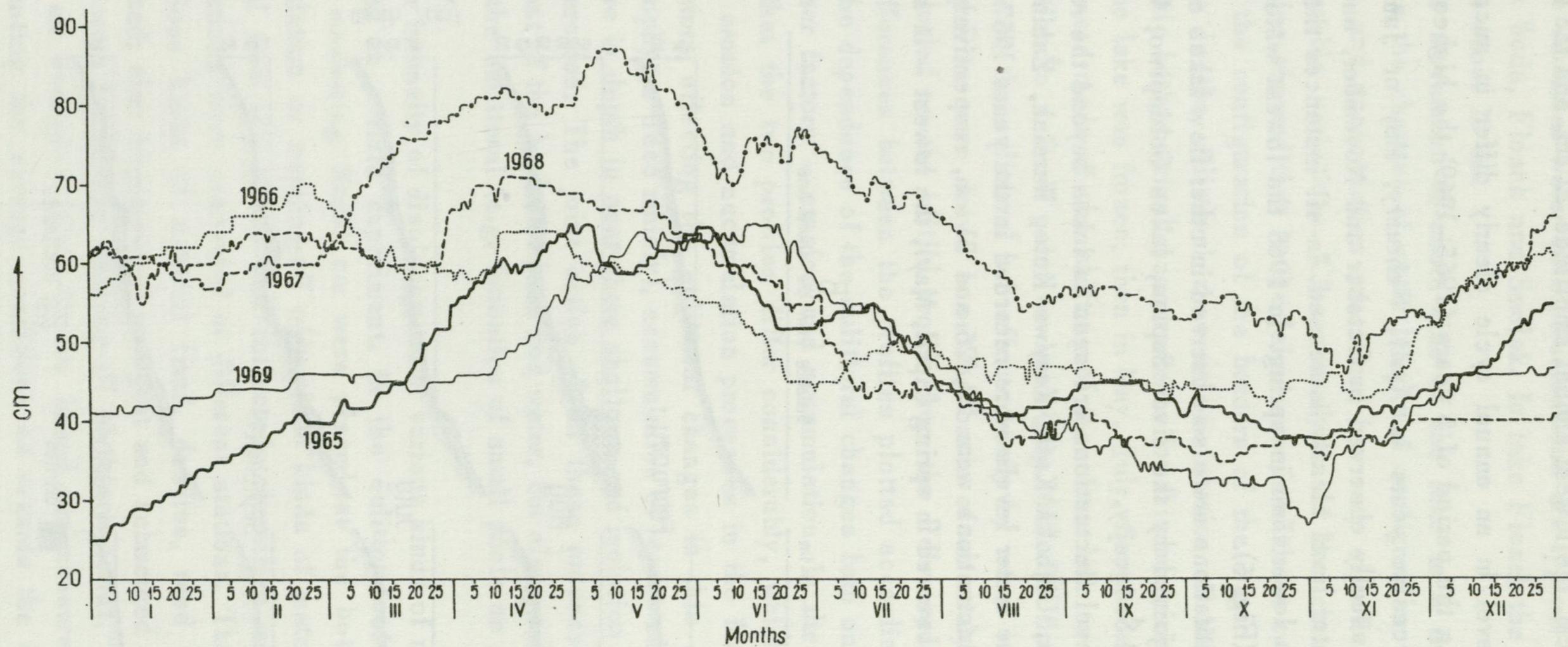


Fig. 5. Changes of water level in Mikołajskie Lake in 1965–1969
(Prepared using data from the National Institute for Hydrology and Meteorology)

of water levels was 114 cm, the lowest annual amplitude 22 cm, and the highest one 80 cm (Fig. 4).

Changes in water level in an annual cycle clearly differ in successive years (Fig. 5). Examining the period of 5 years (1965–1969) the highest water level was noted in successive years in April, February, May or June. The lowest water level was usually observed in October and November, and after them in December the water level clearly increased. In all instances the water level in winter was much lower than in spring. In 1965 the lowest water level was observed in January (Fig. 5).

Great water level fluctuations are also observed in other flow lakes examined, especially in those joined by the river Sapina, lakes Gołdopiwo, Wilkus, Przyleśne, Pozezdrze and Świącajty.

Much smaller water level fluctuations are seen in lakes beyond the route of main flows (Czarna Kuta, Głęboka Kuta, Krzywa Kuta, Warniak, Żabinki). In lake Warniak, in which the water levels were recorded in the years 1967–1969, the annual water level fluctuations were 28, 26 and 31 cm, respectively. The highest water level was observed in spring (April, May), the lowest – in summer (July, August).

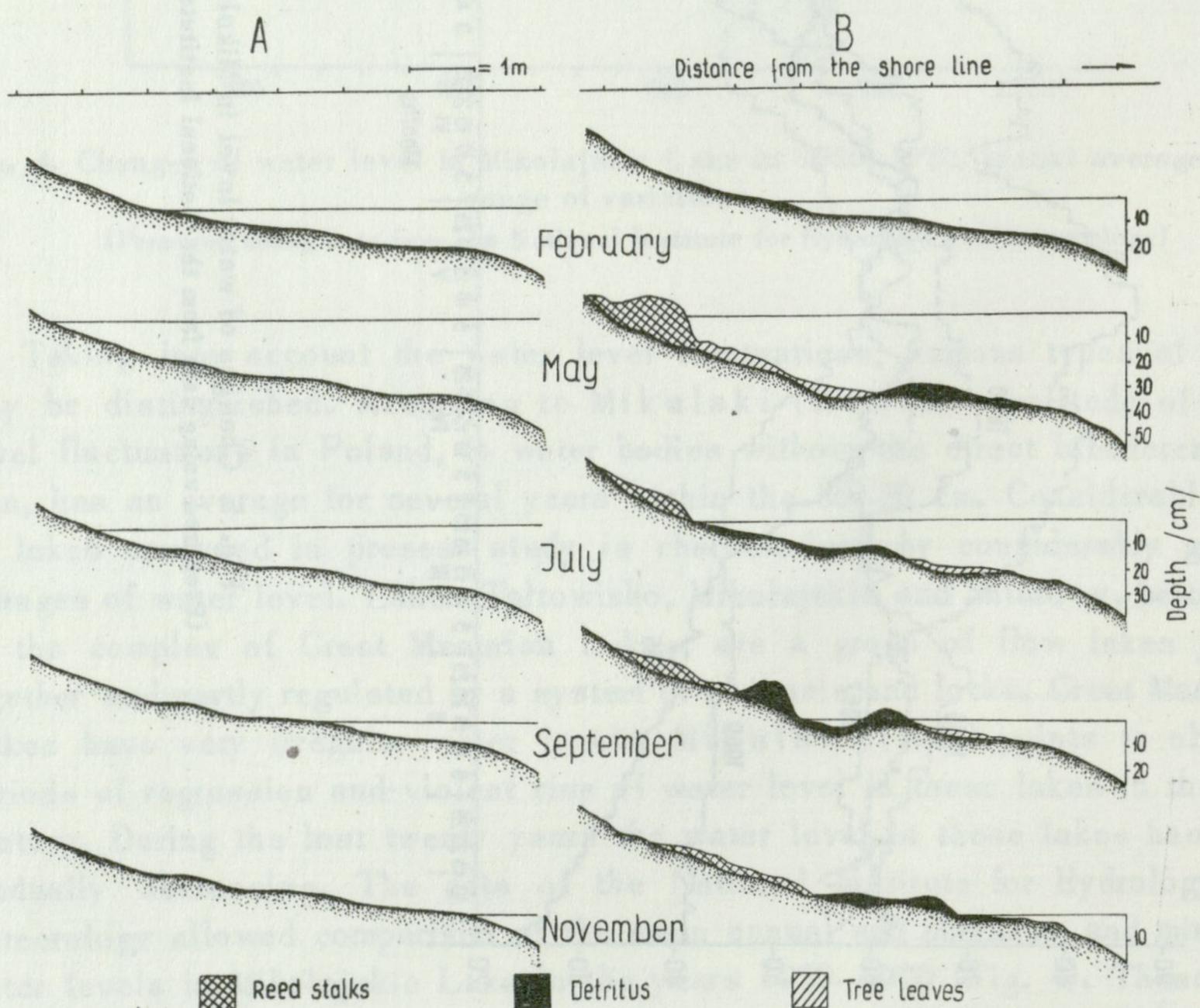


Fig. 6. Eulittoral change at one station of Mikołajskie Lake in 1967

The smallest water level fluctuations are typical of lakes without outflow: Czarna Woda, Flosek and Smolak. In lake Flosek the annual amplitude of water level is about 10 cm.

The movement of shore line of the lake is a resultant of many factors. Besides the changes of water level and configuration of the shore terrace, the erosion and accumulation processes are very significant and subject to quite considerable variations. Closer analysis of the changes in formation of the shore line showed that in the lakes examined these two last factors frequently decide the configuration of the borders of the water body. Figure 6 presents changes in the eulittoral zone at one station of Mikołajskie Lake in 1967. The basic bathymetrical measurements for this analysis were made in February, when the lake was frozen; then in May, July, September and November measurements were made of the shifting of the shore line and eulittoral configuration in relation to a fixed point on land (Fig. 6B). To find out to what extent the changes in the eulittoral are affected only by water level fluctuations, theoretical profiles were drawn – on the basis of an analysis of changes of water level plotted on the initial profile from the February measurements (Fig. 6A). The differences between the profiles plotted according to these two methods prove the dependence of the eulittoral changes both on water level fluctuations and other factors – erosion and accumulation. In the example studied it was found that the two profiles differ considerably, which points to the decisive rôle of erosion and accumulation processes in the formation of the eulittoral.

Factors affecting the eulittoral changes in this case were: accumulation of macrophytes (reed mainly), accumulation of leaves of lake-side trees (causing decrease in depth in near shore shallows and isolation of part of eulittoral) and shore erosion. The joint action of all these processes decides not only the movement of the border of land and water, but also produces some modifications within the eulittoral (e.g. formation of small pools as observed in September – Fig. 6).

The intensity of displacement of various kinds of material in eulittoral was analysed in a field experiment. In the eulittoral of Mikołajskie Lake glass plates measuring 20x50 cm were placed at the bottom, and every day the accumulation or washing-off of various kinds of material were analysed. The material from the plates was collected, classified and weighed. 12 series of observations were conducted at different stations. The intensive accumulation of various kinds of material (mud, detritus, reed leaves and tree leaves dominated; also fragments of emergent and submerged macrophytes and mollusc shells were found) and washing-off of this material, were observed. The data given as examples (Fig. 7) are based on measurements made in habitats representing the average conditions as regards the exposure to wave action in the habitat examined. In habitats more exposed to waves this process is

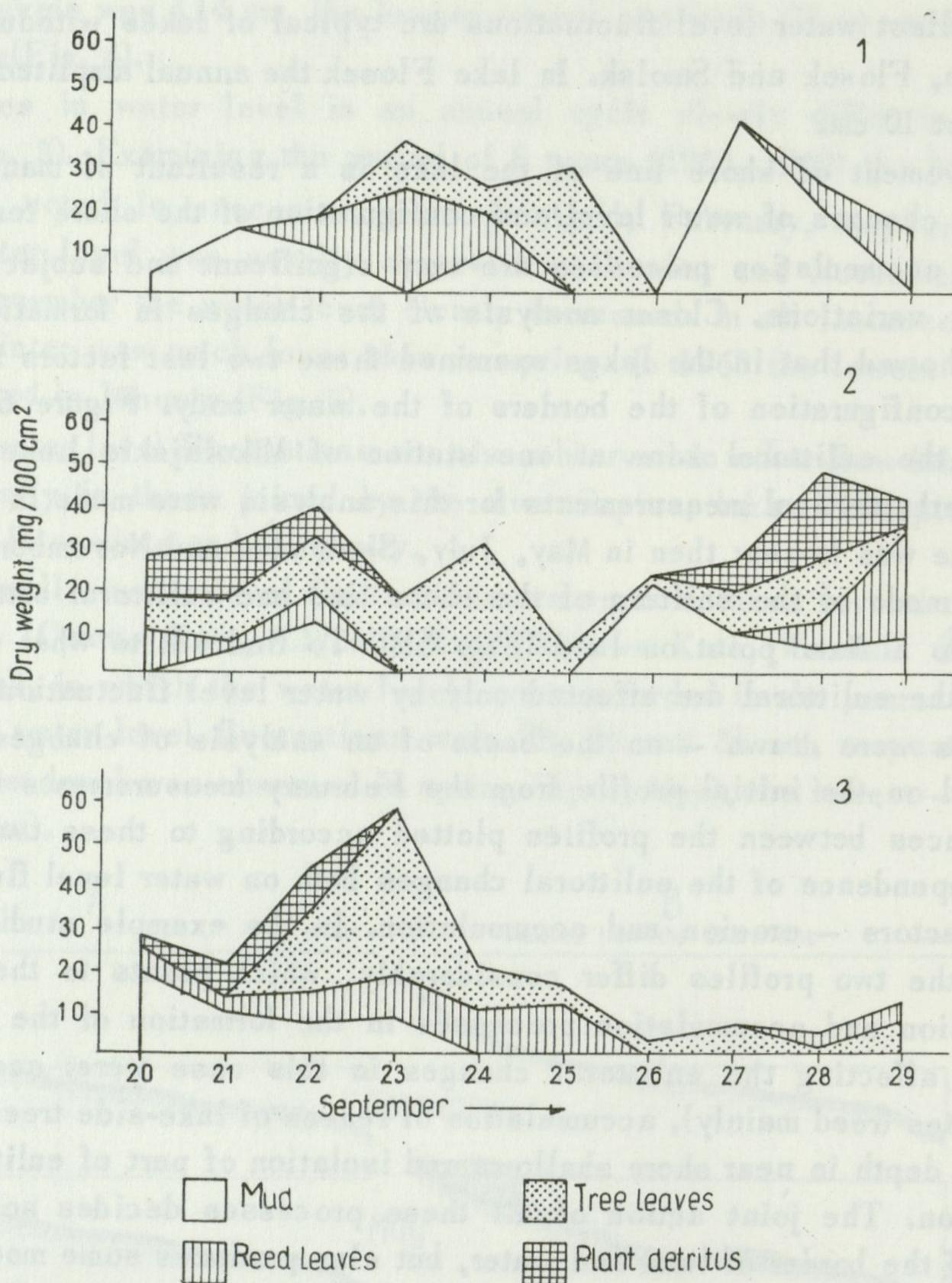


Fig. 7. Movements of sediments in the eulittoral of Mikołajskie Lake
 Changes in the abundance and composition of material collected on glass plates lying on the
 bottom
 1-3 - stations

more intense, and of much lesser significance in sheltered bays. Similar conclusions on the great displacement variability of sediments in the littoral shallows were reached in the studies by Jopkiewicz (1971) carried out on Mikołajskie Lake, some even at the same stations.

The material accumulating on the shores frequently causes, as already discussed (Fig. 6), the separation of part of the eulittoral. Thus small lake-side water bodies are formed, partly separated from the lake. The extent of this separation was analysed according to the method already described with fluorescein solution. 600 measurements were made in lakes Mikołajskie and

Warniak. More than 90% of small pool habitats, periodically separated from the lake, were connected with the lake as the water filtered through the barrier. In 20% of instances apart from solutions small suspensions also penetrated the barrier. In 80% of instances the water flow ran from the lake-side pool to the lake. Small lake-side pools, which were due to accumulation of the vegetation on shores, lasted from a few days up to two months; but not usually longer than two weeks. After that time, as a result of changes in water level, they dried up (at lowering of water level) or joined the lake (at higher water level than the height of the barrier). Alternatively, due to wave action, the barrier was destroyed. Small lake-side pools from tens of cm^2 to tens of m^2 in area, partly separated from the lake, were observed in all examined lakes and they are an important element differentiating the eulittoral.

Taking into consideration the eulittoral range and the factors modifying it in all the lakes studied the following conclusions can be reached:

1) Stony and sandy eulittorals, devoid of vegetation, play a small part in these lakes. They are most frequent in large water bodies with strong wave action (Gołdopiwo, Śniardwy, Święcajty). In all lakes macrophytes are important factors differentiating the eulittoral zone;

2) The rôle of erosion and accumulation processes in the formation of the eulittoral zone depends on the type of substrate and extent of exposure to wave action. In sheltered places with hard substrates, separated from the central part of littoral, the changes in shore configuration are almost exclusively conditioned by the water level fluctuations and the morphological structure of the shore terrace. In habitats exposed to waves, shore erosion and accumulation processes are of considerable significance. Steep shores and poorly developed shore terrace favour erosion processes. In these habitats the material from the land or brought by waves does not accumulate but is transferred to further parts of the lake. This type of eulittoral is rarely found in the examined water bodies – most frequently in lakes Gołdopiwo and Śniardwy. Wide shore terrace and differentiated shore lines favour the accumulation processes. Accumulation of various kinds of material is observed in all the lakes studied over the greater part of the eulittoral;

3) The eulittoral has the greatest range and differentiation in large post-glacial lakes with vast shore terrace, differentiated shore lines and considerable water level fluctuations (Gołdopiwo, Śniardwy, Święcajty);

4) Dystrophic lakes, despite the small level fluctuations, usually have an extensive eulittoral due to their low and wet shores. This zone is little differentiated because the shore line is uniform (Czarna Woda, Flosek, Smolak);

5) Small eutrophic lakes with slight changes of water level have a small eulittoral range, but it is greatly differentiated (Czarna Kuta, Głęboka Kuta, Warniak).

2. Light, thermal conditions and freezing

Light. Light conditions in the littoral overgrown by emergent vegetation are discussed in the paper by Straškraba and Pieczyńska (1970). It also includes a discussion of the material collected in the eulittoral and littoral of Mikołajskie Lake. In the reed belt of this lake light reduction was observed to depend on the density of plants, from 26% (as compared with light conditions in the central part of the lake) at a density of 20 shoots/m² to 90% at a density of 170 shoots/m². The average reed density in Mikołajskie Lake (60 shoots/m²) results in about 50% light reduction. Light reduction is also due to lake-side trees. At the sites studied it was on the average 40% as compared with non-forested areas. Littoral differentiation, both from the point of shore afforestation and the density of macrophytes, results in considerable variation of light conditions. And so, for example, an analysis of 30 littoral stations showed that the light intensity at a depth of 30 cm ranges from 120 to 1060 lux at various stations on a cloudy day and at full solar radiation from 480 to 4100 lux.

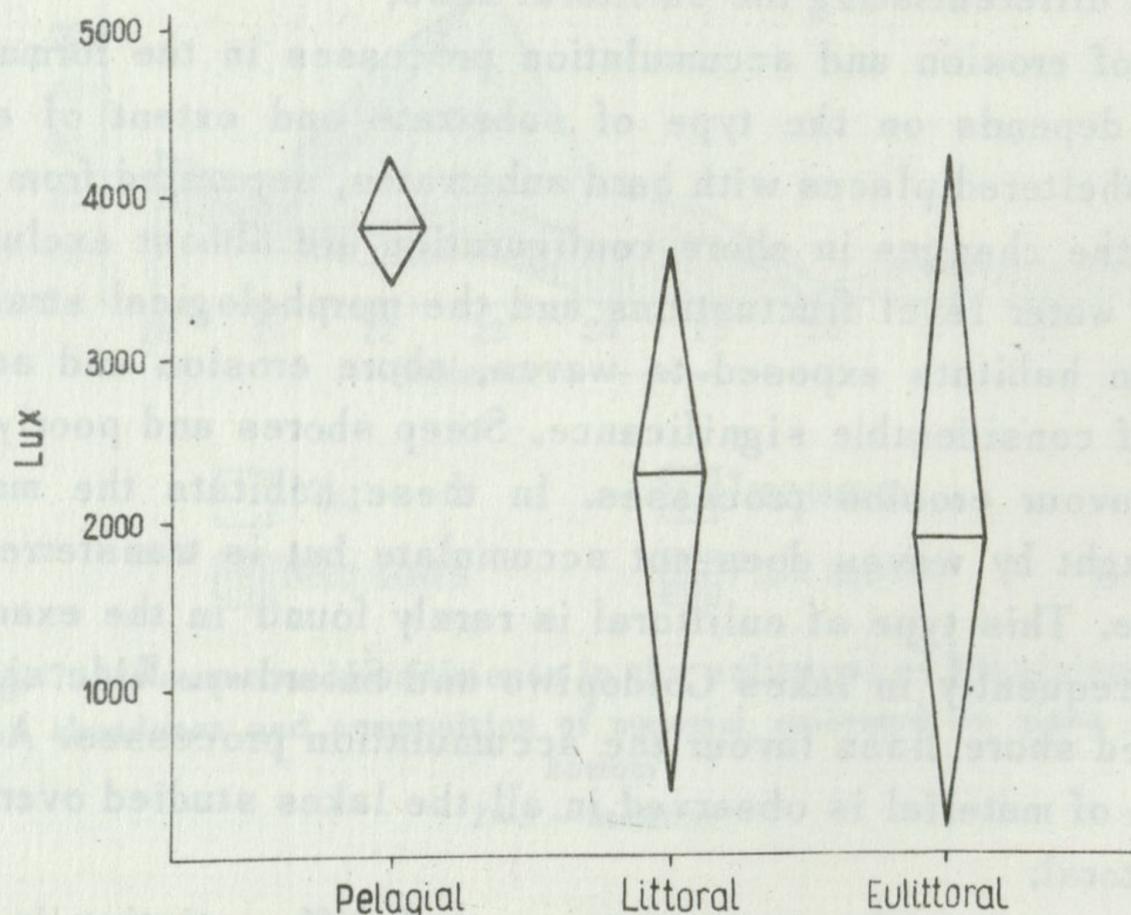


Fig. 8. Light conditions in the pelagial, littoral (reed belt) and eulittoral of Mikołajskie Lake (light on water surface; average values and range of variations)

In the eulittoral, just as in the littoral, emergent vegetation limits and differentiates the light conditions, but here shore afforestation is of greater significance. Thus light intensity reductions (mean values) and considerable increases of variation (ranges of values) are observed in the sequence from

pelagial to eulittoral. Figure 8 presents selected data from the measurements made in September 12, 1966 between 9.30 a.m. and 11 a.m. At each site examined 30 points placed in various parts of the lake were analysed. And so, in the littoral there was an average 60% of light reaching the zone of open water, and 50% in eulittoral. The greatest differentiation of light conditions was observed in the eulittoral. The maximal values (bare shores not overgrown by macrophytes) were close to the values recorded for the pelagial and were higher than the maximal values in the littoral overgrown with emergent vegetation. Minimal values (shores shaded by trees, high density of macrophytes) were lower than minimal values in a reed belt (Fig. 8).

Light measurements made during the year, every two weeks at 30 stations in eulittoral, littoral and pelagial, show that although the absolute light values differ depending on cloudiness, time of the day and the like, the differences between the habitats compared are on a similar level all the year round. In 85% of the analysed instances (measurements in different periods) the recorded light intensity in the eulittoral is on the average 50% lower than in the central zone of the water body.

In the margins of lakes the influence of wind on the variation of light conditions is especially marked.

This influence is due to: 1) greater water turbidity in periods of wave action, chiefly in shallow places with a muddy substrate, 2) movements of tops of emergent plants and 3) movement of lake-side trees producing intermittent shading of the water. The influence of these factors is greatest in the shallowest places with a muddy substrate, average density of macrophytes and shaded by trees. This problem is discussed in detail in the paper by Straškraba and Pieczyńska (1970). Examples of data illustrating the influence of wind on the differentiation of light conditions are presented in Table III.

In other lakes only a small series of measurements were made. These water bodies clearly differ in their light conditions in eulittoral, first due to the differences in degree of afforestation of the surrounding areas and macrophytes overgrowth (Bernatowicz 1960, Kondracki and Szostak 1960, Bernatowicz and Pieczyńska 1965, Bernatowicz, Pieczyńska and Radziej 1968, Bernatowicz 1969). Despite these differences in all lakes, just as in Mikołajskie Lake, the differentiation of light conditions was observed to be several times greater in the eulittoral than in the pelagial and littoral and there was a preponderance of habitats having worse light conditions.

The above generalisations concern the amount of light reaching the water surface. Taking into consideration the light penetration into water, one should remember, that because of the small depth, the whole of the eulittoral has better light conditions, even at the bottom, than many deep lake regions.

The effect of wind-movements of lake-side trees (A) and *Phragmites* tops (B) on the variation of light conditions in littoral of Mikołajskie Lake

Light measured in reed belt at 50 cm depth, expressed in lux* (variability expressed in per cent of the mean values)

Tab. III

		A**			
Time of observation		Sites shaded by trees		Sites not shaded by trees	
Windy day	average	709		986	
	variation (%)	23-196		27-159	
Windless day	average	812		1120	
	variation (%)	60-119		61-123	
		B***			
Time of observation		Density of reed (number of shoots /m ²)			
		25	50	80	110
Windy day	average	1496	1163	857	491
	variation (%)	50-149	36-188	33-159	47-142
Windless day	average	1636	1392	906	518
	variation (%)	63-120	58-128	55-121	71-121

*Data for each kind of observation are based on 150 light measurements.

**Reed belt (65 shoots/m²).

***Sites not shaded by trees.

Thermal conditions and freezing. Changes during the annual cycle of surface water temperatures are similar to the changes of air temperature. The average annual surface temperature of water bodies in Poland is quite constant at 10°C and is $2.5\text{--}3.0^{\circ}\text{C}$ higher than the average annual temperature of air surrounding them (Mikulski 1965).

For a long time the regularities of the thermal changes have already been used as one of the main aspects characterizing the central part of lakes. Littoral habitats have been examined less frequently and there is no significant generalizations. One of the fundamental papers on littoral thermal conditions is that by Gieysztor (1960) including, among others, studies in Mikołajskie Lake. The author found that the thermal conditions in the littoral basically differ from the conditions in the pelagial and are closer to conditions existing in small water bodies. Differences of temperature between the pelagial and the littoral vary in different seasons of the year. The maximal difference was observed in spring (8.9°C).

Zachwieja (1965), comparing daily temperature fluctuations at various depths in the littoral of lake Mamry observed considerable temperature differences between stations at various depths, and a fall in daily fluctuations with increasing depth.

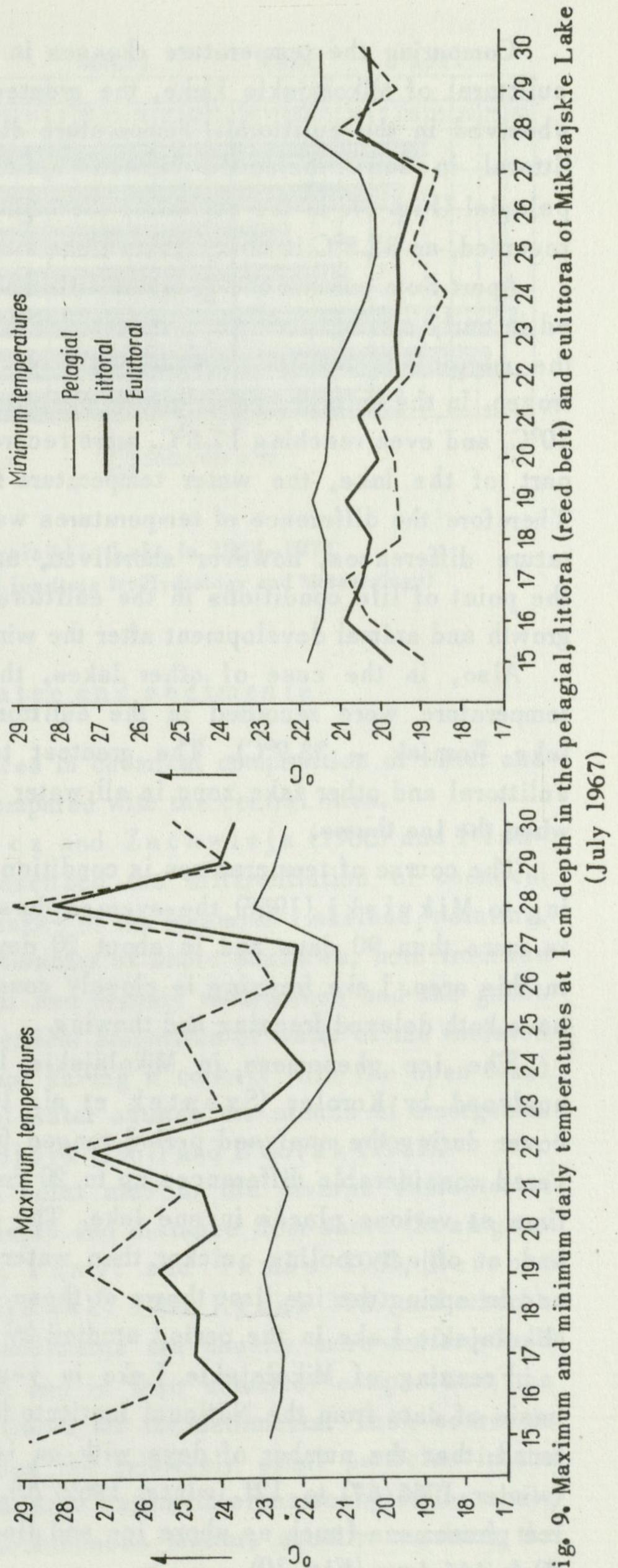


Fig. 9. Maximum and minimum daily temperatures at 1 cm depth in the pelagial, littoral (reed belt) and eulittoral of Mikołajskie Lake (July 1967)

Comparing the temperature changes in the pelagial, littoral (reed belt) and eulittoral of Mikołajskie Lake, the greatest daily temperature fluctuations are observed in the eulittoral. Temperature differences between the eulittoral and littoral in some instances exceed the differences between the littoral and pelagial (Fig. 9). In the eulittoral the highest absolute temperature values were recorded, as 32.5°C in Mikołajskie Lake.

Apart from summer the greatest differences in thermal conditions are observed in early spring, during the thawing of the lake. For a few days to two weeks the margins of the lake are free of ice, while the central part still remains frozen. In the unfrozen parts of the lake, on sunny days, temperatures exceeding 10°C, and even reaching 17.5°C, were recorded. At the same time, in the central part of the lake, the water temperature fluctuated within the range 1–2°C. Therefore the difference of temperatures was 16°C. It seems, that these temperature differences, however shortlived, are of fundamental significance from the point of life conditions in the eulittoral as they allow for quick vegetation growth and animal development after the winter rest.

Also, in the case of other lakes, the highest absolute values of water temperature were recorded in the eulittoral (the highest temperature was in lake Warniak – 33.9°C). The greatest temperature differences between the eulittoral and other lake zone in all water bodies were observed early in spring when the ice thaws.

The course of temperatures is conditioned by ice phenomena in lake. According to Mikulski (1965) the average duration of ice cover on Masurian lakes is more than 90 days and is about 20 days longer than the freezing of rivers in this area. Lake freezing is closely connected with their depth; deeper lakes have both delayed freezing and thawing.

The ice phenomena in Mikołajskie Lake in the years 1952–1958 were analysed by Korolec (Szostak et al. 1961). The maximal thickness of ice cover during the analysed period ranged from 19 to 54 cm. The authors discovered considerable differences up to 20 cm in the thickness of ice at the same time at various places in one lake. The ice appears first in near shore zone and at object cooling quicker than water (reed shoots, stones and the like), and in spring the ice first thaws at these places. The duration of ice cover for Mikołajskie Lake in the period studied by Korolec ranged from 90 to 133 days.

Freezing of Mikołajskie Lake in years 1964–1970 was analysed on the basis of data from the National Institute for Hydrology and Meteorology. It was found that the number of days with an ice cover on the lake ranged from 66 (winter 1966/67) to 121 (winter 1969/70). But considering the entire range of ice phenomena (such as shore ice and floating ice) these periods ranged from 90 to 144 days (Fig. 10).

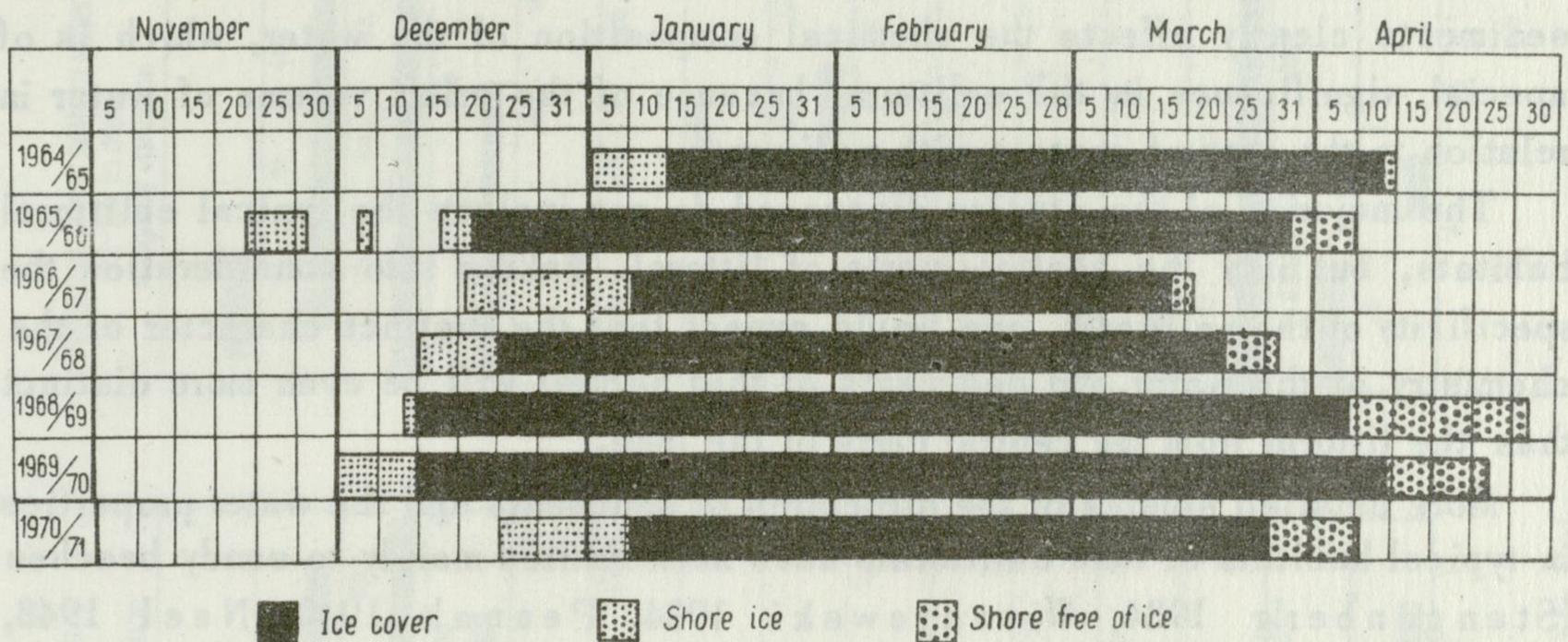


Fig. 10. Ice cover on Mikołajskie Lake in 1964-1971

(Prepared using data from the National Institute for Hydrology and Meteorology)

3. Chemistry of water and sediments

There are several data on differences in chemical composition of water and sediments in marginal lake zones as compared with the central ones.

Zachwieja (1965), Bernatowicz and Zachwieja (1966) and Planter (1970 and unpublished data) described the differentiation of chemical composition of littoral water of some lakes of the Masurian Lakeland, pointing, among other things, to the distinct character of shore shallows, both from the view point of concentration of mineral and organic substances and the gases dissolved in water. Especially the chemical properties of water of the isolated reed-bed (inside part of the stand, not having a contact with the open lake) clearly differed from the properties of water outside the stands of emergents. Similar regularities were observed by Björk (1967) and Dvořák (1971).

Studies of various lake habitats point also to the diverse character of bottom sediments, depending on the depth and distance from shore (Stangenberg and Žemoytel 1952, Entz, Ponyi and Tamàs 1963, Bernatowicz and Zachwieja 1966, Tadjewski 1966, Rybak 1969 and others). In the profundal zone of lakes the sediments are usually more uniform both from the morphological point of view and in their chemical composition, the closer to the shore the more differentiated are the sediments. Their source is matter of various origins, and besides the relatively small particles in the stages of advanced decomposition also large fragments of macrophytes (or whole plants) may be found. Also the allochthonous matter, usually reaching the deeper parts of the water body in the form of small mineral and organic particles,

is found in a more differentiated form in the near shore zone. The character of sediments clearly affects the chemical composition of the water, which is of special significance in the eulittoral because of the small volume of water in relation to the area of contact with sediments.

The majority of the studies discussed do not include the typical eulittoral habitats, but only the shallow parts of littoral. Taking into consideration the specificity of the eulittoral, one would expect that the distinct character of the chemistry of the water and sediments of this habitat will be even more distinct than the littoral from the central parts of the lake.

More detailed studies of the structures of sediments and the water properties in typical habitats of lake eulittorals have been limited mainly to sandy beaches (Stangenberg 1934, Wiszniewski 1934, Pennak 1940, Neel 1948, Ruttner-Kolisko 1962 and others). The considerable distinctness and variety of the sandy eulittoral as compared with the neighbouring lake habitats were observed. Stangenberg (1934) and Wiszniewski (1934), when studying the chemistry of interstitial water in the emergent part of the beach of lake Wigry found that the concentration of many dissolved substances is many times higher than in other lake habitats; but on the other hand the concentration of dissolved oxygen is low. Stangenberg (1934) describes this habitat as an extremely eutrophic.

In these investigations studies of the chemical composition of water and sediments were conducted for an annual cycle in years 1967 and 1968 in the eulittoral of lakes Mikołajskie and Warniak.

In Mikołajskie Lake the chemical composition of water of the submerged eulittoral and the littoral overgrown by emergent vegetation was compared with Rybak's data (Rybak 1972 and unpublished) on the chemical composition of water of the central part of the water body. Figure 11 presents the range of variation of certain features of the water chemistry of these lake zones according to the data obtained in different seasons of 1967 and from various places in the water body. The eulittoral is characterised both by the highest values and the greatest range of fluctuation for the majority of the components analysed. Exceptionally, in the instance of nitrite nitrogen, the greatest fluctuations and the highest maximal values are observed in the near-bottom water layer of the central part of lake. It is significant that in their chemical composition the littoral waters differ more from the waters of eulittoral than from the pelagial (Fig. 11).

Particular eulittoral habitats have different concentrations of mineral and organic substances. In Mikołajskie Lake systematic studies of water chemistry have been conducted in the following habitats (Tab. IV):

A. Habitat with a stony bottom, strong wave action, lack of macrophytes. Samples taken at 0.5 m from the shore line, at 0.2 m depth;

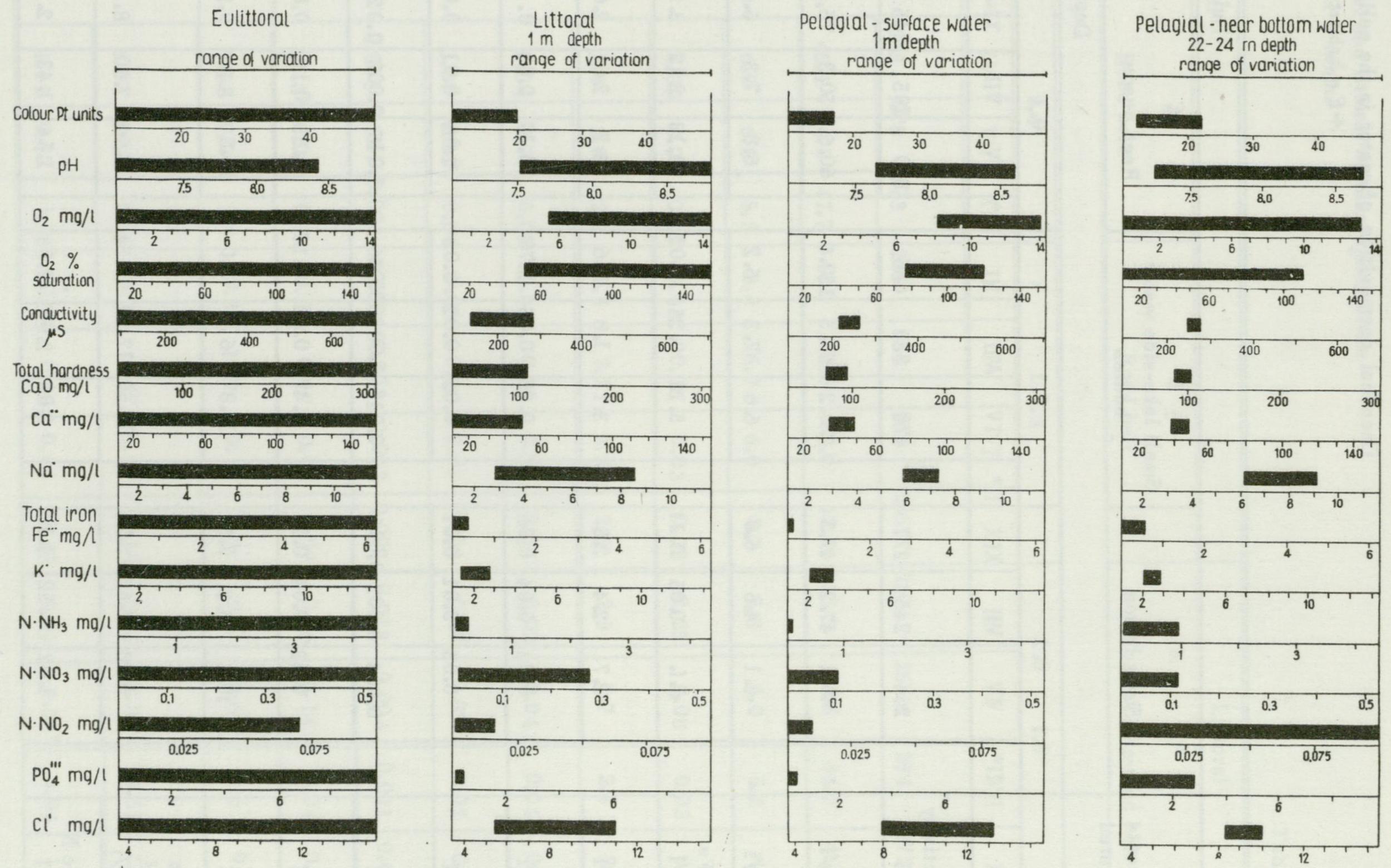


Fig. 11. Chemical composition of water in different zones of Mikołajskie Lake

Chemical composition of water in the eulit-
A-F - habitats,

Eulit												
Elements compared	A Stony bottom				B Small lake-side water bodies				C Reed heaps			
	Depth											
	0.2				0.1				0.1			
	II*	IV	VII	XI	II*	IV	VII	XI	II*	IV	VII	XI
Conductivity μS		264	245	277		470	333	686		360	285	345
Ca ⁺⁺ mg/l		46.1	47.2	49.5		70.2	61.5	150.6		60.6	50.3	75.1
Na ⁺ mg/l		5.1	4.6	6.0		6.6	7.3	6.2		6.8	7.3	6.6
Total Fe mg/l		n.f.	0.06	0.11		5.10	0.26	3.01		4.18	2.12	3.38
K ⁺ mg/l		2.7	2.4	2.5		3.1	1.8	9.6		3.2	2.6	2.6
N-NH ₄ mg/l		0.04	0.04	0.06		0.22	0.06	3.70		0.19	0.08	0.18
N-NO ₃ mg/l		0.05	0.01	0.01		0.06	0.02	0.08		0.06	0.01	0.02
N-NO ₂ mg/l		0.004	0.002	0.005		0.015	0.002	0.036		0.016	0.008	0.029
PO ₄ ^{'''} mg/l		0.13	0.04	0.17		0.47	0.68	7.17		0.35	0.16	0.87
Cl ⁺ mg/l		10.1	8.2	9.3		10.8	6.9	8.0		10.8	8.8	9.5
Oxygen demand O ₂ mg/l		5.98	7.65	5.76		19.60	17.22	19.54		7.99	7.60	8.31
Organic N mg/l		1.02	0.52	1.10		2.84	2.02	7.35		1.54	1.43	2.31

* Ice to the bottom

toral and littoral of Mikołajskie Lake
II-XI — months

Tab. IV

toral				Littoral							
<i>D</i> Reed belt			<i>E</i> Reed belt				<i>F</i> Control site-reed belt				
(m)											
0.1				0.3				1.0			
II*	IV	VII	XI	II	IV	VII	XI	II	IV	VII	XI
	258	278	273	286	263	255	266	250	267	284	272
	46.2	44.2	47.7	47.0	46.0	38.0	43.5	35.5	45.6	44.0	46.1
	6.0	6.5	5.3	5.4	6.7	6.0	3.7	5.3	5.0	5.2	4.7
	0.03	0.07	0.58	0.41	0.06	0.03	0.18	0.25	0.08	0.03	0.09
	2.4	2.3	2.7	2.3	2.7	2.5	2.5	2.3	2.7	2.4	2.6
	0.04	0.05	0.09	0.07	0.06	0.06	0.04	0.03	0.04	0.04	0.05
	0.07	0.02	0.04	0.08	0.06	0.01	0.02	0.10	0.07	0.02	0.04
	0.005	0.001	0.004	0.020	0.005	0.002	0.008	0.013	0.004	0.001	0.004
	0.15	0.03	0.24	0.28	0.12	0.03	0.22	0.26	0.14	0.04	0.05
	7.9	9.0	9.6	9.3	10.9	9.3	8.9	9.5	10.6	8.3	9.1
	6.37	6.43	6.63	5.33	6.37	6.52	6.15	5.45	5.88	6.61	6.01
	1.12	0.67	1.08	0.98	0.94	0.64	1.40	0.91	1.06*	0.94	1.05

B. Small lake-side water bodies, partly separated from the lake by reed heaps, depth 0.1 m;

C. Reed heaps. Samples taken from water from under the reed heaps, 0.1 m from the shore line, depth 0.1 m;

D. Reed belt, 0.5 m from the shore line, depth 0.1 m. Bottom covered with plant detritus. Very little effect of wave action;

E. Reed belt, 2 m from the shore line, depth 0.3 m, sandy bottom with a small amount of detritus. Little effect of wave action;

F. Reed belt, 20 m from the shore line, depth 1 m. Considerable significance of wave action. Typical habitat of the littoral of Mikołajskie Lake. Treated as control for comparison purposes with the eulittoral.

From all these habitats samples were taken six times during the year, from 3 stations in each type of habitat. Detailed comparisons of the materials sampled in February, April, July and November show the following regularities (Tab. IV):

The greatest concentrations of mineral substances are found in small lake-side water bodies, where the maximal values exceed by many times the highest values in other habitats. Very high concentrations of mineral substances are also observed in water under the reed heaps (habitat also partly isolated from the open lake). Other habitats have much lower concentrations of mineral substances. Stony and overgrown by reeds eulittorals exposed to wave action only differ slightly from the deeper parts of reed belts – typical littoral habitat (Tab. IV).

Organic matter (estimated by measurements of oxygen demand and organic nitrogen) also has the highest concentrations in small lake-side water bodies and under reed heaps (Tab. IV).

The variability of hydrological conditions in the eulittoral makes it more difficult to interpret the changes of water chemistry in the annual cycle. Because of the periodical drying up and flooding of the habitat, samples from the chosen eulittoral types were taken in a different place each time, subject previously to various other environmental factors. Thus, one should be extremely careful when interpreting the changes of water chemistry in the annual cycle. In the data presented, attention should be particularly paid to the occurrence of the majority of maximal concentrations of mineral and organic substances in late autumn (November). In many habitats quite high concentrations were also observed in spring. Minimal concentrations were most frequent in summer (July).

An important period specifically for the eulittoral is when the ice and snow are melting, and the lake is supplied by extra water. In the central part of lake this does not much affect the chemical composition. Whereas, because of the small water volume in the eulittoral it is of considerable significance

there. The lowest concentrations of various substances dissolved in water are observed then. And so, e.g., in March 21, 1968 when taking samples during the ice thawing (eulittoral free of ice for an area of about 2 m from the shore) the conductivity was 93 μ S, and the calcium concentration was 9 mg/l Ca, which are lower values than the lowest recorded for pelagial, littoral and eulittoral in all other seasons of the year.

The above description of chemistry of eulittoral waters does not include the stations influenced by municipal sewage. Beside the Mikołajskie Lake there is the town Mikołajki with 3600 residents and several thousand of tourists during the summer. The town has no sewer system. It has few hundreds of dry cesspools. The partly non-purified water is drained off to the lake in a concentrated way (e.g. drain from the restaurant) or directly drained off from the buildings beside the lake. A considerable part of wastes reaches the lake beyond the eulittoral zone (the outlet of sewage pipes several to several hundreds metres from the shore line, or the wastes from boats ferrying on the lake). However, part of sewage waters in the north-eastern part of the lake fertilizes the eulittoral zone. According to the studies of the Department of Hydrobiology, Zoological Institute of Warsaw University (Pieczyńska and others, unpublished) in these environments observed are considerably higher concentrations of some substances than the maximal ones (discussed above) for the not polluted eulittoral station (e.g. chlorides up to 58 ml/l Cl, and ammonia nitrogen up to 20 mg/l N-NH₄). These problems will be a subject of a separate paper.

The dissimilarity in water chemistry between the eulittoral and the central part of the lake has also been observed in lake Warniak. The data of Bernatowicz (1969) concerning the water chemistry of lake Warniak, and of Rybak (1972) on water chemistry of Mikołajskie Lake, show that the central part of lake Warniak has a little lower concentrations of mineral substances. Similarly in the eulittoral of this lake the values of a majority of components are lower than in the eulittoral of Mikołajskie Lake. The greatest concentrations of all substances are recorded in partly isolated shore habitats corresponding to small lake-side water bodies in their hydrological character which in Mikołajskie Lake are characterised by the greatest amounts of mineral and organic substances. Maximal values in eulittoral of lake Warniak are: conductivity 502 μ S, calcium 75 mg/l Ca, potassium 5.70 mg/l K, phosphates 0.7 mg/l PO₄, ammonia nitrogen 1.5 mg/l N-NH₄, nitrite nitrogen 0.005 mg/l N-NO₂, nitrate nitrogen 0.17 mg/l N-NO₃, total iron 4.5 mg/l Fe. Organic substances in lake Warniak were found in greater concentrations than in Mikołajskie Lake (oxygen demand up to 90 mg/l O₂).

The smallest concentrations of various substances were observed at the not overgrown eulittoral; they were either close to or slightly lower than the

concentrations of mineral and organic substances in the stony eulittoral of Mikołajskie Lake (Tab. IV).

The concentrations of various substances in eulittoral habitats of lake Warniak are much higher than the concentrations of these substances in the central part of lake. The greatest concentrations of organic and mineral substances in eulittoral were observed in autumn (October) and spring (April) with the exception of a short period, when, as in Mikołajskie Lake, in some habitats dilution, clearly due to melting ice and snow was observed.

Several of these chemical properties of water in the eulittoral are confirmed by recent investigations of Planter (1970) on the water of reed belts in lakes Mikołajskie, Tałtowisko and Śniardwy. This author recorded much greater concentrations of various substances in the insite parts of reed belts partly separated from the water body, and also much lower values during the thaw.

A regular feature, often described in the central part of lake, is also frequently observed in the eulittoral, i.e. the concentration of mineral substances decreases from the spring to summer. For lake Warniak this is described by Bernatowicz (1969). The author observed an almost 2-fold decrease in the amounts of calcium and potassium during the vegetation season (from April to July). The amounts of phosphorus and inorganic nitrogen also decreased. In the eulittoral this process is clearly modified by water level fluctuations. In the eulittoral of lake Warniak the conductivity decreased between April and June. In July the water level rapidly fell, and the area studied dried up. At the end of September, after flooding of the area, the concentration of analysed substances considerably increased. In the littoral areas examined for comparative purposes, where the fall in water level did not dry up the area, the concentration in September did not increase as compared with July. This regularity was most apparent in the case of the conductivity and also for potassium and calcium (Fig. 12). Similar differences, although not so distinct were noticed for concentration changes of inorganic nitrogen and phosphates.

And so, periodical drying up and re-flooding of the eulittoral renews the habitat, and in consequence enriches it in minerals. But this process does not occur regularly in all lakes, and as it will have been apparent, the increase of water level in autumn is a frequent but not a regular phenomenon, in the habitats examined.

The changes in oxygen concentration in various eulittoral habitats were more thoroughly analysed. The frequencies of occurrence of various levels of oxygen content in lakes Mikołajskie and Warniak were estimated on the basis of material collected from April to November 1968, between 10 a.m. to 12 a.m. In Mikołajskie Lake comparisons of the oxygen content in the eulittoral and

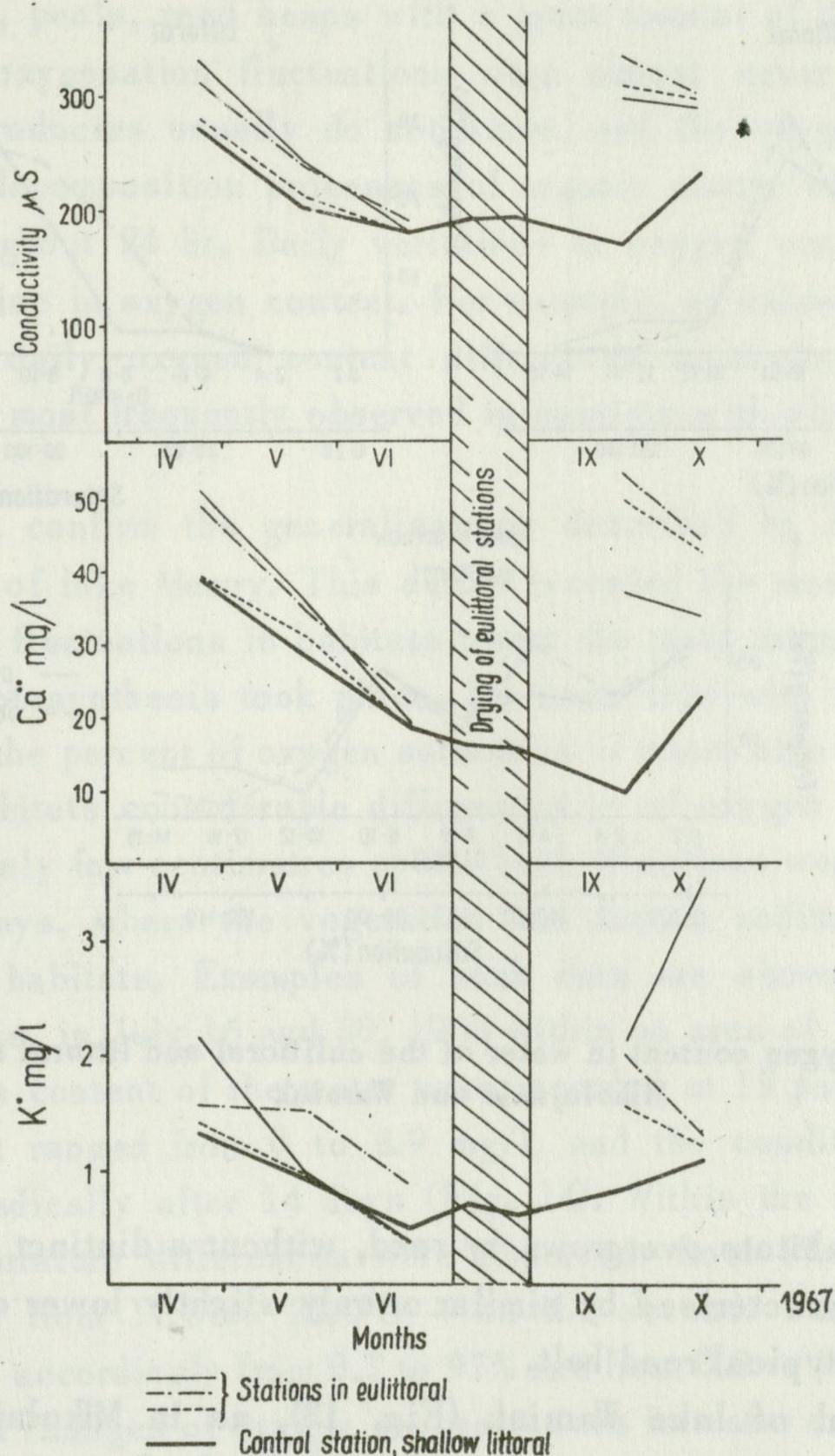


Fig. 12. Seasonal changes in selected features of chemical composition of water in the eulittoral and littoral stations of lake Warniak.

the littoral overgrown by emergent vegetation showed that the former is characterised by much worse oxygen conditions (Fig. 13). Small oxygen concentration (down to 4 mg/l) are quite frequently observed in the eulittoral (36% of instances) but not found in the littoral. They are typical of the small pools along the shore line, the eulittoral covered with reed heaps and the small lake-side water bodies, completely overgrown with *Lemnaceae*. The oxygen concentration values above 14 mg/l are very rarely observed, (2% of occasions), only in eulittoral habitats having a stony or sandy bottom exposed to big

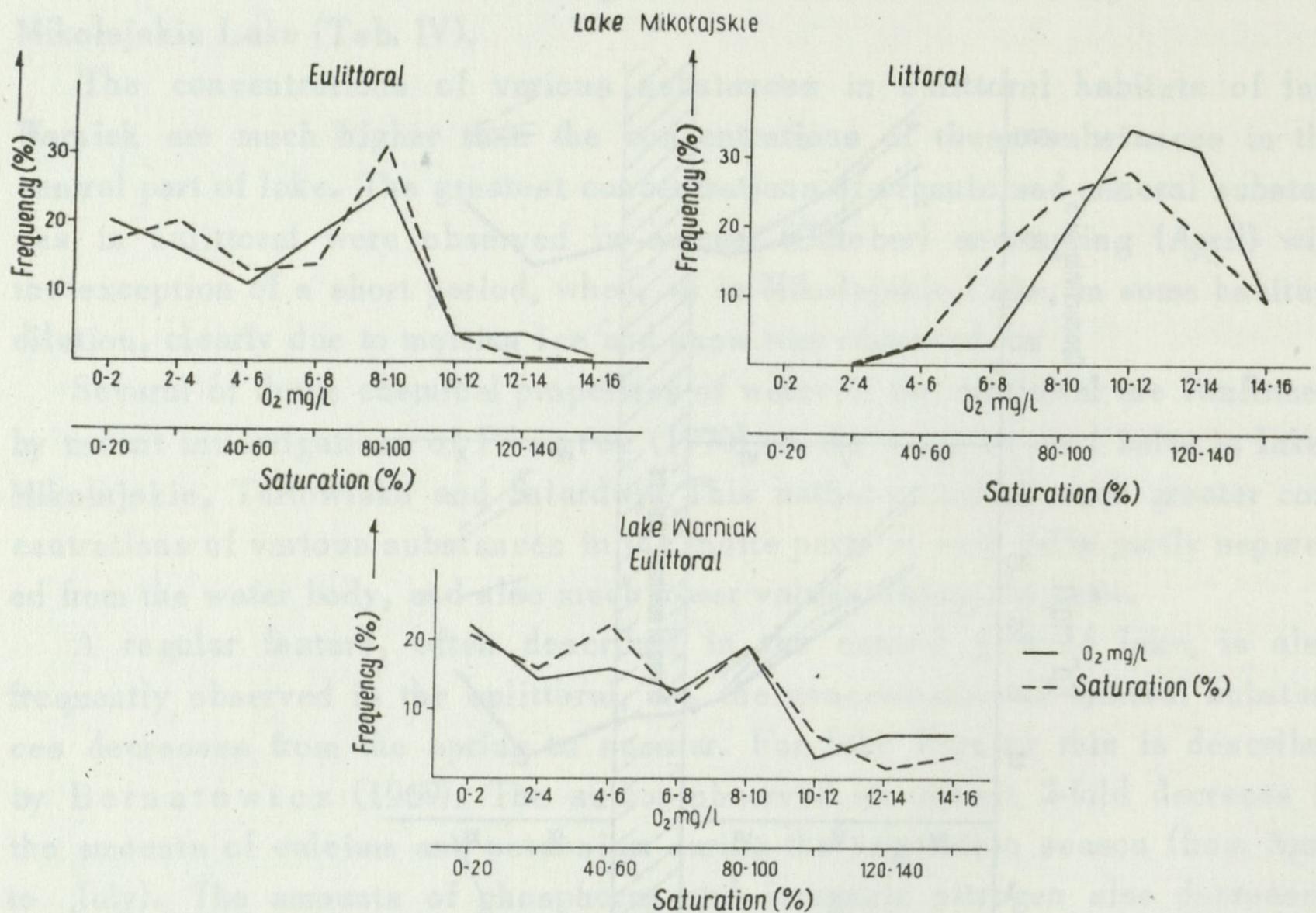


Fig. 13. Dissolved oxygen content in water of the eulittoral and littoral stations of lakes Mikołajskie and Warniak

waves. Eulittoral habitats overgrown by reed, without a distinct border passing into littoral, are characterised by similar or only slightly lower oxygen content as compared with a typical reed belt.

In the eulittoral of lake Warniak (Fig. 13), as in Mikołajskie Lake the occasions with low oxygen contents predominated. In fact, more than 50% of instances included oxygen concentrations below 6 mg/l and 60% saturation. Concentration above 14 mg/l O₂ was observed in 7% of instances, and oxygen saturation above 140% in 4% of instances. In the littoral of this lake, as in Mikołajskie Lake, the oxygen conditions were much better than in the eulittoral (because of the smaller amount of data on the littoral they are not presented in the diagram).

In Mikołajskie Lake the daily changes of oxygen concentration were analysed, taking samples 6 times in 24 hr: at dusk and at dawn, and at 7 and 10 a.m., and 1 and 4 p.m. Such analyses were made at 8 stations, four times in the period June and July. Differences in oxygen concentration during 24 hr are first of all the result of daily algal activity (habitat oxygenation due to photosynthesis

during the day). In the eulittoral characterised by low oxygen concentrations (swampy areas, pools, reed heaps with a great amount of decomposing organic matter) daily oxygenation fluctuations were almost never recorded. In these habitats the producers usually do not occur, and the oxygen concentration is controlled by decomposition processes of organic matter which have a similar intensity throughout 24 hr. Daily variations in oxygen concentration increase together with rise in oxygen content. For example, at values above 12 mg/l O₂ (before noon) daily oxygen content differences approximate 10 mg/l. Such instances were most frequently observed in habitats with abundantly developing algae.

These data confirm the generalisations described by Zachwieja (1965) for the littoral of lake Mamry. This author recorded the smallest amplitudes of oxygen content fluctuations in habitats where the most intensive decomposition and limited photosynthesis took place. He found that with increasing distance from the shore the percent of oxygen saturation of water also increased.

In some habitats considerable differentiation of oxygen content was observed in places only few centimetres apart. Such situations were usually observed in sheltered bays, where the vegetation and bottom sediments distinctly differentiate the habitats. Examples of such data are shown in Figure 14. In Mikołajskie Lake, in July 16 and 30, 1968 within an area of 10 m², the temperature and oxygen content of the water were recorded at 19 points at 10 a.m. The oxygen content ranged from 0 to 8.9 mg/l, and the conditions at each point had changed radically after 14 days (Fig. 14). Within the examined area considerable temperature differences were observed: from 17.2 to 23.2°C on the first date, and from 17.5 to 22.0°C – on the second. Differences of oxygen saturation were accordingly from 0.7 to 97% and from 0.8 to 95%.

Analyses of changes of oxygen concentrations in water during winter showed oxygen deficits in many eulittoral habitats in various lakes. In shallow places, where there are only a few centimetres of water between the ice cover and bottom sediments a lack of dissolved oxygen is usually observed. The further from the shore the better oxygen conditions are observed. And so, e.g., in Mikołajskie Lake, in the profile examined in February 1967, dissolved oxygen was not found up to 1.3 m from shore line. 3 m from the shore line, under the ice, 10 mg O₂/l was recorded and oxygen deficits were maintained only in a small water layer directly adjacent to bottom sediments (Fig. 15). Water temperatures were similar in the area examined (it ranged from 1.6 to 2.1°C), and therefore the changes in the extent of oxygen saturation were directly proportional to the changes in concentration and fluctuated from 0 to 145%.

It has been observed that the oxygen deficits in the shore region under the

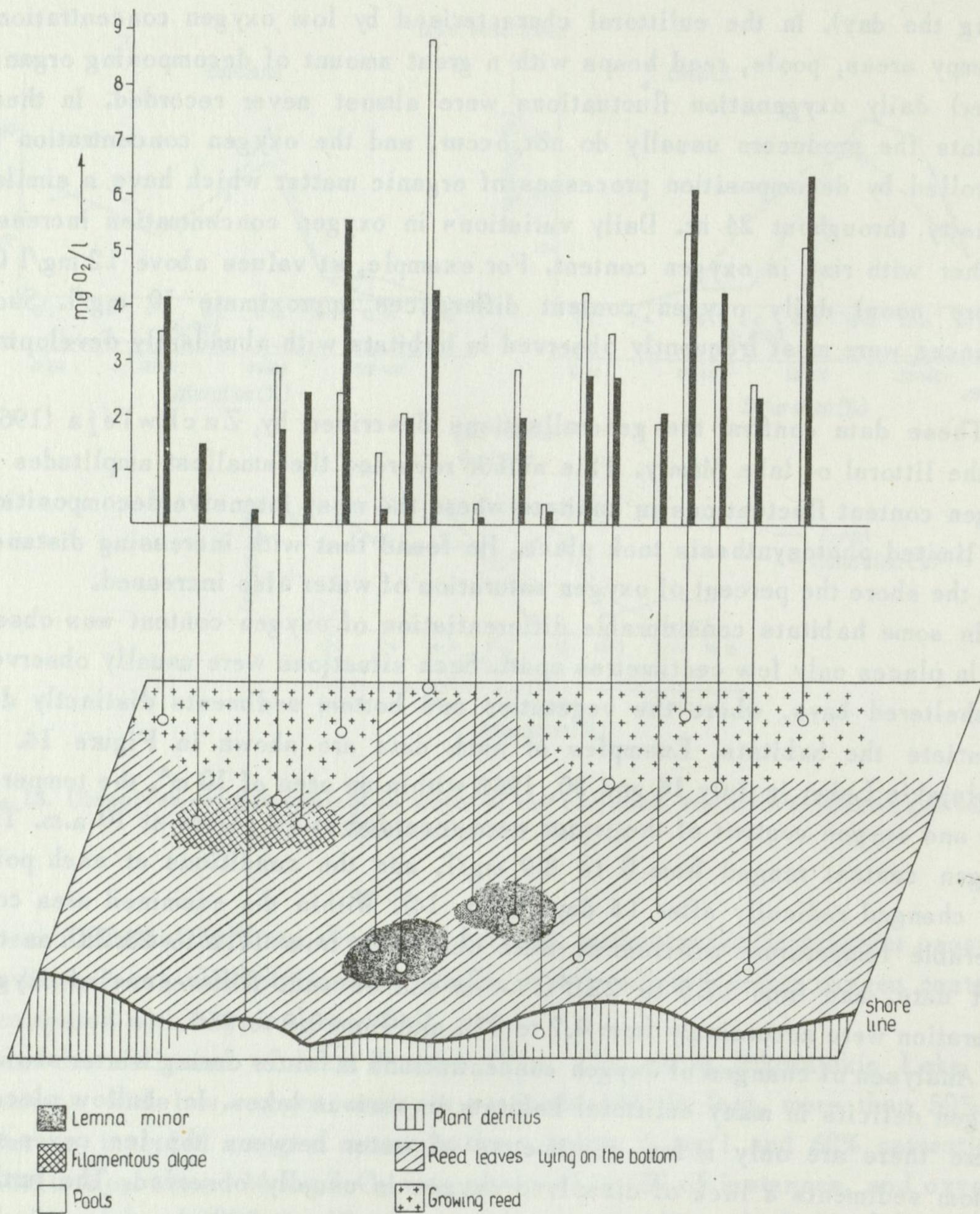


Fig. 14. Distribution of the dissolved oxygen concentrations at one eulittoral station of Mikolajskie Lake

July 16 — white columns, July 30 — black columns

ice are greater when the organic matter content of the sediments is greater. This points to intensive oxygen consumption by sediments despite the low temperature.

Apart from the chemical analyses of free waters of the submerged eulittoral

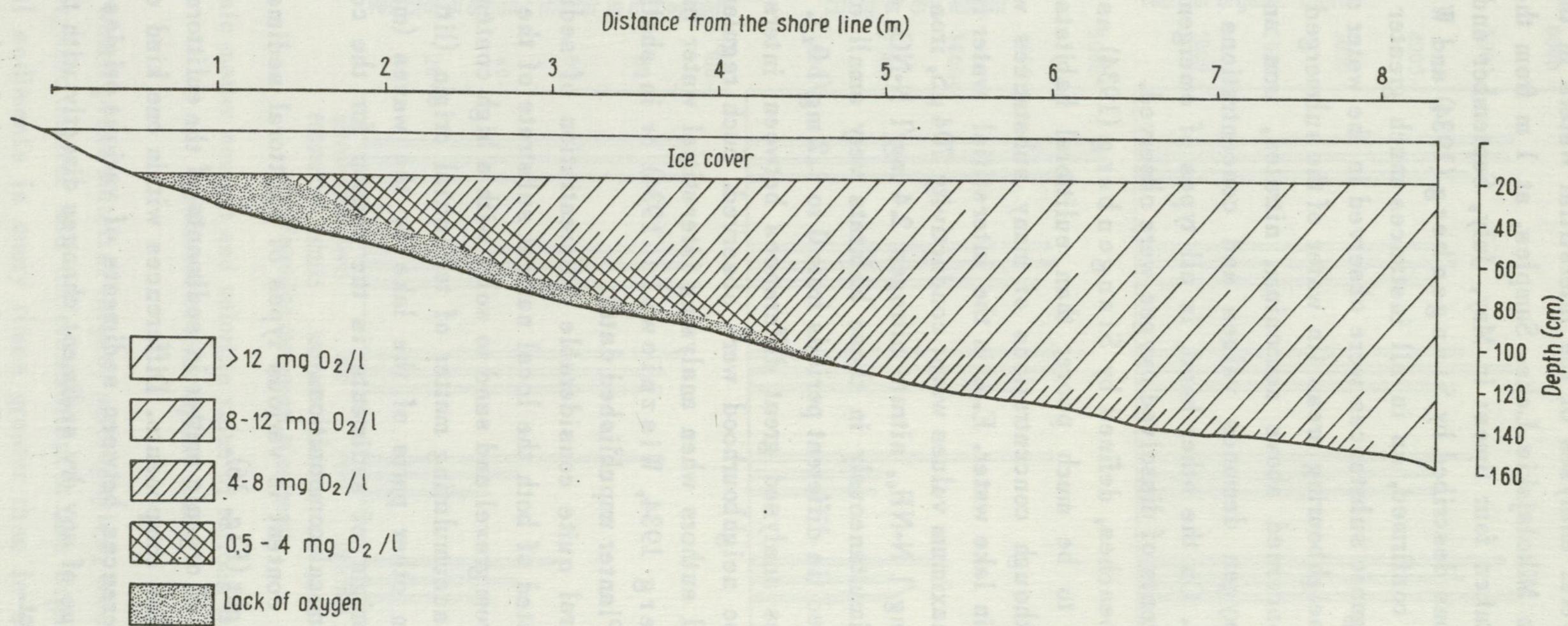


Fig. 15. Dissolved oxygen concentrations at one eulittoral station of Mikolajskie Lake (February 1967)

already discussed, several analyses of the interstitial waters in the emergent eulittoral were made in Mikołajskie Lake. Samples, at 1 m from the border of land and water, were taken four times: in May, July, September and November 1967. The generalisations described by Stangenberg (1934) and Wiszniewski (1934) have been confirmed, as in all instances much greater concentrations of mineral and organic substances were observed in the water of emergent eulittoral than in the neighbouring areas (in water of the submerged eulittoral and littoral). This concerned above ammonium, nitrates, iron and calcium. Also much greater oxygen demands values and concentrations of organic nitrogen were recorded. On the other hand, in all types of emergent eulittoral considerably lower contents of dissolved oxygen were observed.

Habitats of sandy beaches, defined by Stangenberg (1934) as extremely eutrophic, were found to be much poorer than eulittoral habitats, in which detritus dominated, although concentrations of many substances were higher in sandy beaches than in lake water. E.g. in the interstitial water in emergent detritus eulittoral the maximum values were: conductivity 704 μ S, iron 7 mg/l Fe, ammonia nitrogen 5.8 mg/l N-NH₄, nitrate nitrogen 2.4 mg/l N-NO₃ and oxygen demand 98 mg/l O₂. Simultaneously in these habitats very small oxygen concentrations were recorded (in different periods from 0 to 1.2 mg/l O₂).

In all the instances analysed great differences between interstitial water and free water in close neighbourhood were observed. Such regularities were pointed also by several authors when analysing interstitial water in emergent eulittoral (Stangenberg 1934, Wiszniewski 1934) or in shallow part of littoral (Björk 1967, Planter unpublished data).

In the lake eulittoral quite considerable differentiation of sediments was observed, which consisted of both the local natural substrate of the lake shore (various kinds of soil from gravel and sand to soils with a high content of humus or peat), and also of accumulating matter of terrestrial origin (litter fall), or matter brought in from other parts of the lake by the waves (macrophytes, algae). The diverse origin of sediments is the reason for the considerable differences in their chemical composition.

The organic matter content in various types of eulittoral sediments ranges from < 1 to 98% dry weight (Fig. 16).

The calorific value of organic matter in sediments of the eulittoral does not change with the sediment components. Differences within one kind of sediment are similar to the differences between sediments of various origins (Fig. 16). Hence the calorific value of any dry sediment changes directly with the changes in organic matter content.

Habitats with a great amount of organic matter include those types of

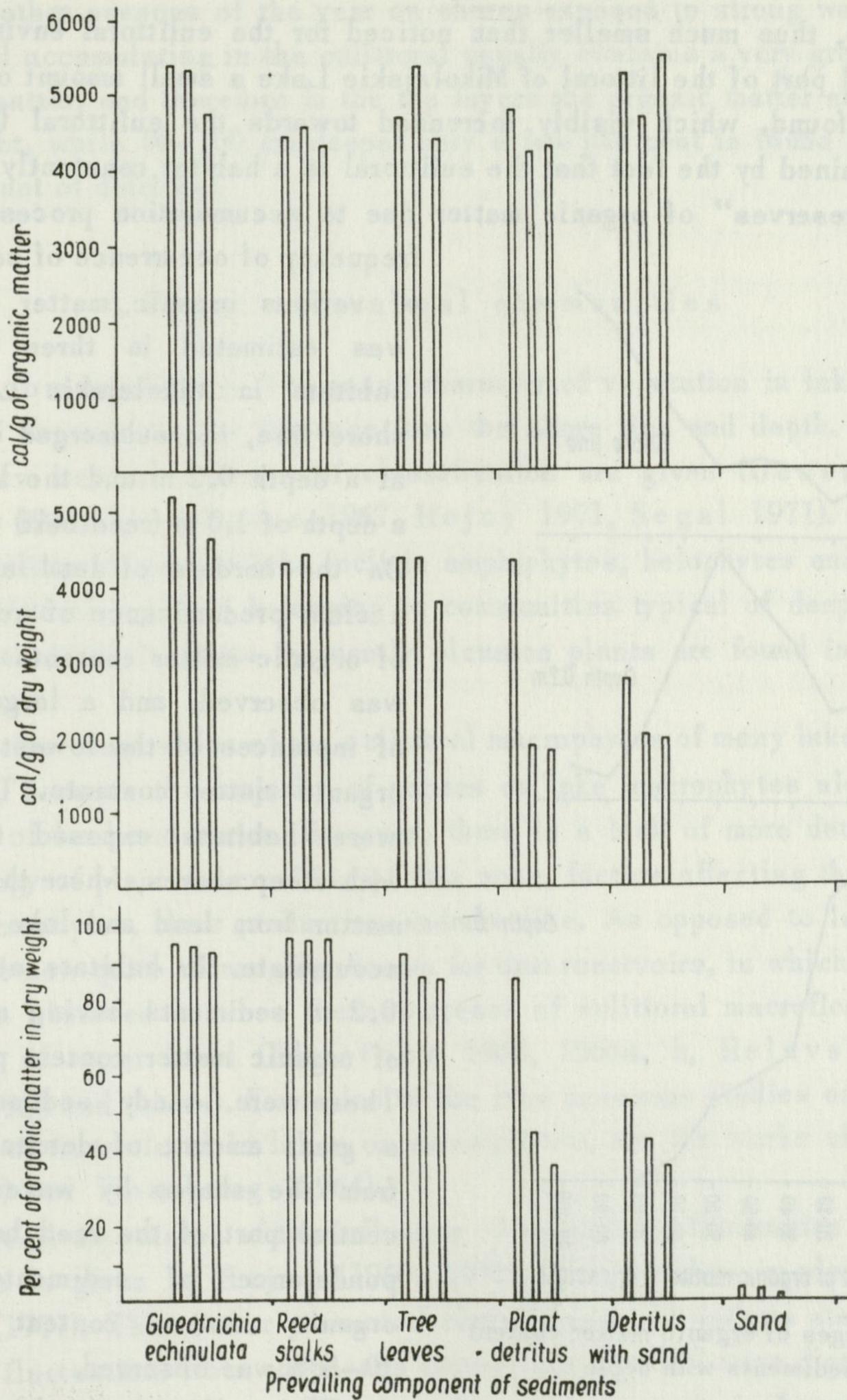


Fig. 16. Organic matter content and calorific value of various types of sediments in the eulittoral of Mikołajskie Lake

eulittoral in which plant material (algae, macrophytes, tree leaves) accumulates. Amount of organic matter and differentiation in the organic matter content in the eulittoral sediments is many times greater than in sediments of the other parts of lake. Rybak (1969) reports differences in the organic matter content of sediments of the part of Mikołajskie Lake beyond the littoral, within the

range 2–30%, thus much smaller than noticed for the eulittoral environments. In the central part of the littoral of Mikołajskie Lake a small amount of organic matter was found, which visibly increased towards the eulittoral (Fig. 17). This is explained by the fact that the eulittoral is a habitat constantly supplied with new „reserves” of organic matter due to accumulation processes. The

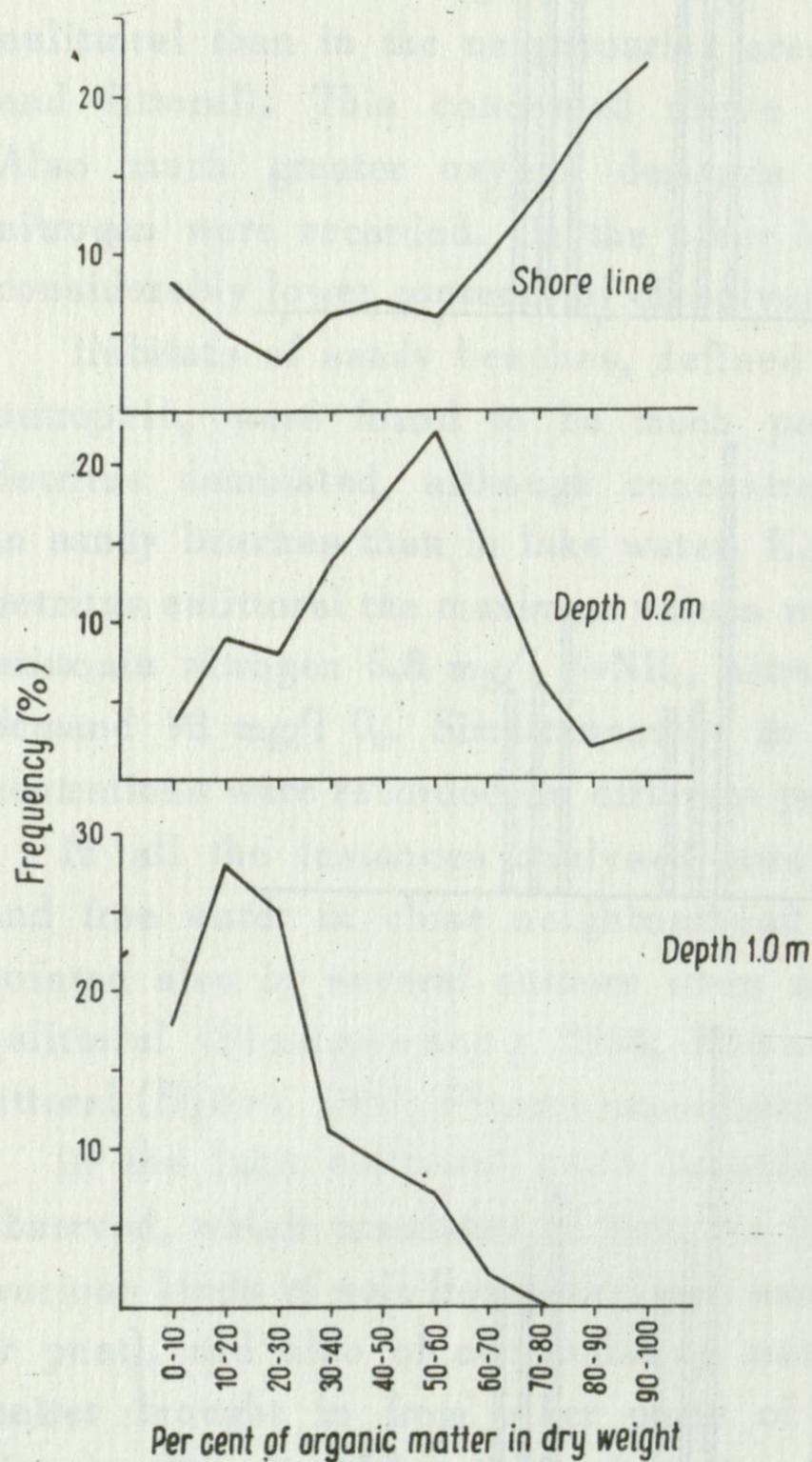


Fig. 17. Changes of organic matter content in sediments with depth

frequency of occurrence of sediments of various organic matter contents was estimated in three types of habitats in Mikołajskie Lake: the shore line, the submerged eulittoral at a depth 0.2 m and the littoral at a depth of 1.0 m (reed belt) (Fig. 17). On the borders of land and water a clear predominance of occurrences of organic matter contents over 80% was observed, and a large number of instances of the lowest (0–10%) organic matter contents. The latter were habitats exposed to waves with steep shores, where the organic matter from land and lake does not accumulate. In habitats at a depth 0.2 m sediments having about 50% of organic matter content prevailed. These were sandy sediments with a great amount of detritus carried from the shores by waves. In the central part of the reed belt a preponderance of sediments of an organic matter content between 10–30% was observed.

The sediments in the eulittoral also have a considerable vertical differentiation, especially in those habitats, where considerable accumulation of material of terrestrial and lake origin takes place. Heaps of reed shoots and submerged macrophytes accumulate periodically on local natural substrates to as much as 80 cm thick. In spring, when the ice thaws, cylinder shaped constructions (composed of reed stalks and leaves, tree leaves, small detritus, and sometimes even sand and mud) with a diameter of 20–30 cm appear on the shores. Similar constructions can

be seen in other seasons of the year on shores exposed to strong wave action. The material accumulating in the eulittoral usually contains a very great amount of organic matter, and therefore in the top layers the organic matter attains 98% of dry weight, while 50–100 cm deeper only a few per cent is found (sand with a small amount of detritus).

4. Plant and animal communities

Plant communities. The zonal character of vegetation in lakes is very distinct and depends on the distance from the shore line and depth. From this point of view several systems of classification are given (Gessner 1955, Starmach 1963, Sculthorpe 1967, Hejný 1971, Segal 1971). Macrophytes in the eulittoral zone of lake include amphiphytes, helophytes and, in some types of eulittoral, species belonging to communities typical of deeper littoral parts (e.g. elodeides). Quite frequently pleuston plants are found in the eulittoral.

The species composition of the eulittoral macrophytes of many lakes is quite well known, because the majority of papers on lake macrophytes also include the borders of land and water. However, there is a lack of more detailed data on the ecology of plant communities of this zone, factors affecting the development of macrophytes, their production and the like. As opposed to lakes these problems are now quite thoroughly known for dam reservoirs, in which a distinct relation was observed between the occurrence of eulittoral macroflora and the fluctuations of water level (Ekzercev 1960, 1966a, b, Belavskaja and Kutova 1966 and others). Examples of the less numerous studies on the effect of changes of water level in lakes on macrophytes, are the works of Lillieroth (1950) and Forsberg (1964).

The general discussion of the influence of water level fluctuation on littoral macrophytes is given by Hejný (1960, 1971). This problem is also analysed by Segal (1971). This author presented classification of various stages of the water level fluctuation. Four ecophases (actual life medium) were distinguished. Each defined in accordance with the adaptative capacities of vegetation in relation to water level fluctuation. There are: 1) the hydrophase – with a high water level; the development of true aquatic plants is characterised, 2) the littoral phase – the water is shallow, even falls dry for a short time, shows the development of mostly amphibious forms, 3) the limnophase – the soil remains constantly water-logged but falls dry at the surface for a considerable length of time, 4) the terrestrial phase – the water level is permanently below the surface of the soil. In the case of aquatic environment only two first typical

ecophases are important, but in the case of eulittoral zone of lakes all ecophases playing a serious rôle, in structure, zonation and succession of macrophytes.

The algae of lake eulittorals are less well known than macrophytes; the research in this respect is limited almost exclusively to sandy and stony eulittorals. Wiszniewski (1947) gives data on the algal occurrence in several habitats of the sandy beaches, and Neel (1948) presents detailed quantitative studies on this subject. Kann (1958, 1959, 1963) pays much attention to the ecology of algae to stony lake eulittorals. This author analysed in detail the occurrence of various species, which depended on the fluctuations of water level and wave intensity. Production of attached algae of the stony eulittoral was investigated by Felföldy (1961), among others.

Eulittorals of lakes examined here clearly differ in species composition, distribution and biomass of macrophytes (Bernatowicz 1960, Bernatowicz and Pieczyńska 1965, Bernatowicz, Pieczyńska and Radziej 1968, Bernatowicz 1969). Taking into consideration five water bodies intensively examined it has been found:

In lakes Śniardwy, Mikołajskie and Tałtowisko most of the shore is overgrown by *Phragmites communis* Trin.;

In lake Warniak the eulittoral is overgrown by several species found in similar proportions: *Phragmites communis*, *Carex* sp., *Equisetum limosum* L., *Menyanthes trifoliata* L., *Calla palustris* L. and *Cicuta virosa* L.;

In lake Flosek a considerable part of the shore is overgrown by *Sphagnum*. *Typha latifolia* L., *Phragmites communis*, *Menyanthes trifoliata* and *Carex* sp. sporadically are found.

The species of *Lemnaceae*, which are not found in deeper parts of littoral (especially in large lakes) are frequently noticed in the eulittoral of lakes Warniak, Mikołajskie, Tałtowisko and Śniardwy. In the eulittoral of all these lakes 3 species were found: *Lemna trisulca* L., *L. minor* L. and *Spirodella polyrrhiza* (L.) Schleiden. These species form two distinct groups: floating (frequently represented by the simultaneous occurrence of all three species or only one of them), and submerged (represented by *Lemna trisulca*). The *Lemnaceae* are a very significant element of the habitat in small lake-side water bodies. They quite often cover the entire surface, thus causing great oxygen deficits. In lake Warniak, during the years of these studies, the increase of the *Lemnaceae* was very pronounced. Bernatowicz (1969), when studying the macrophytes of that lake in 1966, did not observe any representatives of this family. In 1967 all three species were observed, and in the following years they became quite abundant.

Among the eulittoral algae of the lakes studied there are organisms connected to a various extent with the substrate. The attached (periphytonic) algae colonize stones, sticks, macrophytes and the like. In the intensively examined lakes (Mikołajskie, Śniardwy, Tałtowisko and Warniak) *Gloeotrichia pisum* (Agardh) Thuret, *Cladophora glomerata* (L.) Kütz and *Ephitemia argus* Kütz dominate¹. Planktonic forms we may also find in the eulittoral (*Gloeotrichia echinulata* is very abundant) as well as large colonies of blue-green and green algae loosely connected with the substrate, lying at the bottom or floating. Among the latter *Hydrodictyon reticulatum* (L.) Lagerh., *Nostoc pruniforme* Agardh, *Gloeotrichia natans* (Hedwig) Rabenh., and *Spirogyra* and *Cladophora* species are most frequently found. These algal species frequently develop abundantly in the eulittoral and usually are not found in deeper parts of lakes (Pieczyńska 1971). In the dystrophic lake Flosek algal appearances were very rare and they were usually composed of representatives of the genus *Peridinium*.

In other lakes, studied to a smaller extent (Tab. I) (apart from the dystrophic ones), the occurrence of considerable quantities of algae from various ecological groups was observed, as well as frequent monospecific mass appearances.

Fluctuations of water level in all the lakes affected different plants differently. During the years of study they did not affect most of the macrophytes (at least not noticeably). A marked dependence was observed only in the case of the *Lemnaceae*, which developed according to the formation of habitats having the character of quiet bays or small lake-side pools (during increased water level) or withered when the habitat dried up. In contrast the algae clearly reacted rapidly to quickly changing habitat conditions in the eulittoral. Their responses were characterized by violent changes in species composition and abundance, and by frequent brief mass monospecific occurrences (Pieczyńska 1971).

Animal communities. Studies of the eulittoral fauna have concentrated mainly on the microfauna of sandy beaches (Wiszniewski 1934, 1936a, b, 1947, Pennak 1939, 1940, Neel 1948, Stradowski 1964, Andrassy 1967, Altherr 1968 and others). Wasilewska (in press) presented the data on microfauna in several eulittoral habitats (sandy, stony and detritus substrate) in Mikołajskie Lake.

The studies of Rzóska (1935), Ökland (1964) and Furyk (1970) provide information about the macrofauna of several eulittoral habitats. The fauna of stony shores was analysed in detail by Moon (1934, 1935a, b). The fauna of this habitat in Mikołajskie Lake is discussed by Dusoge (1966).

¹I would like to thank Dr. I. Spodniewska, for help in indentifying the algae.

The occurrence of invertebrate macrofauna in
(prepared using the material

Invertebrate macrofauna	Emergent part of eulittoral						
	stones	sand	detritus	tree leaves	reed stalks	pools	Small lake-side water bodies
<i>Enchytraeidae</i> *		X	X	X	X	X	X
<i>Lumbricidae</i> *			X	X	X	X	X
<i>Lumbriculidae</i> *		X	X	X	X	X	X
<i>Naididae</i> *						X	X
<i>Tubificidae</i> *		X	X	X	X	X	X
<i>Hirudinea</i> *				X	X	X	X
<i>Asellus aquaticus</i> *			X	X	X	X	X
<i>Gammaridae</i>					X	X	X
<i>Collembola</i> *	X	X	X	X	X	X	
<i>Odonata</i>							X
<i>Coleoptera</i> *		X	X	X	X	X	X
<i>Heteroptera</i>							X
<i>Lepidoptera</i> *					X	X	X
<i>Ephemeroptera</i> *							X
<i>Trichoptera</i> *				X	X	X	X
<i>Sialis lutaria</i>			X	X	X	X	X
<i>Bibionidae</i> *			X	X	X	X	
<i>Chironomidae</i> *		X	X	X	X	X	X
<i>Culicinae</i> *						X	X
<i>Culicidae</i>							
<i>Chaoborinae</i>						X	X
<i>Cylindrotomidae</i> *			X	X	X	X	X
<i>Heleidae</i> *		X	X	X	X	X	X
<i>Liriopeidae</i> *			X	X	X	X	X
<i>Muscidae</i> *			X	X	X	X	X
<i>Psychodidae</i> *			X	X	X	X	X
<i>Stratiomyidae</i> *			X	X	X	X	X
<i>Syrphidae</i> *			X	X	X	X	X
<i>Tabanidae</i> *			X	X	X	X	X
<i>Tipulidae</i> *			X	X	X	X	X
<i>Araneina</i> *	X	X	X	X	X	X	X
<i>Limnaeidae</i> *				X	X		X
<i>Planorbidae</i> *				X	X	X	X
<i>Valvatidae</i> *							X
<i>Viviparidae</i>							X
<i>Hydrobiidae</i> *				X	X	X	X
<i>Succineidae</i> *				X			X
<i>Zonitidae</i> *	X		X	X	X	X	
<i>Helicidae</i> *			X	X	X	X	
<i>Unionidae</i>							
<i>Sphaeriidae</i> *						X	X
<i>Dreissenidae</i>							

*Organisms found in all 16 lakes.

various types of the eulittoral in Mikołajskie Lake
 compiled in years 1966–1969)

Tab. V

Submerged part of eulittoral				Maximum density (individuals per 1 m ²)
stones	sand	detritus	tree leaves	
	X	X	X	126000
		X	X	4800
X	X	X	X	4590
X	X	X	X	1030
X	X	X	X	18560
X	X	X	X	700
X		X	X	1970
X		X	X	380
				290
X		X		150
X	X	X	X	13700
		X		80
		X	X	420
X	X	X	X	1630
X	X	X	X	2150
X		X	X	120
				5120
X	X	X	X	9800
		X	X	2180
		X	X	80
		X	X	90
		X	X	3370
X		X	X	1540
				370
		X	X	12800
		X	X	398
		X	X	1830
		X	X	990
		X	X	2360
		X	X	470
X		X	X	200
X		X	X	2450
X	X		X	350
X		X		250
X	X	X	X	670
X			X	200
				1270
				280
	X	X		20
	X	X	X	370
X	X			590

Some data on the fauna of the eulittoral zone of lakes may also be found in limnological investigations of various lakes, when the authors included in their observations the eulittoral environments (usually to a small extent) (Borner 1921, Berg 1938, Entz and Sebestyèn 1946, Popov 1969).

All these studies point to an abundance of fauna in the lake eulittoral, and also to its considerable differentiation. In this habitat many species also common in the neighbouring zones of land and the littoral were reported, as well as the organisms typical for this zone. Feuerborn (1923) names the latter as fauna liminaria.

The eulittoral fauna is also discussed (in a little extent) in papers dealing with the effect of changes in water level in lakes on various communities of organisms (Grimås 1962, Hynes 1963).

In the present research quantitative studies of fauna were conducted in Mikołajskie Lake and lake Warniak. In other water bodies only qualitative analyses were made. The main objects of research were the macrofauna communities.

The eulittoral macrofauna of these water bodies includes representatives of several different systematic groups. In Table V the macrofauna of various habitats of the eulittoral of Mikołajskie Lake is compared. Because of the great habitat variability, and to avoid fortuitous conclusions, this analysis takes into consideration only materials from stations, which sustained the defining conditions (distance from the shore line, kind of substrate) for not less than 2 weeks.

In all types of eulittoral the *Oligochaeta* were the most numerous, represented by representatives of the families: *Enchytraeidae*, *Lumbricidae*, *Lumbriculidae*, *Tubificidae* and *Naididae* scarce. Among the *Lumbricidae*, *Eiseniella tetraedra* (Sav.)² clearly dominated, and frequently was the only representative of this family. The *Lumbriculidae* were represented mainly by *Lumbriculus variegatus* Müll., *Rhynchelmis limosella* Hoffm. and *Stylodrilus heringianus* Clap. Great specific differentiation was observed among the *Tubificidae*; *Tubifex tubifex* (Müll.), *Limnodrilus hoffmeisteri* Clap., *L. udekemianus* Clap., *Potamothrix hammoniensis* (Mich.), *Psammoryctides barbatus* (Grube) and *Tubifex ignotus* (Štolc) were abundant. The sporadically found *Naididae* were mainly represented by *Nais communis* Piguet. The *Enchytraeidae* (species not identified) were the most abundant of the *Oligochaeta*, and were found in the majority of eulittoral types.

In the eulittoral of Mikołajskie Lake *Diptera* are very abundant. Representatives of 12 families were found, with different patterns of occurrence (Tab. V).

²I would like to thank R. Wiśniewski, M. Sc. for indentifying the *Oligochaeta*.

The most common are *Chironomidae*, which are very abundant in the submerged eulittoral. In many types of eulittoral the *Culicidae* (mainly *Culicinae* and small numbers of *Chaoborinae*) and *Heleidae* were observed; they are most numerous in pools and small lake-side water bodies. *Tipulidae* and *Tabanidae* are also commonly found in the eulittoral. Representatives of other *Diptera* families are found in several types of eulittoral but their occurrence is rather irregular.

Coleoptera are found in the eulittoral in great numbers and are represented by 11 families³. The greatest number of beetles and the greatest differentiation in qualitative composition were observed in the emergent eulittoral. The *Helodidae* dominated there and in the submerged eulittoral they are found in very small numbers. *Silphidae*, *Driopidae*, *Staphylinidae*, *Carabidae*, *Haliplidae* and *Nitidulidae*, were observed in small numbers only in emergent part of eulittoral. In the submerged eulittoral the *Coleoptera* are much less abundant. Representatives of the *Dytiscidae*, *Hydrophilidae* and some few representatives of the *Gyrinidae*, *Chrysomelidae* and *Helodidae* were observed.

Among the *Mollusca* the representatives of 11 families were recorded (Tab. V). The snails were represented by 8 families with different patterns of distribution. Thus the *Helicidae*, among which *Zenobiella rubiginosa* (A. Schm.) dominated, and the *Zonitidae*, represented mainly by *Zonitoides nitidus* (Müll.) and *Retinella hammonis* (Ström), were found only in the emergent eulittoral. *Bithynia tentaculata* (L.) (*Hydrobiidae*) had the greatest range of occurrence and abundance. It was found in the majority of eulittoral types, but much more abundantly in small lake-side water bodies and in the submerged part of eulittoral. *Radix* sp. (*Limnaeidae*), *Planorbis planorbis* (L.) and *Coretus corneus* (L.) (*Planorbidae*) were found in great numbers. They lived in different habitats, and the two last species were very abundant in small lake-side water bodies. Other species were found in small numbers: *Gyraulus* sp. (*Planorbidae*), *Galba* sp. and *Limnaea stagnalis* (L.) (*Limnaeidae*), *Succinea* sp. (*Succineidae*), *Viviparus viviparus* (L.) (*Viviparidae*), *Valvata piscinalis* (Müll.) and *Valvata cristata* Müll. (*Valvatidae*). In the eulittoral of the lakes examined the bivalves were less abundant than the snails. *Dreissena polymorpha* was observed only in the submerged eulittoral, on sand and stones. Also the *Unionidae* were found in small numbers and only in the submerged eulittoral. The *Sphaeriidae* had a much wider range of occurrence but were not very abundant in the different eulittoral types (Tab. V). This analysis of the occurrence of the *Mollusca*, and of other groups of organisms, takes into account only live individuals. In the

³I would like to thank E. Nowak, M. Sc., for help in identifying the *Coleoptera*. In Table V the *Coleoptera* families are not listed as they only in part of the material have been identified.

case of bivalves numerous dead individuals on areas uncovered by a fall in water level were observed.

Representatives of *Diptera* (with the exception of *Chironomidae*, *Heleidae* and *Culicidae*) and the *Enchytraeidae*, *Lumbricidae*, *Collembola*, *Zonitidae* and *Helicidae* were not found in lake zones other than the eulittoral⁴. Among the other groups of organisms the *Lumbriculidae*, *Tubificidae*, *Gammaridae*, *Coleoptera*, *Culicinae*, *Heleidae*, *Planorbidae* and *Succineidae* are much more abundant in the eulittoral than in other lake zones, whereas the *Naididae*, *Hirudinea*, *Trichoptera*, *Chaoborinae*, *Hydracarina*, *Heteroptera* and *Odonata* are much less abundant there than in the deeper part of the lake, and the two last groups are quite accidental inhabitants of the eulittoral where they are very rare.

Particular types of eulittoral vary in abundance of fauna. The poorest in macrofauna is the habitat of sandy beaches, which, on the other hand, is known to be abundantly inhabited by microfauna (Wiszniewski 1934, Pennak 1939, 1940, Neel 1948, Wasilewska in press and others). It should be pointed out that this habitat can not be examined in detail using the present material, because it is not characteristic of the discussed lakes and it can be found only on small sections of the shore line. The stony eulittoral, abundantly inhabited in the submerged parts, is practically devoid of fauna in the emergent zone. Small lake-side water bodies and pools had the greatest number of components macrofauna. In these habitats the mass occurrence of certain groups of organisms (*Oligochaeta*, *Culicinae*, *Planorbidae*) was also frequently observed. Tree leaves and detritus had a much more abundant fauna in the emergent parts of the eulittoral than in the submerged parts.

In lake Warniak studies of the eulittoral fauna were conducted to estimate the abundance of the food for fish (Pieczyńska 1970). All the groups of fauna found in the eulittoral of Mikołajskie Lake were also found in the eulittoral of lake Warniak and the maximal number of the majority of representatives was approximately the same in both lakes.

In other lakes only qualitative samples were taken at 20–50 stations in each water body. Taking into consideration the whole material from each lake (samples from various stations), a great similarity in the composition of their fauna may be observed in all 16 examined water bodies, despite the fact that they clearly differ in limnological type (Tab. I). Namely, 80% of taxons

⁴To compare the occurrence of animals in the eulittoral and other zones of lake the data collected over several years by the staff of the Department of Hydrobiology of the Zoological Institute of the Warsaw University and Department of Hydrobiology, Institute of Ecology, Polish Academy of Sciences, were used. Part of these papers have been published and are cited in other parts of the present paper.

distinguished were common to all examined lakes (Tab. V). Other groups of organisms were observed in the eulittoral of many of the 16 lakes examined: *Chaoborinae* (9 lakes), *Dreissena polymorpha* (9 lakes), *Sialis lutaria* (8 lakes), *Viviparidae* (8 lakes), *Gammaridae* and *Unionidae* (6 lakes), *Odonata* and *Heteroptera* (5 lakes). Some of them (*Heteroptera* and *Odonata*) were found at a few stations in small numbers as in Mikołajskie Lake.

It was found that if a eulittoral type (sandy beach, stones, reed heaps, small lake-side pools) is represented in a particular lake, then its fauna contains characteristic representatives – the same in lakes of various limnological types. Thus, the great differentiation of eulittoral habitat in all examined lakes, previously described, explains the considerable similarity of fauna composition between particular water bodies treated as a unit. Dystrophic lakes (Tab. I) have the most distinctly characteristic fauna, and their small numbers. However, it is striking that dystrophic water bodies, having such a different eulittoral zone from the other lakes, have as much as 80% of macrofaunal groups in the eulittoral common with the other lakes.

Particular faunal groups, as in Mikołajskie Lake (Tab. V), vary in their development in different habitats of the eulittoral of the lakes examined. So, for example, the *Enchytraeidae* have the widest range of occurrence (observed in all eulittoral types). On the other hand, there are forms observed only in a few types of eulittoral: the *Collembola* – emergent eulittoral, *Dreissena polymorpha* – submerged stony or sandy eulittoral.

The great variety of habitat conditions is the reason why considerable differences are observed in the fauna composition and abundance on small areas. For a more thorough analysis of this subject 30 series of macrofauna samples were taken from an 8 m long shore section of Mikołajskie Lake in July 1967. The habitat examined (25 m² of surface) included the border of land and water and the neighbouring areas – emergent and submerged eulittoral. In this section the following habitats were distinguished: sand, gravel, tree leaves, reed stalks, plant detritus and pools (Fig. 18). On the area examined great differentiation in the abundance of fauna was observed: from 7 to 880 individuals per 100 cm² of substrate surface. As in the case of the differentiation of fauna in the eulittoral of Mikołajskie Lake, previously discussed, here also the macrofauna was most abundant in the pools on land close to the water line. Great density of fauna was also observed on the detritus in emergent part of eulittoral, and least density among tree leaves (in water) and in gravel and sand of the submerged and emergent eulittoral (Fig. 18 and 19). The average number of organisms in samples taken from under water was much smaller (31 individuals per 100 cm² of substrate surface) than in samples from the emergent part of

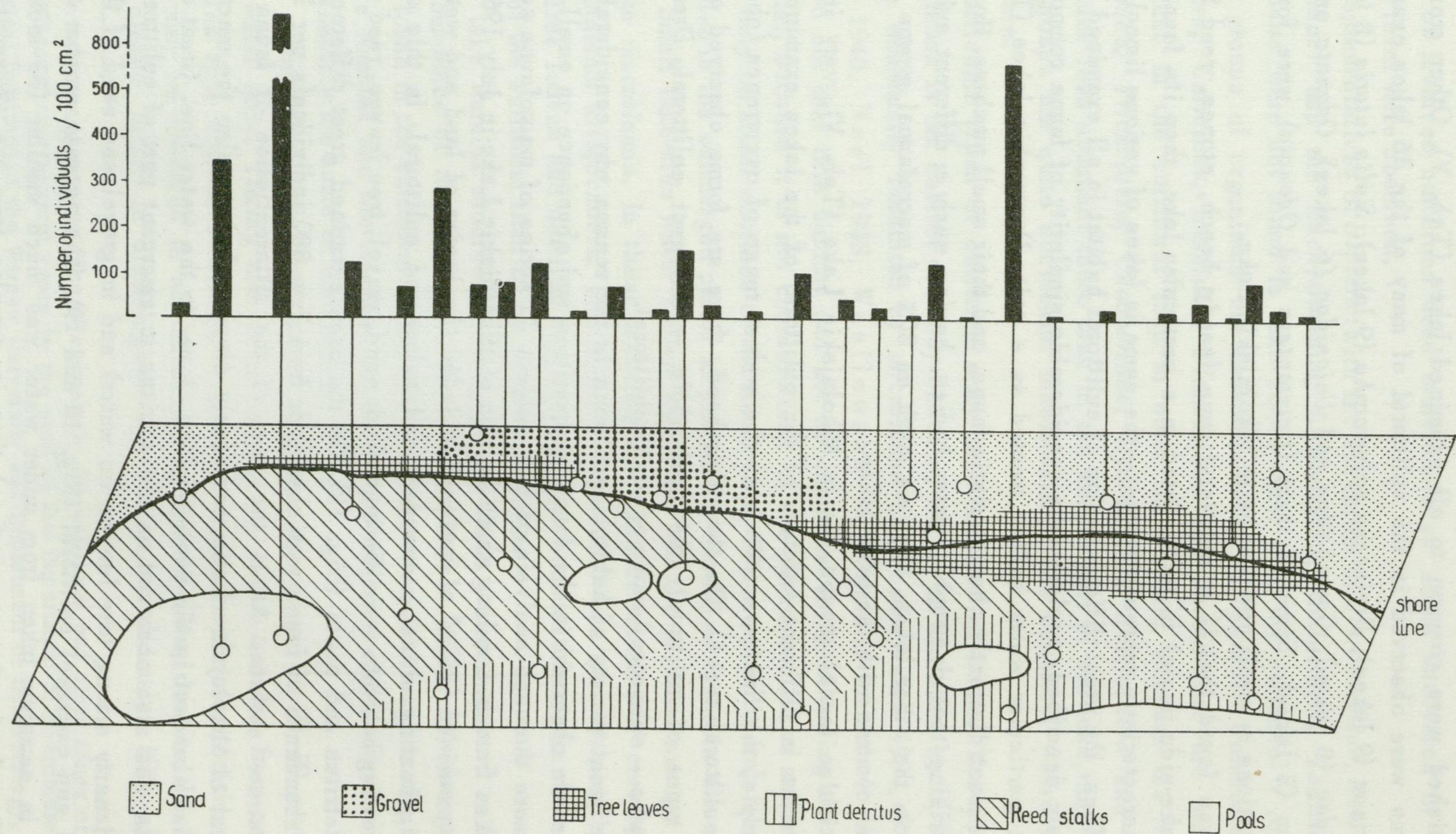


Fig. 18. Distribution of habitats and macrofauna densities in a chosen part of the eulittoral in Mikołajskie Lake (July 1967)

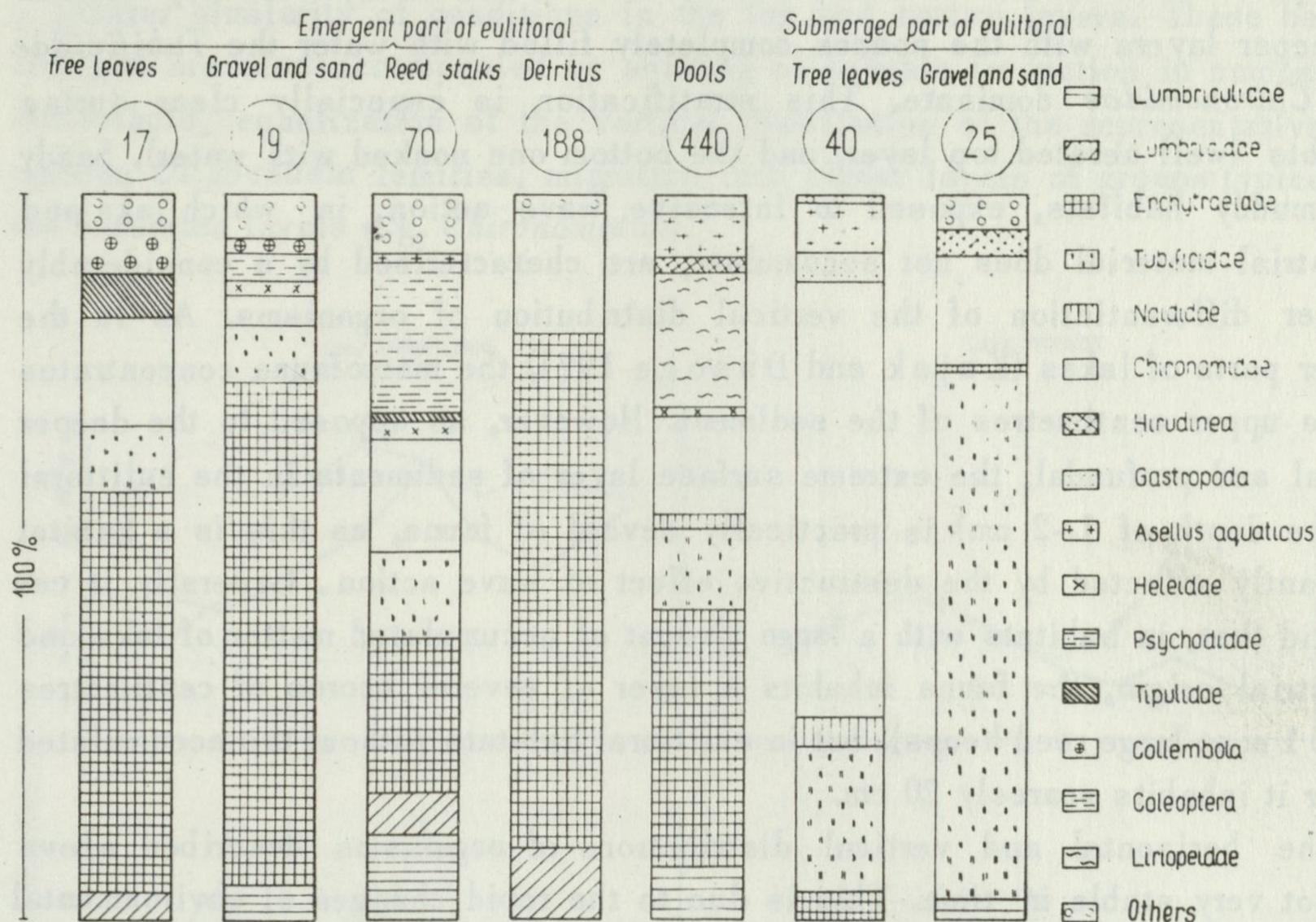


Fig. 19. Composition and density of macrofauna in various habitats in a chosen part of the eulittoral in Mikołajskie Lake

(Numbers in circles are the average numbers of all fauna groups per 100 cm² of substrate surface)

For the habitats see Fig. 18

eulittoral (98 individuals per 100 cm² of substrate surface). In the majority of samples from the emergent eulittoral the *Enchytraeidae* dominated, whereas in samples from under water it was the *Chironomidae* and *Tubificidae*. Pools and reed stalks in the emergent eulittoral were the most differentiated from the point of view of qualitative composition (Fig. 19). The fact that representatives of all five *Oligochaeta* families and the eight *Diptera* families were found in one sample (200 cm² surface) points to the great variety of this habitat.

The vertical faunal distribution in the eulittoral was found to be considerably differentiated. As has been previously described, the heaps of reed shoots, submerged vegetation, tree leaves and detritus form distinct layers creating different conditions for the fauna (varying water content, spatial structure, nutritive value and the like). The greatest differentiation of the vertical distribution has been observed on the border of land and water in habitats with a great amount of accumulated matter of terrestrial and lake origin. Top layers with large spaces filled with air are inhabited by terrestrial organisms (*Collembola*)

or amphibious ones (*Lumbricidae*, *Lumbriculidae*, and *Enchytraeidae*), whereas in deeper layers with the spaces completely filled with water the *Tubificidae* and *Chironomidae* dominate. This stratification is especially clear during droughts (well aerated top layer, and the bottom one soaked with water). Sandy and muddy habitats, exposed to intensive wave action, in which lake and terrestrial material does not accumulate, are characterised by a considerably smaller differentiation of the vertical distribution of organisms. As in the deeper parts of lakes (Kajak and Dusoge 1971) the macrofauna concentrates in the upper centimetres of the sediment. However, as opposed to the deeper littoral and profundal, the extreme surface layer of sediments in the eulittoral (to the depth of 1–2 cm) is practically devoid of fauna, as this is a habitat constantly affected by the destructive effect of wave action. Generally it can be said that, in habitats with a large amount of accumulated matter of lake and terrestrial origin, the fauna inhabits a layer of several scores of centimetres (up to 1 m at large reed heaps), but in eulittoral habitats without the accumulated matter it inhabits scarcely 20 cm.

The horizontal and vertical distributions of organisms described above are not very stable in time. This is due to the rapid changes of environmental conditions, especially water level fluctuations, accumulation and washing out of various kind of material. And so, changes in the composition and abundance of the fauna due to the shifting of the border of land and water have been observed. The point is that the number of typical aquatic forms (*Chironomidae*, *Tubificidae*, *Asellus aquaticus* and others) increased, whereas the number of amphibious forms (*Collembola*, *Lumbricidae*, *Enchytraeidae*) decreased in newly flooded areas. And reciprocally, when the water level fell in the open areas a reduction in number of the former, and the appearance of the latter was observed. The fauna also moves corresponding to other changes in the habitat. For example, it has been observed that on poorly colonized sandy shores, after the accumulation of macrophytes thrown out by the waves, various groups of organisms concentrate (*Mollusca*, *Oligochaeta* and others). These are very rapid changes. The colonization by macrofauna of new, convenient areas takes place on the average after three days. Subsequently the changes in composition of the macrofauna and their abundance are not great. Similarly, quick shifts of the eulittoral macrofauna, accompanying water level fluctuations and changes in trophic conditions of the habitat, have been observed by Moon (1935a). He gives an example of the appearance of actively moving fauna (*Gammarus*, *Ecdyonurus*, *Isopteryx*) in areas flooded only for 8 hours.

The vertical distribution of organisms in the emergent eulittoral, and at the border of land and water, changes depending on precipitation, which produces

a greater similarity of conditions in the top and bottom layers. These habitat changes are also accompanied by shifting of animals (reduction in numbers of *Collembola*, equalization of the vertical distribution of the representatives of various *Oligochaeta* families, migration into higher layers of groups typical for the saturated layers e.g. *Chironomidae*).

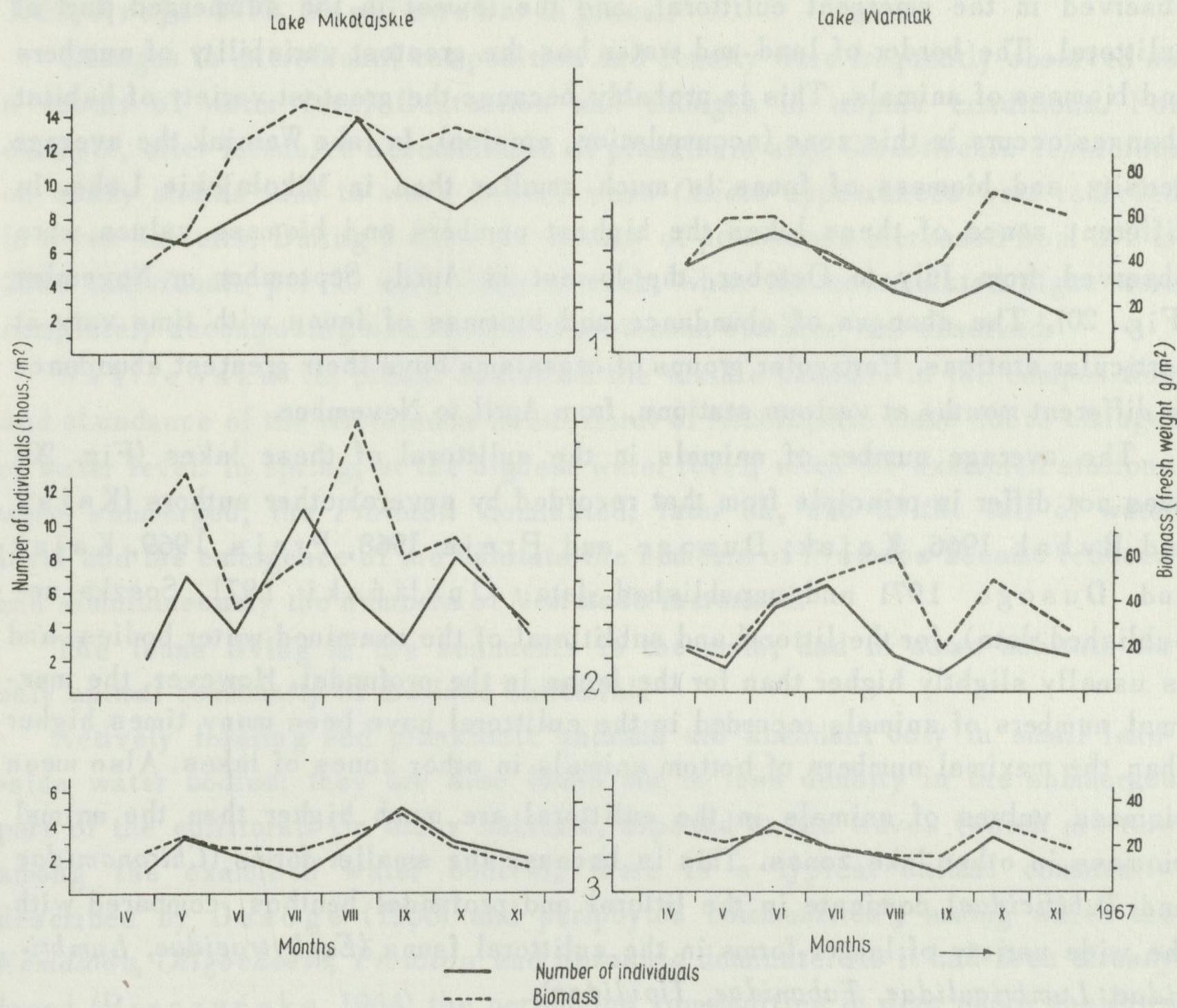


Fig. 20. Changes in macrofauna numbers and biomass in the eulittoral of lakes Mikołajskie and Warniak

1 - emergent part of eulittoral, 1 m from the shore line, 2 - shore line, 3 - submerged part of eulittoral, 1 m from the shore line

Frequent and variable changes in habitat conditions and the accompanying changes in composition and abundance of the fauna produce great difficulties in estimating the dynamics of faunal numbers in the annual cycle. Changes with time in the faunal composition and abundance are a result of regular seasonal changes and irregular changes in living conditions (periodical flooding and emergence, brief improvement or worsening of oxygen, trophic condition and the

like). The latter are different for various stations, even within one water body. Despite these difficulties the seasonal changes of the number and biomass of macrofauna inhabiting sediments in the eulittoral of lakes Warniak and Mikołajskie were compared (Fig. 20). The averages of 12 stations for each lake are used.

In both lakes the highest density and biomass of macrofauna have been observed in the emergent eulittoral, and the lowest in the submerged part of eulittoral. The border of land and water has the greatest variability of numbers and biomass of animals. This is probably because the greatest variety of habitat changes occurs in this zone (accumulation, erosion). In lake Warniak the average density and biomass of fauna is much smaller than in Mikołajskie Lake. In different zones of these lakes the highest numbers and biomass values were observed from July to October, the lowest in April, September or November (Fig. 20). The changes of abundance and biomass of fauna with time vary at particular stations. Particular groups of organisms have their greatest abundance in different months at various stations, from April to November.

The average number of animals in the eulittoral of these lakes (Fig. 20) does not differ in principle from that recorded by several other authors (Kajak and Rybak 1966, Kajak, Dusoge and Prejs 1968, Prejs 1969, Kajak and Dusoge 1971 and unpublished data, Opaliński 1971, Soszka unpublished data), for the littoral and sublittoral of the examined water bodies, and is usually slightly higher than for the fauna in the profundal. However, the maximal numbers of animals recorded in the eulittoral have been many times higher than the maximal numbers of bottom animals in other zones of lakes. Also mean biomass values of animals in the eulittoral are much higher than the animal biomass in other lake zones. This is because the smaller forms (*Chironomidae* and *Tubificidae*) dominate in the littoral and profundal benthos, compared with the wide variety of larger forms in the eulittoral fauna (*Enchytraeidae*, *Lumbricidae*, *Lumbriculidae*, *Tabanidae*, *Tipulidae*).

The microfauna colonizing the eulittoral sediments of the examined lakes is composed of the abundant *Nematoda*, *Protozoa* and *Rotatoria* and the less numerous *Tardigrada*, *Copepoda*, *Cladocera* and *Ostracoda*. The studies conducted in Mikołajskie Lake within the present research, and the paper by Wasilewska (in press) show that the *Protozoa* (among which the *Ciliata* dominate) are most abundant at the water body border and in the submerged eulittoral, the *Rotatoria* dominate on the border of land and water and in the emergent eulittoral, and the *Nematoda* are most abundant in the emergent part of eulittoral. The variability in composition of the microfauna and their abundance is quite large and considerably exceeds the previously described differentiation of the

macrofauna. The groups dominating in the eulittoral of Mikołajskie Lake attain the following maximal densities (per 10 cm² of substrate surface): *Protozoa* 5500 individuals, *Rotatoria* 980 and *Nematoda* 1650. The average and maximal microfaunal numbers in the eulittoral are in the majority of instances higher than the microfaunal number in the bottom sediments of littoral and profundal (Stańczykowska 1967, Stańczykowska and Przytocka-Jusiak 1968, Prejs 1970, Wasilewska in press).

Changes in microfaunal composition and density were frequently observed as a result of water level fluctuation and changes in trophic conditions. For example, after intensive accumulation of planktonic alga *Gloeotrichia echinulata* on sandy shores (due to wave action) mass *Ciliata* appearances were recorded in these habitats. During 3 days the density of protozoans increased from 292 to 2880 individuals per 10 cm². After a week, when the accumulated algae were completely decomposing a reduction of protozoan numbers was observed.

Wasilewska (in press) described the visible changes in the composition and abundance of the microfauna in eulittoral of Mikołajskie Lake due to changes of water level. In spring, at the highest water level, when the examined stations were submerged, the *Protozoa* dominated; later on, due to the fall of water level and the emergence of the habitats the numbers of *Protozoa* became reduced and simultaneously the numbers of *Nematoda* increased.

The fauna living in the sediments is the main, and in some habitats the only animal community of the lake eulittoral.

Actively floating and planktonic animals are abundant only in small lake-side water bodies; they are also found but in less density in the submerged part of the eulittoral. On stony habitats, exposed to the waves (which are rare among the examined water bodies), there is a typical animal community described by Dusoge (1966) and periphyton communities⁵, among which the *Nematoda*, *Oligochaeta*, *Protozoa* and *Rotatoria* dominate. As it had been already found (Pieczyńska 1964) the periphyton communities in near shore shallows have a much greater variability in time and space than the periphyton in deeper littoral parts.

In a very few eulittoral habitats distinct communities of animals related to the macrophytes can be distinguished as well as the communities of bottom fauna. Such differentiation has been observed for example in lake Warniak in submerged eulittoral overgrown by *Menyanthes trifoliata* and *Stratiotes aloides*, which are sheltered from the waves. In these habitats the quantitative samples

⁵The term periphyton as used in this paper means both plant and animal organisms colonizing all kinds of submerged substrates projecting above the bottom. The terminological problems were discussed earlier by Pieczyńska (1964).

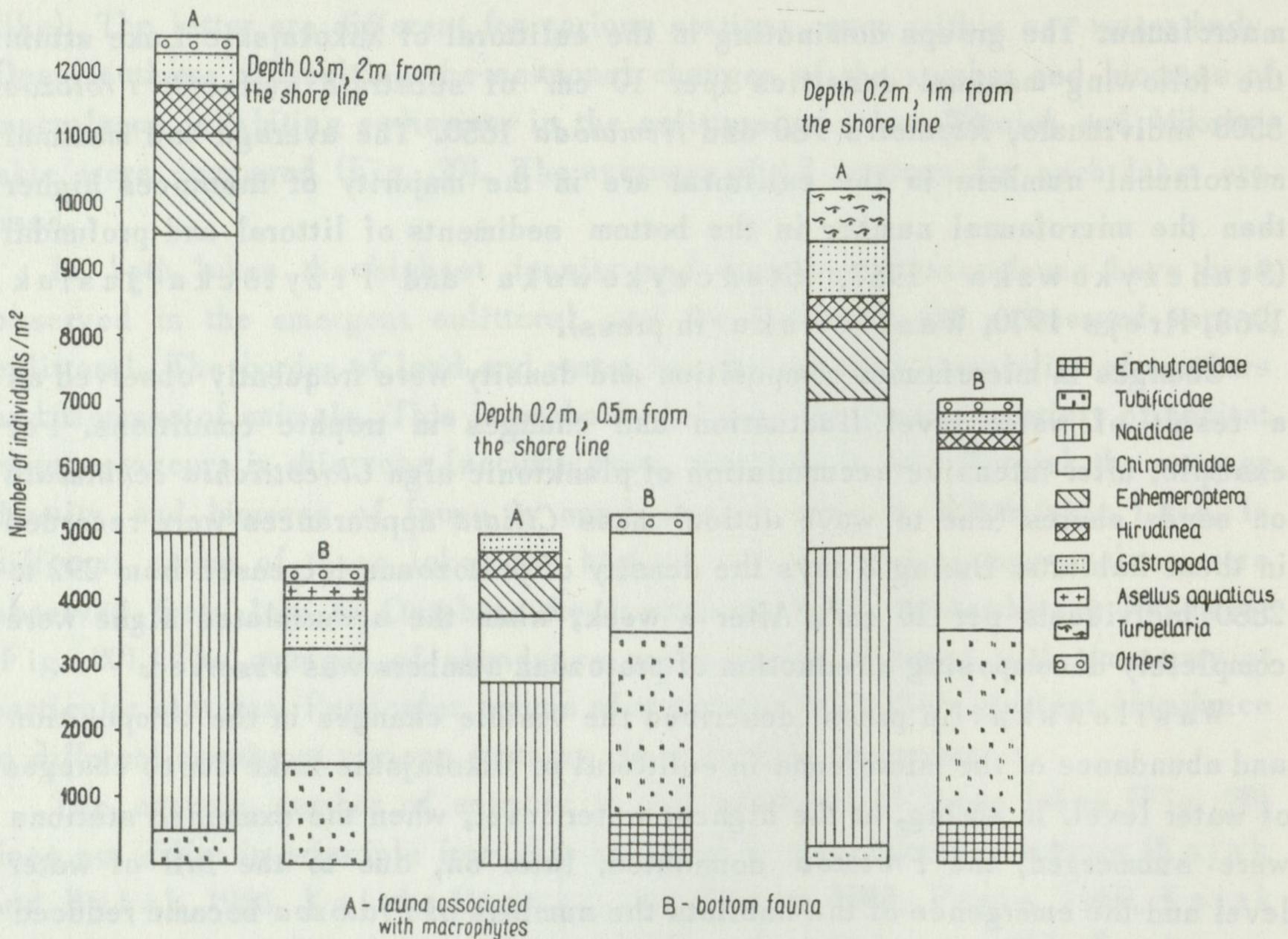


Fig. 21. Numbers and composition of macrofauna in bottom sediments and on macrophytes at three stations of lake Warniak

of benthos and fauna on vegetation were taken separately. This comparison is shown in Figure 21. Each station represents the average of 20 samples. Although at all stations the water depth did not exceed 30 cm, separate communities may be observed differing basically in their qualitative composition (Fig. 21). In the majority of instances the numbers of animals living on plants were greater than of those living in the sediments (density of animals is expressed in numbers of individuals per 1 m² of surface of examined eulittoral station). The differentiation of communities described is very rarely observed in the eulittoral. Most frequently the small depth, water movement and activity of fauna are the reasons why the eulittoral fauna clearly forms one community.

V. PRIMARY PRODUCTION AND ALLOCHTHONOUS MATTER

In the eulittoral of the examined lakes three sources of organic matter may be distinguished: 1) Matter produced in the eulittoral by the producers living in this habitat; 2) Accumulated matter of lake origin (produced in other

parts of the lake but brought into eulittoral due to wave action); 3) Accumulated matter of terrestrial origin.

The great variety of conditions existing in the eulittoral, previously discussed, suggests that the proportions of these kinds of matter, their rôle and their fate in various eulittoral habitats may be different.

The material reaching the eulittoral from the adjacent areas not only provides organic matter, but is also the source of mineral salts.

1. Primary production

Primary production of macrophytes and algae has been examined in lakes Mikołajskie, Flosek, Śniardwy, Tałtowisko and Warniak.

In Mikołajskie Lake net primary production in the eulittoral is 2100 kcal/m², of which 72% is algal production (Pieczyńska 1972a). The algae are the most variable element of primary production in the eulittoral. Attached to the substrate, planktonic and loosely connected with substrate or lying on the bottom algae are all represented by species having various life cycles and ecological requirements. Thus, in different eulittoral habitats and in different periods of time considerable differences are observed in the production and the composition of the producing community. In papers on the littoral primary production of the examined lakes (Pieczyńska 1965, 1968, 1971, Pieczyńska and Szczepańska 1966) the decisive significance of mass algal appearances is pointed out. In the eulittoral, as compared with other lake habitats, mass appearances are much more frequently observed, and during their occurrences the biomass and production rate is several times higher than in other lake habitats (Pieczyńska 1971). This is true of different ecological groups of algae. Thus, the studies conducted in Mikołajskie Lake in the years 1966–1969 gave the following values for the maximal planktonic algae biomass (in mg fresh weight per dm³): pelagial – 31 (Spodniewska unpublished data), littoral overgrown with submerged vegetation – 34, littoral overgrown with emergent vegetation – 41, and in the submerged eulittoral – 86. Mass algal appearances in the pelagial are usually formed by several species occurring in similar proportions (Spodniewska 1967, 1969). Most of the planktonic algae which form blooms in the pelagial are often abundant in the littoral but the one species, *Gloeotrichia echinulata* occurs most frequently and in larger quantities. In the eulittoral only this species is abundant among planktonic algae during their mass appearance. The great quantities of this species may, in

some eulittoral habitats, be partly the result of accumulation due to wave action. This will be discussed further in the paper. The greatest intensity of mass appearance of other groups of algae was also observed in the eulittoral. In the same years the highest biomass of attached algae was 810 mg/dm³ in the eulittoral while 590 in littoral. Biomass of loosely connected with substrate, lying on bottom or floating algae (*Hydrodictyon reticulatum*, *Gloeotrichia natans*, *Nostoc pruniforme*, and *Spirogyra* and *Cladophora* species) was the highest. Maximal value 5324 mg fresh weight per dm³, was several times higher than the maximal biomass of all other groups of algae in remaining part of the lake.

The algal biomass during the period of mass appearance calculated per 1 m² of surface of the discussed zones is also much greater in the eulittoral than in littoral and pelagial despite the considerable differences in the depth of these zones and therefore the size of accessible habitat. In Mikołajskie Lake the mean depth of pelagial is 15.5 m, in littoral overgrown with emergent vegetation 1.0 m, and in eulittoral only 0.3 m. For example in 1966 in the eulittoral the algal biomass was the highest, 1407 g fresh weight per m², while in the littoral (emergent vegetation zone) it was 405 g per m², and in the pelagial 104 g per m².

Differences between the production rate of algae in compared zones of lake are less distinct but the greatest values were also observed in the eulittoral. Maximal value of gross primary production in the submerged eulittoral of Mikołajskie Lake was noticed in August 1967 during mass appearance of *Hydrodictyon reticulatum* and it was 40.7 mg O₂ per dm³ per day (Pieczyńska 1971).

Among the eulittoral macrophytes in Mikołajskie Lake the most abundant is reed (63% of biomass of all plants). In the majority of instances this species has greater biomass in the eulittoral than in deeper littoral parts. Kowalczewski and Wasilewski (1966) say that the average reed biomass (in g of dry weight/m²) during the time of flowering, treated as annual production, is 810 at 0.1 m deep, 690 at 0.3 m, and 502 at 0.7 m. These differences are the result of reed density increasing as depth decreases.

Among other macrophyte species *Equisetum limosum* and *Acorus calamus* have greater biomass in the eulittoral than in the deeper littoral parts of this lake, and *Potamogeton lucens* and *P. perfoliatus* have lesser biomass.

Undoubtedly the main factor responsible for the high primary production values in the submerged eulittoral is the previously described great quantity of mineral salts. On the other hand, the light conditions are a factor limiting the production in many habitats. In shaded parts of the eulittoral the recorded production values were never greater than the primary production in pelagial and littoral.

The occurrence of producers, and especially algae, in the eulittoral is characterized by a great variability as compared with the littoral and pelagial. In some habitats the producers develop abundantly, and in others not at all. Furthermore, production in the eulittoral is taking place for only part of the year, because of the periodical emergence of this part of the water body due to water level fluctuation and total freezing during the winter. Therefore, despite such great periodical intensities of production processes the mean annual values of algal production are lower than the primary algal production in the zone of emergent vegetation.

The annual macrophyte production in the whole eulittoral is smaller than in the zone of emergent vegetation. This is because relatively large parts of the eulittoral are devoid of macrophytes.

The share of various groups of producers in the yearly net primary production of the eulittoral and littoral overgrown with emergent vegetation in Mikołajskie Lake

Tab. VI

Producers		Eulittoral		Littoral overgrown with emergent vegetation	
		kcal/m ²	%	kcal/m ²	%
Macrophytes		588	28	2711	57
Algae	planktonic	210	10	929	20
	attached to the substrate	861	41	1096	23
	loosely connected with the substrate and floating	441	21	—	—
Total		2100	100	4736	100

Annual net primary production (all groups of producers) in the eulittoral of Mikołajskie Lake is 2100 kcal/m², and is much lower than the annual primary production of littoral overgrown with emergent vegetation (4736), of littoral overgrown with submerged vegetation (3376), and of pelagial (3312 kcal/m²).

The share of various groups of producers in the eulittoral production is basically different than in the neighbouring zone — littoral overgrown with emergent vegetation (Tab. VI). In the latter the macrophytes are the main producers (57%), which only contribute 28% of annual production in the submerged eulittoral. The most important producers in the eulittoral are the attached (periphytic) algae (41%). Loosely attached to the substrate, floating and lying at the bottom algae are also of great importance (21%). They are practically not represented in the littoral zone overgrown with emergent vegetation (Tab. VI).

Primary production of the eulittoral has also been analysed, but less intensively, in lakes Flosek, Śniardwy, Tałtowisko and Warniak, limiting the studies of algae. These lakes clearly differ in the species composition of pelagic algae and in their production (Hillbricht-Ilkowska and Spodniewska 1969, Hillbricht-Ilkowska et al. 1972).

In the littoral of these lakes the studies of primary production included only some groups of producers (Bernatowicz and Pieczyńska 1965, Pieczyńska 1965, Pieczyńska and Szczepańska 1966, Bernatowicz, Pieczyńska and Radziej 1968, Pieczyńska 1971). A comparison of the above mentioned lakes and the previously discussed Mikołajskie Lake showed that primary production in the littoral was the most intensive in Mikołajskie Lake, slightly lower in the littoral of lakes Tałtowisko and Warniak, much lower in lake Śniardwy and the lowest in lake Flosek.

The submerged eulittoral of all these lakes is characterised by a considerably higher biomass of algae and more intensive primary production than the littoral and pelagial. Determining the biomass of different ecological groups of algae during the mass appearances in littoral and eulittoral zones, it was found that the highest values in all lakes were observed in the eulittoral. Also in this habitat the greatest frequency of occurrence of mass appearances was noticed. In 1966–1969 the greatest biomass values of periphytonic algae (1020 mg fresh weight/dm³) and loosely connected with the substrate (6110 mg/dm³) were found in the eulittoral of lake Śniardwy, and of planktonic algae (86 mg/dm³) in the eulittoral of Mikołajskie Lake (Pieczyńska 1971).

Primary production of algae was observed to be most intense in the eulittoral of lake Śniardwy, lower in lakes Mikołajskie and Warniak, much lower in lake Tałtowisko and lowest in lake Flosek. At various stations and at different time various groups of producers were observed to be the dominant.

The variability in intensity of gross primary production in four lakes was compared on the basis of measurements made in July, August and September 1967, on 6 stations of each lake (Fig. 22). The fact that, despite the considerable differences in production between the compared lakes, the differences in the share of particular ecological groups of algae are greater in the successive months in one water body than in different lakes (Fig. 22) points to the great variability of conditions in the eulittoral.

Intensity of primary production in the pelagial and littoral of the lakes compared is different from that in the eulittoral (only in lake Flosek have both these habitats the lowest production values). The greatest differences are observed in lake Śniardwy. In the pelagial and littoral of this lake lower primary production values are observed than in the corresponding zones of

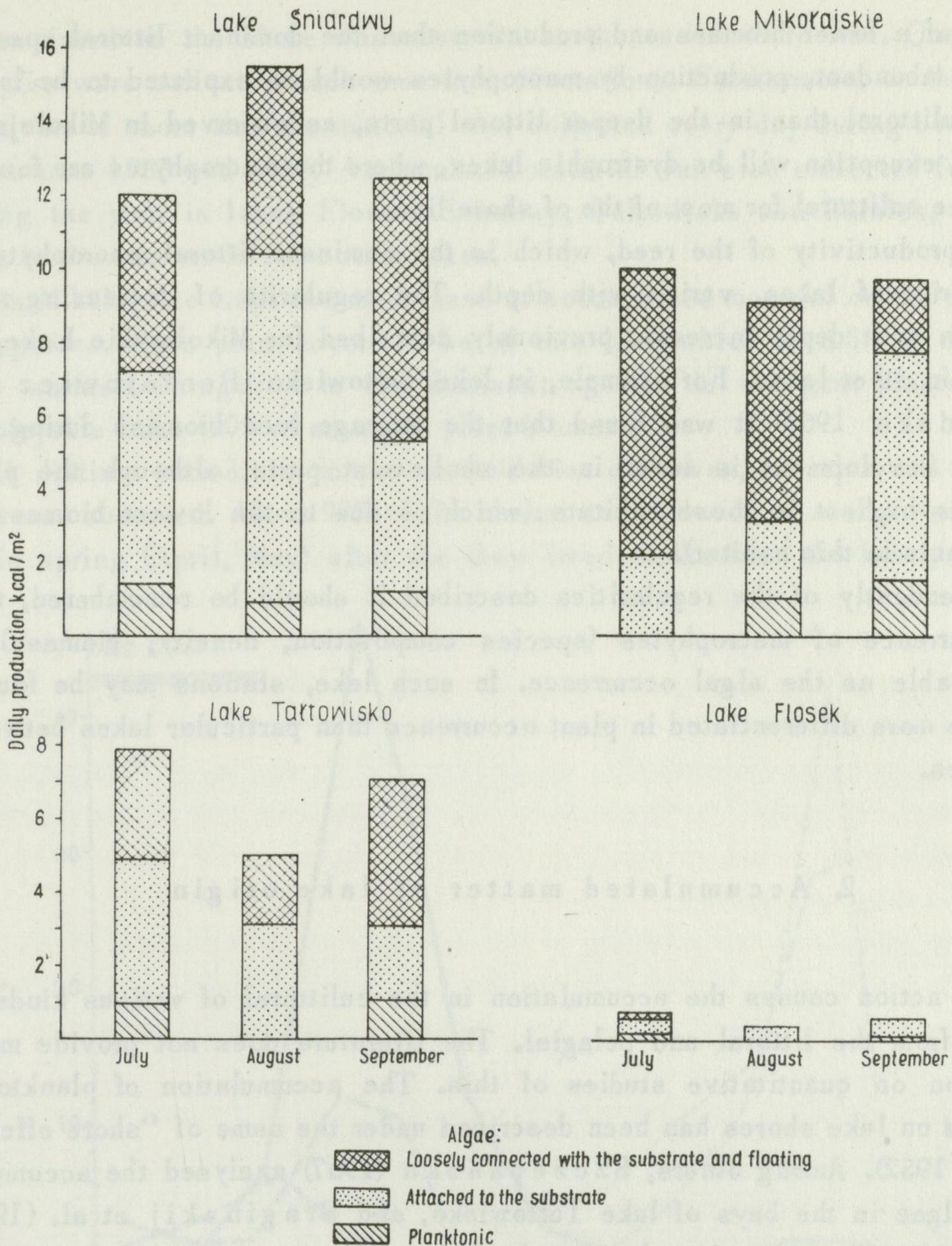


Fig. 22. Gross primary production of algae in four Masurian lakes, summer 1967

lakes Mikołajskie and Tałtowisko (Kajak, Hillbricht-Ilkowska and Pieczyńska 1972). Whereas in the eulittoral the greatest primary production values are observed and the most frequent mass algal appearances (Fig. 22, Pieczyńska 1971). The vast eulittoral of lake Śniardwy, partly isolated from the central part of the lake, have a good light condition, and is rich in nutritive substances. Such habitats are good for intensive primary production.

The macrophytes production in the other water bodies, apart from Mikołajskie Lake, has not been examined, but taking into consideration that some eulittoral parts of all lakes are not overgrown with vegetation, and that plant

species of a lower biomass and production than the dominant littoral species are more abundant, production by macrophytes would be expected to be lower in the eulittoral than in the deeper littoral parts, as observed in Mikołajskie Lake. An exception will be dystrophic lakes, where the macrophytes are found only in the eulittoral for most of the of shore line.

The productivity of the reed, which is the dominant littoral macrophyte of the majority of lakes, varies with depth. The regularity of decreasing reed production with depth increase, previously described for Mikołajskie Lake, is different in other lakes. For example, in lake Tałtowisko (Bernatowicz and Pieczyńska 1965) it was found that the average reed biomass during the maximum development is least in the shallowest parts, although the plant density is highest in these habitats (which is due to the lowest biomass of single plants in this habitat).

Independently of the regularities described it should be remembered, that the occurrence of macrophytes (species composition, density, biomass) is very variable as the algal occurrence. In each lake, stations may be found, which are more differentiated in plant occurrence than particular lakes between themselves.

2. Accumulated matter of lake origin

Wave action causes the accumulation in the eulittoral of various kinds of material from the littoral and pelagial. The literature does not provide much information on quantitative studies of this. The accumulation of planktonic organisms on lake shores has been described under the name of "shore effect" (Welch 1952). Among others, Szczepańska (1967) analysed the accumulation of algae in the bays of lake Tałtowisko, and Braginskij et al. (1968) the accumulation of blooming algae on the shores of dam reservoirs.

Young (1945) describes the accumulation of plankton and periphytic organisms detached from the substrate on the shores of lake Douglas exposed to strong waves. Neel (1948), conducting his studies in the same lake, gives numerous examples of accumulation of planktonic organisms and detritus on the shores. Also Sebestyèn (1950) describes the accumulation of detritus of various origin on the shores of lake Balaton. Some data on accumulation of macrophytes due to wave action are given by Björk (1967) and Hejný (1971).

Quantitative studies of the accumulation of various materials of lake origin, with consideration to the changes in the annual cycle, were conducted in Mikołajskie Lake in the years 1967 and 1968. Once a month, the material

accumulated on the shore was observed on the entire shore line. Quantitative samples were collected each time from 60 stations. Furthermore, on the chosen sections of shore line the material was collected every day during two months in summer 1967 and 1968. Accumulated material was also collected four times during the year in lakes Flosek, Śniardwy, Tałtowisko and Warniak, and only once in the summer in some other lakes.

In Mikołajskie Lake the main mass of accumulated material on the shores is *Phragmites*. This plant covers 39 ha of this lake which is 8.5% of the total lake surface. *Phragmites* is the dominant species in emergent plants zone of Mikołajskie Lake (90% of emergent plant biomass).

A distinct periodicity in the accumulation of leaves, panicles and stalks of reed was observed. About 90% of the annual accumulation of stalks was observed in spring (April, May) after the thaw (reed stalks from the last year). The

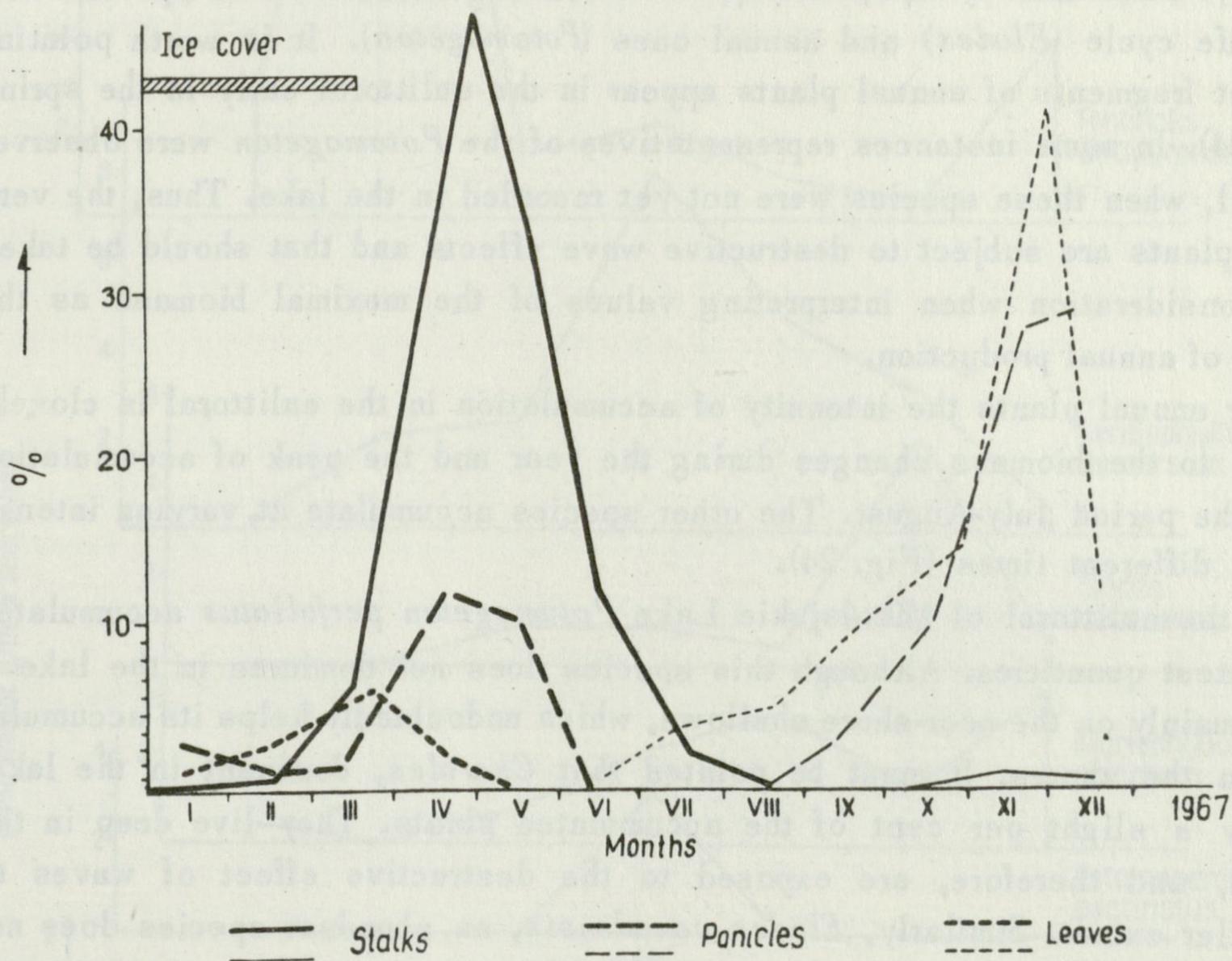


Fig. 23. Accumulation of panicles, leaves and stalks of reed in the eulittoral of Mikołajskie Lake (in % of total yearly accumulation)

Thin lines — this year's plants, thick lines — last year's plants

leaves accumulate in the eulittoral mainly in late autumn (over 80% of annual accumulation — leaves of this year's plants) and in spring (last year's — over 10%). The panicles accumulate most intensively in autumn and spring. During

the summer (June-September) the accumulation of reeds is minimal (Fig. 23). The factors differentiating the intensity of reed accumulation in the successive years and different lakes are first of all the freezing period, velocity and wind direction. Because the stalk forms the main mass of the parts of the plant aboveground, the periods of most intensive stalk accumulation therefore, decide the changes in the annual cycle of the total reed mass accumulation. The yearly accumulation of reed in eulittoral of Mikołajskie Lake is on the average 7900 g of dry weight per 1 m of shore line.

The accumulation of all species of submerged vegetation recorded in Mikołajskie Lake has been observed on its shores. In this lake the submerged vegetation covers 48 ha, which is 10.4% of the lake surface. The following species dominate (proportion in biomass is taken into account): *Charales*, *Ceratophyllum demersum*, *Elodea canadensis*, *Fontinalis antipyretica*, *Potamogeton perfoliatus* and *Myriophyllum spicatum*. Among these we find species with long life cycle (*Elodea*) and annual ones (*Potamogeton*). It is worth pointing out that fragments of annual plants appear in the eulittoral early in the spring (Fig. 24). In some instances representatives of the *Potamogeton* were observed in April, when these species were not yet recorded in the lake. Thus, the very young plants are subject to destructive wave effects and that should be taken into consideration when interpreting values of the maximal biomass as the amount of annual production.

For annual plants the intensity of accumulation in the eulittoral is closely related to the biomass changes during the year and the peak of accumulation is in the period July-August. The other species accumulate at varying intensities at different times (Fig. 24).

In the eulittoral of Mikołajskie Lake *Potamogeton perfoliatus* accumulates in greatest quantities. Although this species does not dominate in the lake it grows mainly on the near-shore shallows, which undoubtedly helps its accumulation on the shores. It must be pointed that *Charales*, dominant in the lake, is only a slight per cent of the accumulated plants. They live deep in the littoral, and therefore, are exposed to the destructive effect of waves to a smaller extent. Similarly, *Elodea canadensis*, an abundant species does not accumulate very intensively. *Ceratophyllum demersum* and *Fontinalis antipyretica* observed in great quantities in the lake, have been also found in considerable numbers in the eulittoral.

In the eulittoral of Mikołajskie Lake the accumulation of *Myriophyllum spicatum*, *Potamogeton lucens*, *P. pectinatus* and *Batrachium circinatum* was also often observed (Fig. 24). The *Charales*, *Nuphar luteum*, *Nymphaea alba*, *Utricularia vulgaris*, *Potamogeton compressus* and others were found sporadically.

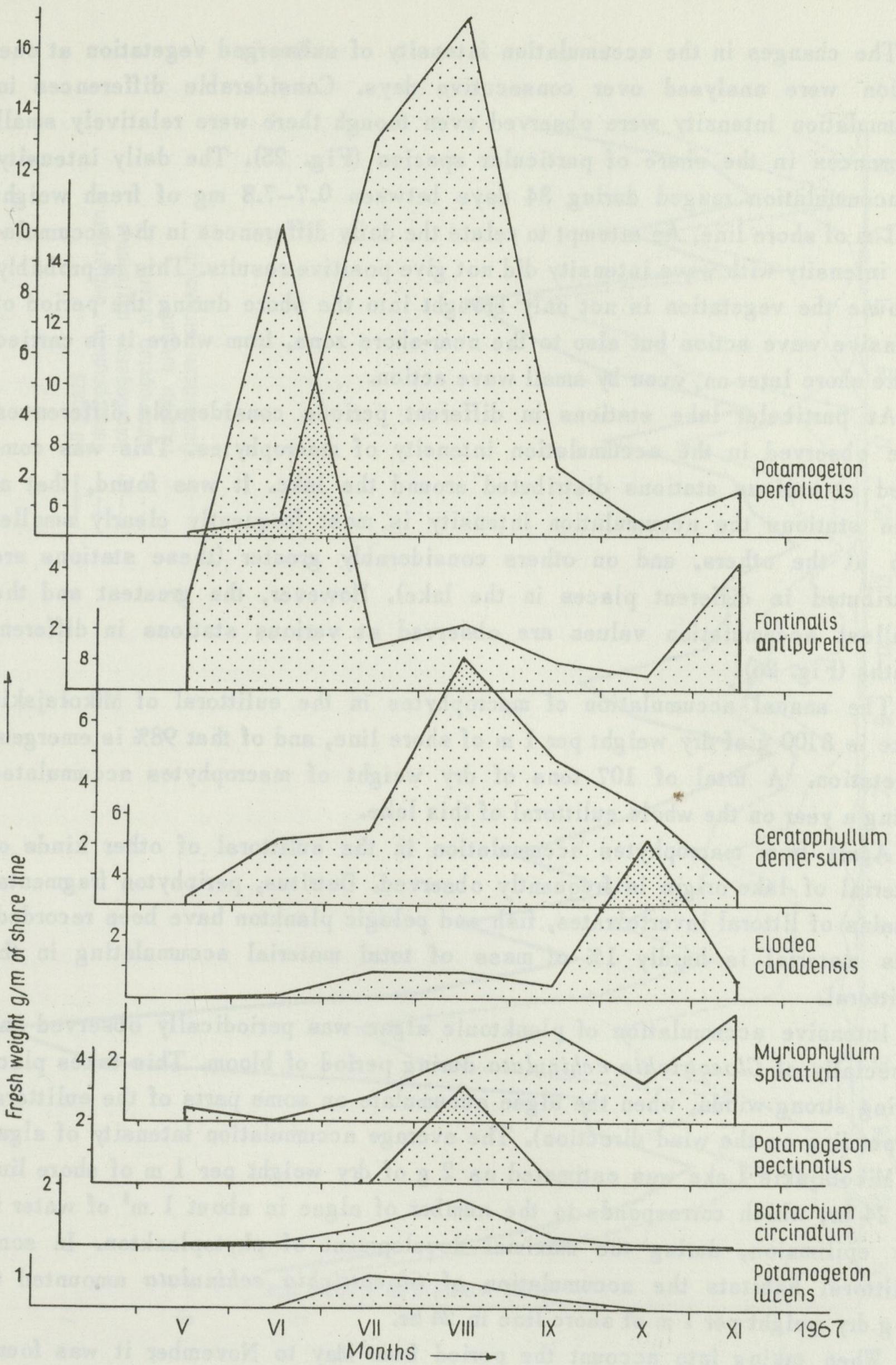


Fig. 24. Accumulation of dominant species of submerged vegetation in the eulittoral of Mikołajskie Lake

The changes in the accumulation intensity of submerged vegetation at one station were analysed over consecutive days. Considerable differences in accumulation intensity were observed even though there were relatively small differences in the share of particular species (Fig. 25). The daily intensity of accumulation ranged during 34 days between 0.7–7.8 mg of fresh weight per 1 m of shore line. An attempt to relate the daily differences in the accumulation intensity with wave intensity did not give positive results. This is probably because the vegetation is not only brought into the shore during the period of intensive wave action but also to the near-shore zone, from where it is carried to the shore later on, even by small wave action.

At particular lake stations in different periods considerable differences were observed in the accumulation intensity of macrophytes. This was compared at various stations distributed around the lake. It was found, that at some stations the accumulation intensity is most frequently clearly smaller than at the others, and on others considerably greater (these stations are distributed in different places in the lake). However, the greatest and the smallest accumulation values are observed at various stations in different months (Fig. 26).

The annual accumulation of macrophytes in the eulittoral of Mikołajskie Lake is 8100 g of dry weight per 1 m of shore line, and of that 98% is emergent vegetation. A total of 107 tons of dry weight of macrophytes accumulates during a year on the whole eulittoral of this lake.

Apart from macrophytes accumulation in the eulittoral of other kinds of material of lake origin is frequently observed. Detritus, periphyton fragments, remains of littoral invertebrates, fish and pelagic plankton have been recorded. This material is hardly 1% of mass of total material accumulating in the eulittoral.

Intensive accumulation of planktonic algae was periodically observed and especially of *Gloeotrichia echinulata* during period of bloom. This takes place during strong winds, when the algae accumulate on some parts of the eulittoral (depending on the wind direction). The average accumulation intensity of algae in Mikołajskie Lake was estimated as 2 g of dry weight per 1 m of shore line in 24 hr, which corresponds to the number of algae in about 1 m³ of water in the epilimnion, during the maximal development of phytoplankton. In some eulittoral habitats the accumulation of *Gloeotrichia echinulata* amounted to 20 g dry weight per 1 m of shore line in 24 hr.

When taking into account the period from May to November it was found that each time 90% or more of shore line length was covered by the accumulated material of lake origin.

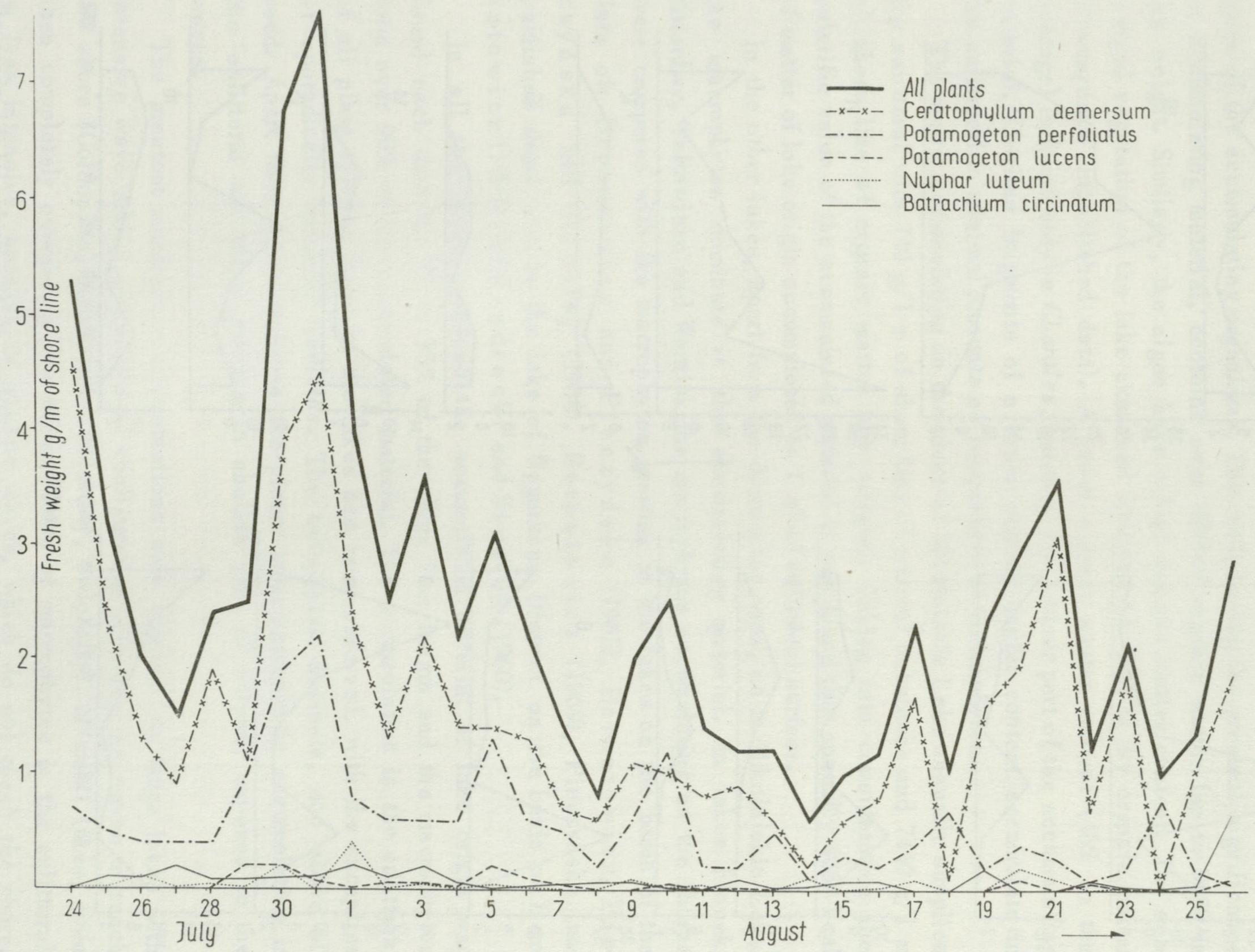


Fig. 25. Daily changes in accumulation of submerged vegetation at one eulittoral station in Mikołajskie Lake

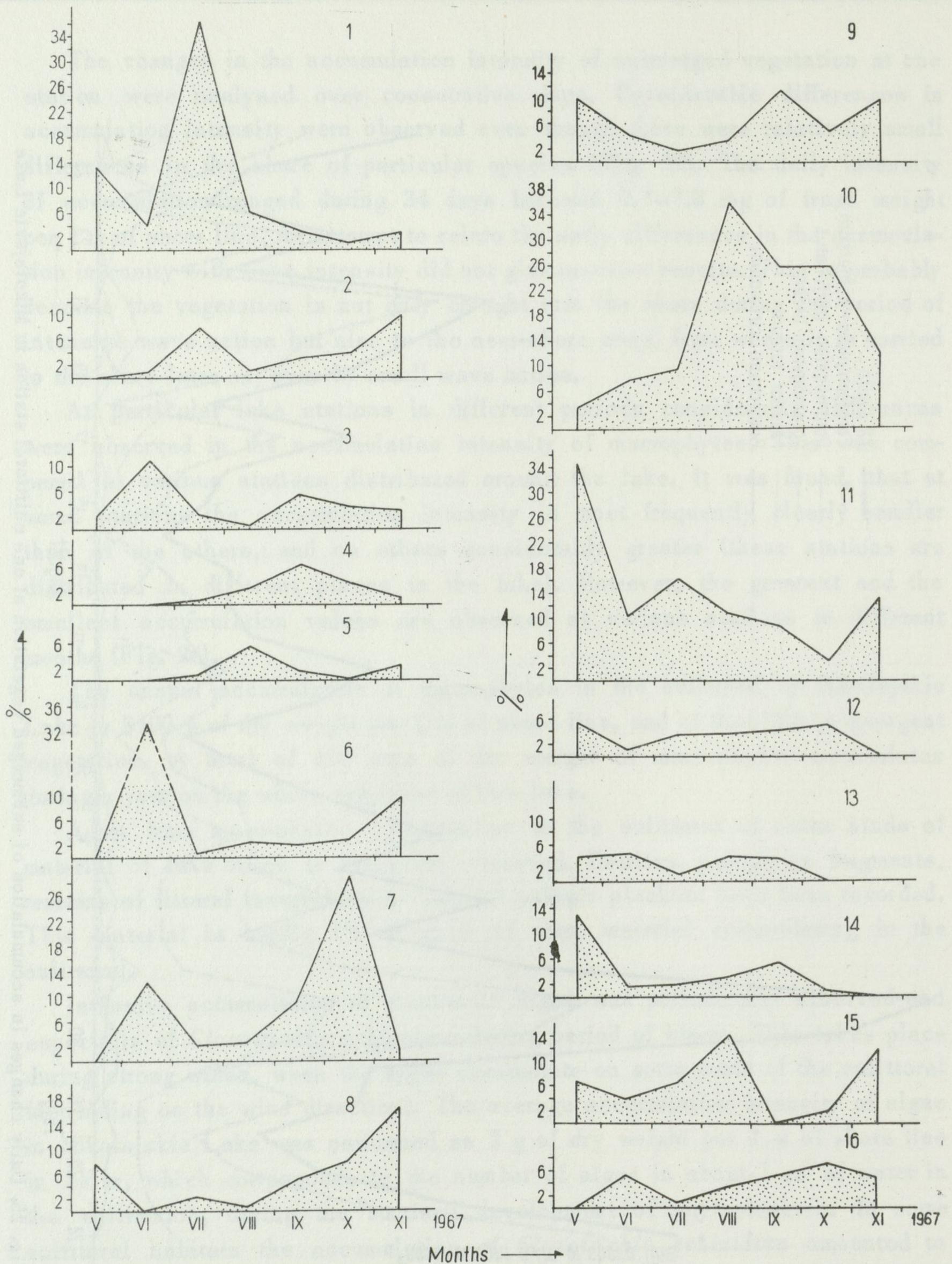


Fig. 26. Accumulation intensity of submerged vegetation on 16 stations of the shore of Mikołajskie Lake (in % of cumulated material on the given station as related to the total accumulation in the given period)

1-16 - stations

The material of lake origin in the eulittoral is almost exclusively a source of organic matter, because of the small proportion of inorganic matter in the mass of the accumulating organisms. The reed, having the greatest significance in accumulating material, contains over 90% of organic matter (up to 98%) in dry weight. Similarly, the algae have a high organic matter content. The submerged vegetation of the lake examined contains 65–90% of dry organic matter (Pieczyńska unpublished data). A lower organic matter content (45% on the average) is found only in *Charales*, but they are a minor part of the accumulating material. Detritus fragments of a lower organic matter content accumulate in the eulittoral in minimal amounts as compared with macrophytes.

The matter accumulating on the shore of Mikołajskie Lake annually supplies the eulittoral with 740 g/1 m of shore line of mineral substance and 7440 g/1 m of shore line of organic matter (dry weight). Taking into consideration the calorific value of the accumulated material it was found that annually 4860 kcal of matter of lake origin accumulates on 1 m² of eulittoral surface.

In the other lakes, apart from the dystrophic ones, as in Mikołajskie Lake, the macrophytes dominate in the accumulating material. In lakes Flosek, Śniardwy, Tałtowisko and Warniak the macrophytes accumulating on the shores were compared with the macrophytes growing in the lakes on the basis of the data of: Bernatowicz and Pieczyńska (1965), Bernatowicz, Pieczyńska and Radziej (1968), Bernatowicz (1969), Pieczyńska (unpublished data), and in the lake of Węgorzewo District on the basis of Bernatowicz (1960) and Kondracki and Szostak (1960).

In all the lakes examined the accumulated material of lake origin was found each time for 70 to 95% of the shore line length and the macrophytes form over 90% of the accumulated material. The accumulation in the eulittoral of all plant species found in the lakes has been observed, with the exception of sporadically recorded *Charales*. The helophytes dominate, and above all reed. Apart from the helophytes the plants most intensively accumulating in the eulittoral are those growing in shallow part of littoral, exposed to the waves.

The greatest macrophyte accumulations were observed in large lakes with intensive wave action and a littoral configuration allowing the waves to reach the shore (Gołdopiwo, Mikołajskie, Śniardwy, Święcajty). In small lakes, even when completely overgrown, the accumulation of macrophytes in the eulittoral is less intensive, because of smaller waves, which do not reach the shore. In dystrophic lakes the accumulation in the eulittoral of matter of lake origin is very small, and it looks as if this had no special bearing on the matter circulation in the eulittoral.

3. Accumulated matter of terrestrial origin

The literature does not provide many complete surveys on the amount of matter of terrestrial origin reaching lakes.

Quantitative studies of the allochthonous matter are difficult and, therefore, frequently only indicative assessment of the influence of surroundings areas on the lakes (basing on the dependences between the fertility of water body and the size and character drainage basin) are applied (Ohle 1934, 1965, Patalas 1960d, Schindler 1971).

More detailed quantitative studies are usually dealing with only one kind of allochthonous material entering a water body and this is usually the litter fall which is relatively simple to estimate (Smirnov 1964, Szczepański 1965, Minshall 1967, Mathews and Kowalczewski 1969 and others).

The most significant sources of allochthonous matter in the lake are: a) river inflows, b) underground inflows, c) atmospheric precipitation, d) domestic wastes, e) industrial wastes, f) products of shore erosion, g) products of erosion of drainage basin soils and h) litter fall (the role of these kind of matter is discussed in another paper by Pieczyńska 1972b).

The most significant for the eulittoral zone are the three last sources of allochthonous matter, which usually initially reach the eulittoral, and only later on are they carried further into the lake. The other kinds of matter of terrestrial origin reach the eulittoral to a smaller extent, and most of these get straight into the central part of the lake. In some cases artificially introduced anthropogenic matter plays important role in the eulittoral.

In the case of all lakes examined in present study the point indicatory system of Patalas (1960d) was used for comparative estimation of the extent to which drainage basins affect lakes. Patalas determines the influence of surrounding areas on the lake taking into consideration the size of the drainage basin, its fertility (estimated on the basis of share of forest, fairly fertile soils, fertile cultivated soils and buildings), fertility of main influent of drainage basin, intensity of water exchange and so on. The estimations are expressed in points. For example, the highest score (5 points) was reached by lakes with 75% of their surroundings with fertile arable lands and at the same time with over 20% of the shore line in contact with buildings. The lowest score (1 point) was reached by lakes with their neighbouring areas covered by forest for more than 75% of shore line. Analysed in this paper lakes of Węgorzewo District (Tab. IB) have already been treated from this view point in the paper by Patalas (1960d). The fundamental data used in the estimation in the cases of other lakes (Tab. IA) are presented in Table VII and VIII.

Characteristics of the fertility of the drainage basins of some Masurian lakes
A – forests, *B* – fairly fertile soils (pastures, fallows, meadows, sandy cultivated soils), *C* –
 fertile cultivated soils, *D* – buildings

Tab. VII

Lake	Ground surrounding the lake							
	in percentage of the shore line length				in percentage of drainage basin surface			
	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>
Flosek	91	9	0	0	94	6	0	0
Mikołajskie	35	33	17	15	30	27	31	12
Śniardwy	17	46	29	8	45	24	29	2
Tałowisko	3	74	23	+	39	23	38	+
Warniak	23	29	48	+	23	20	57	+

+ determines the value < 0.2%.

The area of the drainage basins and the water exchange of some Masurian lakes*

Tab. VIII

Lake	Surface area (ha)		Volume of water (mln m ³) <i>V</i>	Yearly outflow (mln m ³) <i>H</i>	$\frac{F}{f}$	$\frac{F}{V}$	$\frac{H}{V}$
	lake <i>f</i>	drainage basin <i>F</i>					
Flosek	4	46	0.1	(0.07)	11.5	4.6	0.7
Mikołajskie	460	810	50.6	151.6	1.8	0.2	3.0
Śniardwy	10970	14230	650.2	460.5	1.3	0.2	0.7
Tałowisko	327	1163	45.8	107.4	3.6	0.3	2.3
Warniak	38	382	0.5	(0.6)	10.1	7.6	1.2

*Prepared using the data of the National Institute for Hydrology and Meteorology. In lakes Flosek and Warniak the field investigations of water exchange were not carried out. The exchange was calculated using hydrographic maps of the area.

The comparison of my own data and of Patalas (1960d) allowed the lake examined to be put in order of increasing direct drainage basin effect:

1) Lakes not much affected by the drainage basin (Czarna Woda, Flosek, Krzywa Kuta, Smolak);

2) Lakes with an average affect of the drainage basin (Gołdopiwo, Śniardwy, Święcajty);

3) Lakes greatly affected by the drainage basin (Czarna Kuta, Głęboka Kuta, Tałowisko, Wilkus and Żabinki);

4) Lakes, where the effect of the drainage basin is the greatest (Mikołajskie – because of the municipal sewage, Pozezdrze, Przyleśne and Warniak).

Studies on the amount of matter of terrestrial origin reaching the lake and especially the eulittoral were conducted in Mikołajskie Lake by the following determinations: shore erosion, litter fall, municipal sewage and erosion of drainage basin soils. The data on shore erosion and litter fall were obtained by my own field investigations. The erosion of drainage basin soils was determined by Mikulski (unpublished data) on the basis of estimation of the size of drainage basin, precipitation intensity and susceptibility to soil erosion in various parts of the basin.

The amount of matter in municipal sewage from Mikołajki town was estimated on the basis of data on the number of inhabitants (resident and visitors), sewerage system, and fragmentary data on the amounts of inflowing sewage and its chemical composition. The calculations were made using the indices given by Imhoff (1957). Another calculation was made in parallel, based on data dealing with quantities of water sold in town, sewerage system and calculation of amount of sewage water discharged to the lake. Both methods of calculation give only approximate values. The great consistency of results obtained using these methods points to the reliability of obtained data. However, it should be taken into account that these values may be higher, because of the great number of holidaymakers staying near the lake.

The total amount of analysed allochthonous matter reaching the lake was estimated as 263 tons dry weight per year, which is 59 g dry weight per 1 m² of the total surface of the lake. The greatest part is from municipal sewage (83.6%), and the smallest from shore erosion (0.8) (Tab. IX).

Some sources of allochthonous matter reaching to
Mikołajskie Lake

Tab. IX

Origin of inflowing matter	Total amount of dry weight per year	
	tons	%
Municipal sewage	220	83.6
Erosion of drainage basin soils	34	12.9
Litter fall	7	2.7
Shore erosion	2	0.8
Total	263	100.0

The amount of municipal sewage reaching the eulittoral is not easy to estimate quantitatively on the basis of available data. Their significance is partly indirect (acting through the lake) in this instance, as the majority of the sewage water is carried out to the central lake beyond the eulittoral zone.

Shore erosion and litter fall, the allochthonous matter of the greatest importance in eulittoral were quantitatively measured.

Shore erosion in Mikołajskie Lake is highly variable. Only high shores (in the western part of the lake) are affected to a great extent by these processes. The most intensive erosion was observed in these habitats in May 1967. Then from one metre of shore line 3–4 kg of soil were washed out in 24 hr., while in other periods this value did not exceed 0.5 kg. Erosion, close to the average for the lake, was observed on the south-western shore. Examples of erosion effects in this habitat are presented in Figure 27.

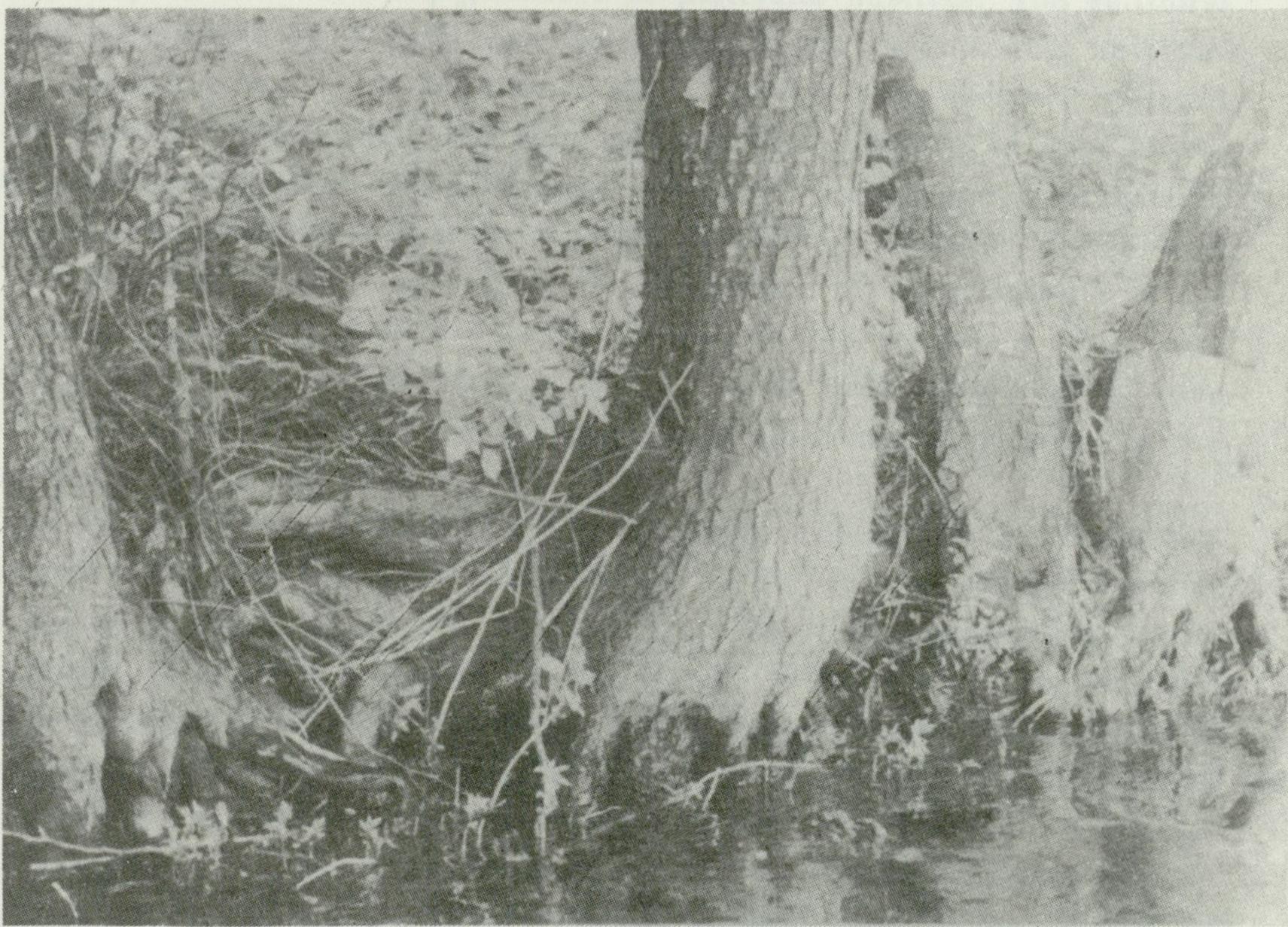


Fig. 27. Tree roots exposed by shore erosion (Mikołajskie Lake, June 1967)

The amount of tree leaves falling into Mikołajskie Lake was determined earlier by Szczepański (1965) for the autumn period (September–November). He found the value as 3.8 tons of dry weight, which is 0.2% of the autochthonous production in analysed lake. In my investigations annual measurements

of the litter fall were carried out and showed that during the autumn (September-November) the falling is highest (70% of yearly amount of material). However, the amount of material falling down in other months is sufficiently great not to be overlooked in studies on the amount of matter brought in (Fig. 28). Among the falling to eulittoral material tree leaves dominate. They are, in various periods, 55 to 93% of the mass of falling matter. Apart from the leaves, flowers, seeds, bark and twigs are recorded. The small fraction of fauna (insects) periodically observed never exceeds 0.2% of plant material mass.

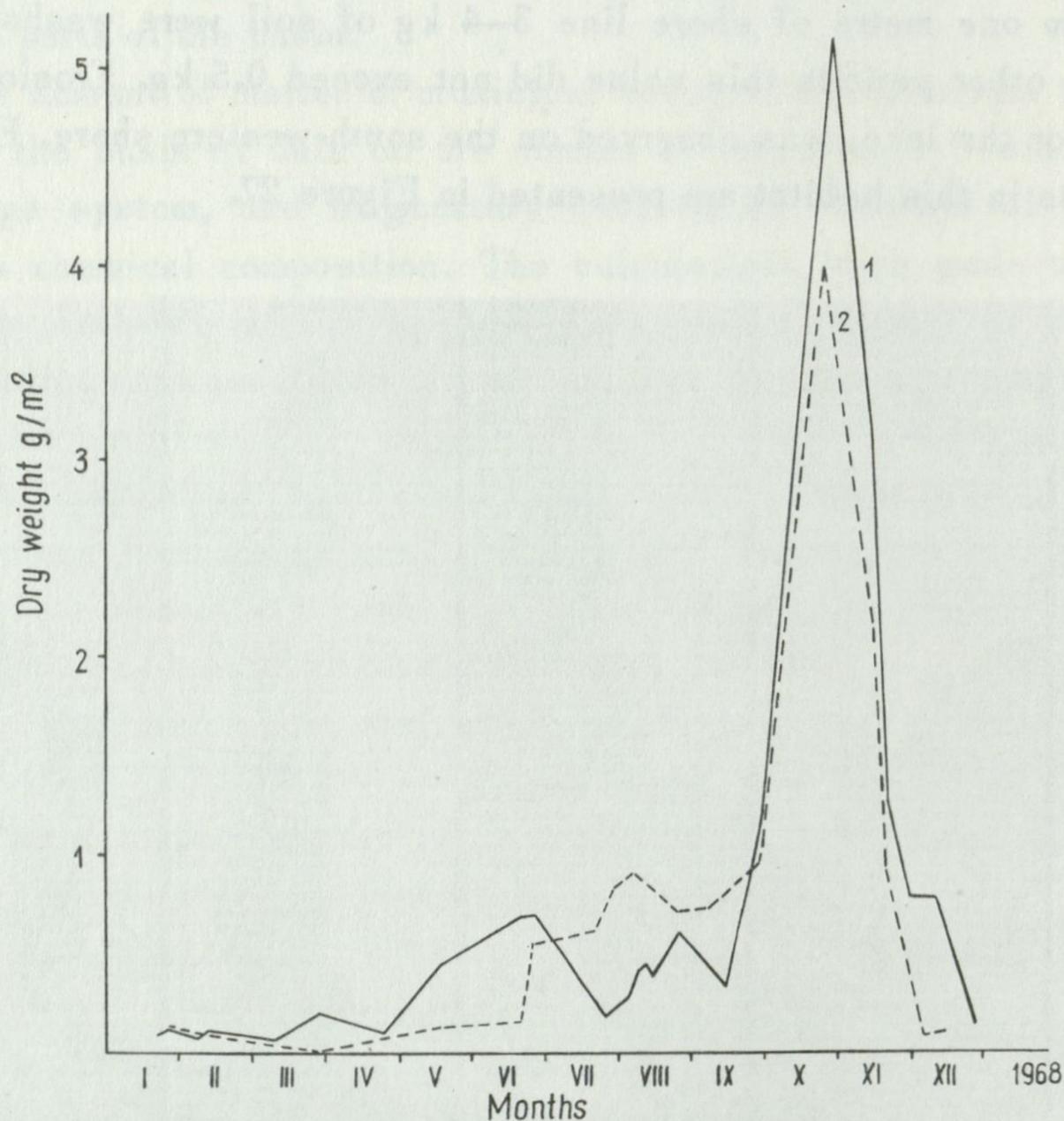


Fig. 28. Changes in the yearly cycle of the amount of litter fall into Mikołajskie Lake
1-2 - stations

The form in which the matter of terrestrial origin reaches the eulittoral varies greatly. It is a source of organic and mineral substances. The falling fragments of terrestrial vegetation may in the high organic matter content exceed 90% of dry weight (the highest values recorded 93%). In the domestic sewage the content of organic matter is about 50% and there is a considerable share of dissolved matter. The smallest share of organic matter is typical for eroded soils.

The total amount of matter of terrestrial origin reaching during one year the eulittoral of Mikołajskie Lake was estimated as 30 tons of mineral substance and 13 tons of organic matter. Taking into consideration the calorific value of the accumulated material, it was found that annually 1940 kcal of matter from surrounding land area accumulates on 1 m² of eulittoral surface.

VI. DECOMPOSITION PROCESSES

The variability of environmental conditions in the eulittoral, and the variety of organic matter found there, point to the possibility of finding considerable differences in the intensity of decomposition processes in this habitat.

The consumers living in the eulittoral are represented by various trophic groups, and the variability of faunal composition and abundance previously discussed points to their different rôle in particular habitats. The eulittoral is also penetrated by several species living in the neighbouring habitats. Fish feeding can be of great importance here. This has been analysed in detail in lake Warniak (Prejs unpublished data) by studying the feeding of carp, bream, tench, roach and crucian carp in the gut content of which several exclusively eulittoral forms were found (*Cylindrotomidae*, *Tipulidae*, *abanidae*, *Liriopeidae* and *Stratiomyidae*). The regularity of the occurrence of these animals in gut contents of fish points to their constant feeding in this habitat. A factor conditioning the intensity of penetration by fish is the great variability in case of access to the eulittoral due to water level fluctuation, isolation by the accumulating plants and the like.

The eulittoral is penetrated also by terrestrial vertebrates (mainly amphibians and birds), the feeding of which is one of the ways of using the matter produced or accumulated in this habitat. The rôle of this penetration varies in different lakes. For example, Dobrowolski (1961), when studying the avifauna of lakes of Węgorzewo District, points to the considerable differences in the number of species and density of birds in lakes of varying trophic types, size, depth and extent of overgrowth. In many lakes included in these investigations (especially of the Great Masurian Lakes) the eulittoral penetration by vertebrates is limited by the considerable tourist traffic. This is confirmed by very rare traces of vertebrates (e.g. faeces of birds) found in the eulittoral of these lakes.

Undoubtedly, the processes of matter utilization by microorganisms are of great significance in the eulittoral. This is, on one hand, due to the distinct domination of matter (macrophytes, tree leaves), which is little used as direct food for the majority of animal groups, and on the other hand, due to the occur-

rence in this habitat of considerable numbers of bacteria, which, according to the studies by Godlewska-Lipowa in Mikołajskie Lake (unpublished data), are higher than the maximal abundances in other lake habitats.

Within the present research, studies were conducted on the decomposition of falling tree leaves, macrophytes accumulating in the eulittoral and algae accumulating or developing in this habitat.

Data on the decomposition of these kinds of matter are not common in the literature. As examples we may mention the studies on decomposition of macrophytes (Gorbunov 1953, Koreljakova 1958, 1959, Solski 1962, Ulehlová 1971) and of falling tree leaves (Kaushik and Hynes 1968, 1971, Mathews and Kowalczewski 1969). In the considerable number of papers on algal decomposition this problem was analysed on pelagic material. Furthermore such investigation was carried out using various methods and in different habitats, frequently in laboratory conditions. This makes the comparison of results more difficult.

Several authors point to the basic significance of microbiological processes in making resistant matter accessible for the aquatic fauna (Sorokin 1967, Kaushik and Hynes 1968, 1971, Mathews and Kowalczewski 1969).

The intensity of decomposition processes has been examined in the eulittoral of Mikołajskie Lake, as described in the chapter on methods, by the analysis of loss of weight of various kind of material placed in nylon bags and exposed in natural conditions. The experiments were conducted in four types of habitats: *A* – emergent eulittoral, 1 m above the shore line of the lake, placing the bags on the surface of the sediments; *B* – reed heaps on the shore line, placing the bags under the reed heaps; *C* – swampy shore area, with periodical pools or a few centimetres of water, placing the bags in the sediments at the depth of 3 cm; *D* – (control habitat) littoral overgrown by reed, 0.5 m deep, 2 m from the shore line, placing the bags on the surface of the sediments. The systematic studies included: the *Potamogeton lucens* and *P. perfoliatus*, leaves of *Phragmites communis* accumulating in the eulittoral and leaves of *Salix* sp. (each time the leaves were used immediately after falling off the trees). Three examples of these experiments conducted in 1967 are presented in Figure 29. As the period of 10 days was the most frequently used in the experiments on disappearance rate, the results were expressed in the weight loss after 10 days. Differences in temperature during particular series were as following: in the first series (June 12–21) the average water temperature (measured daily at 8 a.m., in water 20 cm from the shore, at the depth of 10 cm) was the lowest, 16.6°C. The other two periods had higher and similar temperature: second series (July 30 to August 8), 21.8°C, and third series (September 6–15), 21.0°C.

obvious oxygen deficits (0–0.5 mg O₂/l), high conductivity (490–620 μS) and oxygen demand (41–56 mg O₂), pH ranged during the studies from 7.1 to 7.4. The sediments were composed mainly of plant detritus (remains of tree leaves and reed stalks and leaves). The organic matter content in the sediments was within the range of 57–62% of dry weight.

The smallest disappearance was observed in the emergent part of eulittoral (A) (not more than 7% of the weight loss in 10 days). A high disappearance intensity was observed under reed heaps (B) – up to 50% of weight loss in case *Potamogeton perfoliatus*. In this habitat the humidity was constantly very high; the reed heaps were on top of the detritus similarly to that in habitat C.

In a well oxygenated littoral habitat, in which the water exchange was continuous, the loss of weight from submerged plants (*Potamogeton lucens* and *P. perfoliatus*) took place slowly (up to 8% of weight loss). This was probably because the plants accumulating on the shore were still alive and because they remained in their “own” habitat for some time they did not die. Terrestrial plants (leaves of *Salix* sp.) and emergent parts (leaves) of reed disappeared in the littoral much more intensively – up to 25% of weight loss in 10 days (Fig. 29). The studies carried out later, in 1968 and 1969, from May to September, confirmed the regularities described above. The only exception was the disappearance rate of material exposed in the emergent eulittoral (1 m from the shore line) which was definitely higher (up to 32% of weight loss in 10 days). This was observed in periods of intensive rainfall when the decomposing material was constantly wet.

In habitats having the greatest decomposition intensity (C), further series of experiments were systematically carried out in the years 1968–1970. Each time the disappearance rate was as high as before. The maximal value (97% of weight loss after 10 days) was observed in *Potamogeton perfoliatus* exposed during June 12–21, 1969. The mean temperature measured at 8 a.m. was then 18.9°C, and the amplitude (estimated using the maximum-minimum thermometers), 9°C.

Experiments to estimate the disappearance of other macrophyte species accumulating on the shore were also conducted (*Batrachium circinatum*, *Myriophyllum spicatum* and stalks of *Phragmites communis*). In the case of the first two species the disappearance intensity was slightly lower (on the average about 10%) than that recorded for *Potamogeton*. Over the periods of exposure used (up to two months) the reed stalks weight did not decrease. A longer time of exposure was not used because of the changes taking place in the habitat – flooding or drying of the eulittoral, which causes profound differences in the decomposition conditions and makes it impossible to compare the data. Syste-

matic observation of accumulating reed stalks in the eulittoral showed that the essential process preceding and making the decomposition easier is mechanical crumbling by the waves. In the sediments of the near shore zone of lakes small fragments of reed stalks, a few millimetres in size, were frequently found in masses. Taking into consideration the previously described marked periodicity of reed accumulation in the eulittoral, the time necessary for such size-reduction may be estimated as one year.

The decomposition intensity depends to a great extent on the age of the plant material. The experiments conducted in June 1968 and 1969 showed that the disappearance rate of willow leaves, which fell late in autumn, wintered under the ice and remained till summer of the next year in the eulittoral, was half that of the leaves which fell off trees directly before the start of the experiment. Despite the obvious differences in the disappearance rate of particular species, parts of plants, and also material of various age, all series of experiments confirmed the regularity presented in Figure 29, a considerably, frequently over 10 times, greater disappearance rate in the eulittoral habitats (B, C) than in the neighbouring emergent eulittoral and littoral habitats.

The decomposition intensity of plant material observed in eulittoral conditions is much higher than that recorded for other habitats by various authors. For example, Mathews and Kowalczewski (1969), using the same methods in their studies, found that the total disappearance of oak, sycamore and willow leaves falling into the River Thames took place within one year, but the slowest disappearance was of the oak leaves. In habitats examined within the present work, a similar decomposition rate was only observed on the land and in some instances in the littoral. In typical eulittoral habitats the decomposition rate was several times higher. Two months of experiments allowed the conclusion to be reached that total disappearance took place in a habitat under reed heaps (B) – from 39 days (*Potamogeton lucens*) to 58 days (*Salix* sp.) and in a habitat of swampy area (C) – from 18 days (*Potamogeton lucens*) to 50 days (*Salix* sp.).

As a better estimate of decomposition intensity the coefficient of daily rate of disappearance (r_i) after Wiegert and Evans (1964) was applied, basing the calculations on the equation introduced by the authors and commonly used in the ecology of terrestrial habitats:

$$r_i = \frac{\ln (W_0/W_1)}{t_1 - t_0}$$

where: r – daily disappearance in mg/g, W_0 – initial weight, W_1 – final weight, $(t_1 - t_0)$ – exposure time in days. This analysis gave a range of variability

of the disappearance values expressed by the coefficient r as following: emergent eulittoral (habitat A) 0.5–10.3, reed heaps on the border of land and water (B) 22.8–79.6, swampy shore area (C) 44.3–435.0 and littoral (D) 1.5–37.2. These results differ considerably from those of Wiegert and Evans (1964) and other authors (Traczyk 1968) for terrestrial habitats. In these habitats the recorded values of disappearance did not exceed 10 mg/g per 24 hr, and were frequently below 2 mg (disappearance of grasses in meadow habitats).

All results discussed are based on experiments where nylon bags of mesh size 4.00 mm² were used. A series of experiments have been set up where dense nets of mesh size 0.25 mm² (unabling the access of fauna) and thin nets of mesh size 20.0 mm² (enabling the access of macroinvertebrates) were used in parallel. It was found that the results using these nets were similar – the differences were irregular and did not exceed 15% (Tab. X).

Decomposition rates of plant material exposed in nylon bags of various mesh size
Losses of dry weight after 10 days of exposure (in per cent of initial)

Tab. X

Plant material	Series*	Mesh size of bags in mm ²		
		0.25	4.0	20.0
<i>Phragmites communis</i> (leaves)	I	21.3	19.4	24.0
	II	47.8	41.2	45.0
	III	12.6	13.3	12.2
<i>Potamogeton perfoliatus</i>	I	36.5	39.1	31.3
	II	80.2	73.5	76.1
	III	8.5	7.8	9.0

*Series of experiment: I – July 1967, reed heaps on the shore line; II – September 1967, emergent part of eulittoral, 1 m from the shore line, small pools; III – June 1969, submerged part of eulittoral, 1 m from the shore line, 20 cm depth.

This shows that the disappearance of organic matter despite the presence of a great amount of detritus feeders was caused principally by microorganisms. These results are confirmed by analogous conclusions reached by Mathews and Kowalczewski (1969) in their experiments conducted on the River Thames.

Decomposition intensity of algae was estimated on the basis of two series

of experiments conducted in July and September 1967. The periphyte *Cladophora glomerata* colonizing the stones in eulittoral and *Gloeotrichia echinulata*, which accumulate in the eulittoral were exposed in the habitats discussed above. An estimation of decomposition intensity using the method of weight loss is much more difficult for algae than for macrophytes, because of the difficulties in separating the analysed material from various kinds of impurities. As for macrophytes the decomposition rate are the most intensive in swampy shore areas (habitat C). Total disappearance of *Cladophora glomerata* took place in 5 days, and of *Gloeotrichia echinulata* in 3 days. Under the reed heaps the disappearance of *Gloeotrichia* took place in 4 days, and of *Cladophora* in 6 days (the average values from two experiments). Total disappearance of these species in emergent eulittoral and in littoral took place in 9–18 days. This is a much greater decomposition rate than found by Kacieszczenko (unpublished data) in the pelagial of the same lake. He analysed the weight loss of *Gloeotrichia echinulata* mass by exposing the dried algal colonies in bags of mesh size 180 and 60 μ , or in glass cylinders. Exposing the material for 17 days in the epi- and metalimnion he observed a weight loss not exceeding 22%.

The great decomposition intensity observed in the eulittoral, which is not found in other habitats, is confirmed in a microbiological analysis of this habitat by Godlewska-Lipowa (unpublished data). She found, in these habitats, which have the greatest decomposition rate, great numbers of bacteria, 10 times exceeding the highest values in other lake habitats. For example, in June 1969 in the eulittoral (habitat C), where the highest decomposition rate was observed (97% of weight loss of *Potamogeton perfoliatus* after 10 days of exposure), the number of bacteria amounted to 57 millions in 1 ml of water (water taken from sediment in habitat C). In comparison the highest number of bacteria in the epilimnion during 2 years of studies was 6 millions in 1 ml (Godlewska-Lipowa unpublished data).

The decomposition rate in this habitat was also estimated on the basis of an analysis of oxygen consumption by the detritus (habitat C). 10 series of measurements were made in between July and August 1967. Fluctuations of oxygen consumption were observed in the range 1.9–2.9 mg/hr per g dry weight. These values considerably exceed the oxygen consumption by bottom sediments of lakes of various trophic types (Rybak 1969). When analysing the oxygen consumption by bottom sediments from a few Masurian lakes Rybak has recorded a maximum of 1.3 mg oxygen/g dry weight/hr. Also Fenchel (1970), when analysing the oxygen consumption by plant detritus from *Thalassia testudinum*, growing in a shallow marine eulittoral, found an oxygen consumption of from 0.7 to 1.4 mg O₂/hr per dry weight. Both in the instance of my own analyses

and the studies of the cited authors the oxygen consumption has been estimated by detritus containing the natural community of organisms. The above comparison is one more proof of the extremely intensive decomposition processes in the some habitat of lake eulittoral, much more intensive than in other habitats.

VII. CONCLUSIONS AND DISCUSSION OF RESULTS

The eulittoral is a border zone between the water body and the land surrounding it. This zone, directly and without any marked line, passes into littoral, and for this reason is treated as a part of littoral by many authors. In this paper a distinction is made, and the eulittoral is presented separately because of its specific significance in the lake ecosystem, and because of several specific biological processes observed there.

The range of the eulittoral varies according to the water level fluctuation in the lake and the configuration of the shore terrace. Within one water body, depending on the morphological configuration of the shore regions, we find habitats with a vast eulittoral zone and others, where this zone has a very small range (Tab. II). In successive years the water level fluctuations determine the area covered by the eulittoral in one and the same water body.

Taking into consideration the range of the eulittoral zone, and the factors modifying it in the lakes investigated (Tab. I), the following conclusions have been reached:

1) In all lakes the macrophytes (amphiphytes and helophytes mainly) are an important factor differentiating the eulittoral zone.

2) Stony and sandy eulittorals, devoid of vegetation, are very few in the examined lakes. They are most frequent in large lakes with strong wave action (Gołdopiwo, Śniardwy, Świącajty).

3) The erosion and accumulation processes play an important role in the formation of the eulittoral. Accumulation processes are of great significance within the eulittoral area in all lakes. In many habitats the aquatic vegetation accumulating on the shore isolates part of the eulittoral, thus producing small, periodical, lake-side water bodies. The prevalence of erosion processes has been observed in a few eulittoral habitats, mainly in lakes Gołdopiwo and Śniardwy.

4) The eulittoral has the greatest range and the greatest differentiation in large post-glacial lakes having a vast shore terrace, a differentiated shore line and considerable water level fluctuation (Gołdopiwo, Śniardwy, Świącajty).

5) Dystrophic lakes, despite the small water level fluctuation, usually have vast eulittoral. Straight, undeveloped shore line are the reason, why this zone is poorly differentiated (Czarna Woda, Flosek, Smolak).

6) Small eutrophic lakes, with small changes of water level, have a small eulittoral range but it is greatly differentiated (Czarna Kuta, Głęboka Kuta, Warniak).

The above analysis of the range and transformation of eulittoral includes natural influence. In many water bodies the eulittoral is to a great extent affected by human activity. For example Sukopp (1971) points to a clear destructive influence of recreational activities on shore transformation and littoral macrophytes in the Berlin water bodies. This author presents also a review of data on the subject.

The eulittoral is characterized by a great variability of physico-chemical conditions. Light intensity (light on surface of water) is as a rule smaller there than in other lake zones, which is primarily due to shading by macrophytes and trees at the lake-side. The maximal values of light intensity in the eulittoral (no trees on the shore, lack of macrophytes) approximate the values recorded in the pelagial and are greater than the maximal values in the littoral (reed belt). The minimal values (trees on the shore, high density of macrophytes) are clearly lower than the minimal values in the littoral (Fig. 8). The thermal conditions in the eulittoral as compared with other parts of the lake have a very distinct character. Differences in water temperature between the eulittoral and littoral are in some instances greater than those between the littoral and pelagial (Fig. 9). The greatest temperatures in eulittoral are observed on sunny days early in spring when ice on the lake thaws, and the eulittoral parts of the lake are already free of ice, but the central part of the lake is still frozen. In all lakes examined the highest absolute temperatures are observed in the eulittoral.

The chemical composition in the eulittoral, as compared with the littoral and pelagial, is characterized both by the highest values and the greatest variation range of the majority of components determined (Fig. 11). The greatest concentrations of mineral and organic substances (frequently more than 10 times greater than concentrations in the littoral and pelagial) are observed in small lake-side water bodies, partly isolated from the lake by the vegetation accumulated by the waves; considerable concentrations are also found in water under the reed heaps accumulating on the shore. Other eulittoral habitats, exposed to the waves, differ slightly from the deeper parts of reed belts, the typical littoral habitat (Tab. IV).

In the eulittoral much lower oxygen concentrations have been observed than in the littoral. Oxygen deficits were observed in pools forming along the shore line, in eulittoral habitats covered with reed heaps and in small lake-side water bodies completely covered with the *Lemnaceae*; and also as a rule in

winter under the ice in all habitats, where there is a small water layer between the bottom sediments and ice cover.

Also the bottom sediments vary considerably. The organic matter content in the sediments of the eulittoral of one lake ranges at the same time from < 1 to 98% dry weight (Fig. 16). On the border of land and water, because of the vegetation accumulating there, habitats having a high organic matter content (above 80%) dominate (Fig. 17).

The plant and animal communities in the eulittoral are represented by many forms, terrestrial, aquatic and specific for this zone. Among the algae there are planktonic and periphytic (attached to the substrate) species, and those loosely connected with the substrate and lying at the bottom. Among the latter large colonies of blue-green and green algae are frequently found, which frequently develop abundantly in the eulittoral and usually are not found in deeper part of lakes (Pieczyńska 1971). There are for example *Hydrodictyon reticulatum*, *Nostoc pruniforme*, *Gloeotrichia natans*, *Spirogyra* spp. and *Cladophora* spp. The macrophytes are represented by many amphiphytes and helophytes. The pleuston plants (mainly *Lemnaceae*) are recorded in great abundance in the eulittoral of several lakes.

The macroinvertebrates in the eulittoral zone are represented by many organisms not found other than in the eulittoral parts of lake (9 *Diptera* families, *Lumbricidae*, *Enchytraeidae*, *Collembola*, *Helicidae*, *Zonitidae*). Among the other groups of organisms the *Lumbriculidae*, *Tubificidae*, *Gammaridae*, *Coleoptera*, *Culicinae*, *Heleidae*, *Planorbidae* and *Succineidae* become much more abundant in the eulittoral, than in other lake zones, whereas the *Naididae*, *Hirudinea*, *Trichoptera*, *Chaoborinae*, *Hydracarina*, *Heteroptera* and *Odonata* are less numerous in this habitat than in other lake zones. The greatest faunal numbers and also their greater differentiation is recorded in small lake-side water bodies, partly connected with the lake. 80% of the taxons distinguished are common to all the lakes examined, although they represent various trophic types (Tab. V). It has been observed that if a type of eulittoral (sandy, stony, reed heaps, lake-side pools and the like) is represented in a given lake, of whatever trophic type, then the characteristic faunal representatives are found there.

Among the microfauna of the eulittoral of the lakes examined the *Protozoa*, *Rotatoria* and *Nematoda* dominate. They attain definitely greater numbers in that habitat than in other lake zones.

Due to the changing conditions, and especially water level fluctuations, some parts of the eulittoral become inaccessible to fauna in some periods, while at other time several new biotopes suitable for colonization are formed.

The habitat conditions in the eulittoral are to some extent similar to those existing in small water bodies, the principal feature of which is their discontinuity due to the periodical flooding and drying up. The organisms living in such places adapt to these conditions by shortening their life cycle, which allows them to develop during the short period of habitat accessibility, or in other ways enabling them to survive the periods of droughts and other changes of habitat connected with drying (Klekowski 1966).

In the lake eulittoral it seems that the movement of fauna is of the greatest significance. Animal organisms leave the unsuitable habitats and colonize them again when the conditions change; they move together with the shifting of border of land and water. Water level fluctuation in natural, not man-regulated lakes are so small that the slow movement of the border of land and water allows for the simultaneous movement of even the less active organisms (e.g. *Oligochaeta*). Also earlier studies by Moon (1935a) show that in lake conditions the movement of eulittoral fauna accompanies the water level fluctuation and is quite intensive.

New areas are colonized by the migratory fauna from other habitats, and another population source is the reproduction of the initially settled forms. In the case of organisms having a short life cycle (*Protozoa*, *Rotatoria*), it may be assumed that the regulation of density takes place primarily through the changes in the reproduction intensity. Violent changes in numbers of organisms having a long life cycle (*Oligochaeta*) or partly developing in an another habitat (*Insecta*) are mainly due to migrations.

The worsening of habitat conditions, despite all the migration or adaptation possibilities of organisms to survive unfavourable conditions, produces higher mortality. For example, the mortality of large numbers of animals living in the near-shore shallows (mainly molluscs) as a result of lowering the water level in the Great Masurian Lakes was pointed out by Dziekan (1965).

In the eulittoral of the examined lakes three sources of organic matter are distinguished: 1) Matter produced in the eulittoral by the producer community living in this habitat; 2) Accumulated matter of lake origin (produced in other parts of the lake which has been accumulated in the eulittoral due to wave action); 3) Accumulated matter of terrestrial origin.

Primary production in the eulittoral is periodically very intense. Much more frequently than in other lake habitats we come across the monospecific mass appearance of different algae. The main factor favouring the intense production is undoubtedly the great abundance of mineral salts. On the other hand, there are many factors limiting the primary production in the eulittoral, such as unfavourable light conditions, periodical desiccation of the habitat,

total freezing at winter time and the like. Therefore, despite such a high periodical intensity of production, the average values of annual primary production in the eulittoral are smaller than in other zones of the lake.

In all lakes examined the matter of lake origin reaching the eulittoral is mainly represented by macrophytes, which are over 90% of the accumulating material of this kind of matter. Apart from the macrophytes, accumulations of plankton, periphyton and various kinds of detritus are observed.

In the matter of terrestrial origin the following are of considerable significance in eulittoral: litter fall, products of erosion of drainage basin soils and products of shore erosion. In some lakes examined the municipal sewage is of considerable significance.

The material of lake and land origin accumulating in the eulittoral is not only a source of organic matter, but also of mineral matter, which undoubtedly affects the considerable concentration of nutrients in this habitat.

The share of particular sources of organic matter in the eulittoral in Mikołajskie Lake is as follows (comparison on an annual basis): primary production – 2100 kcal/m² of the eulittoral surface, accumulated matter of lake origin – 4860 kcal/m² and accumulated matter of terrestrial origin – 1940 kcal/m² of the eulittoral surface.

Different habitats in the eulittoral, even within one lake, vary in the significance of the sources of organic matter mentioned above. In each lake there are habitats constantly under the influence of matter of terrestrial origin, and also some, where the accumulation of lake material or primary production in situ are of decisive significance. In many lakes, shaded by trees, sections of eulittoral of several metres length are observed, where primary production practically never occurs and the habitat remains under the influence of matter of terrestrial origin carried in large quantities. Also parts of the eulittoral exposed to waves with a broad shore terrace are frequently observed, where the lake matter constantly accumulates. Primary production is usually of the utmost significance on non-shaded, flat shores and quiet bays separated from the lake by a broad reed-belt. Great differentiation in the eulittoral is the reason why all types of eulittoral are found in each of the lakes examined.

Taking into considerations such great differentiation it must be pointed that the division of sources of organic matter on an annual scale as presented above is rather artificial and plays the rôle of general description only. From the view point of ecosystem metabolism we can say that in eulittoral of each lake a number of functioning "subsystems" exist which are variously connected with the surrounding areas. This connection changes in time due to periodical isolation of some eulittoral section from the lake.

The organic matter in the eulittoral is utilized in various ways. It is used by local consumers and by organisms living in the neighbouring habitats, which periodically penetrate the eulittoral (amphibians, birds, fish and invertebrates). In the case of rising water levels the matter produced and accumulated in the eulittoral reaches other parts of the lake in various stage of decomposition, where it can be used by the representatives of various trophic levels.

The processes of matter utilization by microorganisms are of basic importance in the eulittoral. This is due to the clear dominance of matter, which only to a slight extent can be direct food for fauna (macrophytes, tree leaves). The intensity of decomposition processes in the eulittoral is considerably greater than in the neighbouring habitats, that is on land and in the littoral. The most intensive decomposition processes have been observed on a swampy area, where small pools were formed. The greatest numbers of bacteria were also recorded there, which exceeded, by several times, the bacteria numbers in other lake habitats.

The varying accessibility to consumers, and also the varying susceptibility to bacterial decomposition of organic matter in the eulittoral is the reason why in particular part of lake eulittoral and various times of year, a grazing or detritus food chain may be observed in its extreme form.

The significance of lake zones other than the eulittoral – pelagial, profundal and littoral – in the functioning lake ecosystem is relatively well known. Several structural and functional regularities are described in general terms in text-books. The significance of these zones in the lake metabolism has been also described.

The eulittoral zone has not been yet described in general term and in limnological texts it is usually mentioned only when dividing up the shore region of the lake.

On the basis of some literature data and the present results, it can be said, that the eulittoral is characterized by specific biological processes and its rôle in the lake ecosystem differs from other zones:

- 1) The eulittoral is an extremely differentiated habitat. Great influence of land and lake, and partial separation from the surrounding areas on the other hand favours the occurrence of specific habitats. Eulittoral habitats are to some extent independent from the character of the lake (its size, depth, throphic type etc.).

- 2) The eulittoral is a typical ecotone, in which terrestrial and aquatic organisms are found, and also specific organisms. In the eulittoral of the lakes examined a phenomenon has been observed, which is described in ecology as the "edge effect", and which results in the occurrence of a greater number of species, and greater density of some populations in the ecotone than in the surrounding habitats.

3) The eulittoral is a zone characterised by periodically great primary production rate. The significance of this production for the lake ecosystem is largely decided by the eulittoral area as compared to the surface of the lake.

4) The eulittoral is a "store" of various kinds of matter of terrestrial and aquatic origin, which is accumulated there. Most frequently this is material resistant to decomposition, only to a small extent used as direct food for fauna (tree leaves, macrophytes). The great decomposition rate in the eulittoral allows for its quicker participation in the circulation of material in the water body than the material accumulating in other lake zones. This material, after partial decomposition, at a time of change of hydrological conditions (water level rising) reaches the other lake zones in a reduced amount but in a form accessible for the consumers of these zones.

5) Environment conditions and biological processes in the eulittoral as well as the interactions between eulittoral and surrounding land and lake area are to a considerable extent affected by the fluctuation of water level in the lake. Flooding or drying up causes the appearance or disappearance of the habitat for aquatic or terrestrial organisms. It also affects production and decomposition conditions, the accumulation of allochthonous material, the movement of material to the water body, penetration of eulittoral by typical lake and terrestrial animals and the like.

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EKOLOGIA POBRZEŻA JEZIORNEGO

Streszczenie

Pobraże jest strefą graniczną między zbiornikiem wodnym i otaczającym go pasem łądu (fig. 1). Strefa ta bezpośrednio i bez wyraźnych granic przechodzi w litoral i przez wielu autorów traktowana jest jako część litoralu. W niniejszym opracowaniu wyodrębniono pobraże jako oddzielny obiekt badawczy ze względu na swoistą rolę jaką pełni w ekosystemie jeziornym oraz stwierdzenie w nim szeregu specyficznych procesów biologicznych. Badaniami objęto 16 jezior Pojezierza Mazurskiego (tab. I).

Pobraże charakteryzuje się zmiennym zasięgiem zależnym od wahań poziomów wody oraz ukształtowania wybrzeża i ławicy przybrzeżnej. W obrębie jednego zbiornika, w zależności od morfologicznego ukształtowania partii przybrzeżnych, spotykamy środowiska o rozległej strefie pobraża oraz inne, w których strefa ta ma bardzo mały zasięg (tab. II). W kolejnych latach, w zależności od wahań poziomu wody, obszar jaki zajmuje pobraże w tym samym zbiorniku może być różny. Zasięg pobraża warunkowany jest w dużym stopniu procesami erozji i akumulacji.

Pobraże charakteryzuje się dużą zmiennością warunków fizyczno-chemicznych. Intensywność światła jest tu z reguły mniejsza niż w innych strefach zbiornika, co warunkowane jest przede wszystkim zacienieniem przez makrofity i nadbrzeżne drzewa. Stwierdzono dużą odrębność warunków termicznych w pobrażu w porównaniu z pozostałymi częściami zbiornika. Różnice temperatur wody pomiędzy pobrażem i centralną częścią litoralu często przekraczają różnice między litoralem i pelagialem (fig. 9).

We wszystkich badanych jeziorach w pobrzeżu notowano najwyższe bezwzględne wartości temperatur.

Skład chemiczny wody w pobrzeżu w porównaniu z litoralem i pelagiałem charakteryzuje się zarówno najwyższymi wartościami, jak też największym zakresem wahań większości analizowanych składników (fig. 11). Największe koncentracje substancji mineralnych i organicznych (często ponad dziesięciokrotnie przewyższające koncentracje w litoralu i pelagiału) stwierdzono w małych zbiornikach przyjeziornych, częściowo izolowanych od jeziora zgromadzoną na skutek falowania roślinnością; znaczne koncentracje obserwowano również w wodzie pod zwałami trzcin gromadzącymi się przy brzegu. Inne środowiska pobrzeża, eksponowane na falowanie, różnią się tylko nieznacznie od głębszych partii trzcinowisk — typowego środowiska litoralnego (tab. IV).

W pobrzeżu obserwowano znacznie niższe koncentracje tlenu w porównaniu z litoralem. Deficyty tlenu stwierdzono w kałużach tworzących się wzdłuż linii brzegowej, pobrzeżach przykrytych zwałami trzcin i w małych zbiornikach przyjeziornych całkowicie pokrytych *Lemnaceae*, jak również z reguły w zimie pod lodem we wszystkich środowiskach, w których była mała warstewka wody między osadami dennymi a pokrywą lodową.

Dużą zmiennością charakteryzują się również osady. Zawartość materii organicznej w osadach pobrzeża jednego zbiornika waha się w tym samym czasie od < 1 do 98% suchej masy (fig. 16). Na granicy lądu i wody, ze względu na kumulującą się tu roślinność, dominują środowiska o dużej zawartości materii organicznej — powyżej 80% (fig. 17).

Flora i fauna w pobrzeżu reprezentowana jest przez wiele form lądowych, wodnych oraz specyficznych dla tej strefy. Wśród glonów występują gatunki planktonowe, perifitonowe oraz luźno związane z podłożem i leżące na dnie. Wśród tych ostatnich częste są duże kolonie sinic i zielenic, specyficznych dla strefy pobrzeża, rozwijających się tu masowo (*Hydrodictyon reticulatum*, *Nostoc pruniforme*, *Gloeotrichia natans*, *Spirogyra* sp. sp. i *Cladophora* sp. sp.). Makrofity reprezentowane są przez wiele gatunków amfitów i helofitów. Masowo w pobrzeżu wielu jezior notowano rośliny pleustonowe (głównie *Lemnaceae*).

Makrofauna strefy pobrzeża reprezentowana jest przez wiele organizmów nie występujących w innych, poza pobrzeżem, strefach jeziora (9 rodzin *Diptera*, *Lumbricidae*, *Enchytraeidae*, *Collembola*, *Helicidae*, *Zonitidae*). Spośród pozostałych grup organizmów *Lumbriculidae*, *Tubificidae*, *Gammaridae*, *Coleoptera*, *Culicinae*, *Heleidae*, *Planorbidae* i *Succineidae* osiągają w pobrzeżu liczebności znacznie wyższe, natomiast *Naididae*, *Hirudinea*, *Trichoptera*, *Chaoborinae*, *Hydracarina*, *Heteroptera* i *Odonata* występują w tym środowisku w liczebnościach znacznie mniejszych niż w innych strefach jeziora. Największą liczebność fauny, jak też największe jej zróżnicowanie notowano w małych zbiornikach przyjeziornych, częściowo łączących się z jeziorem. 80% wyróżnionych jednostek systematycznych było wspólnych dla wszystkich badanych jezior, mimo iż reprezentują one różne typy troficzne (tab. V). Zaobserwowano, że jeżeli jakiś typ pobrzeża (pobrzeże piaszczyste lub kamieniste, zwały trzcin leżące na brzegu, itp.) jest reprezentowany w danym jeziorze, znajdują się w nim charakterystyczni przedstawiciele fauny — tacy sami w jeziorach różnych typów troficznych.

Wśród mikrofauny pobrzeża badanych jezior dominują *Protozoa*, *Rotatoria* i *Nemato-da*. Osiągają one w tym środowisku wyraźnie większą liczebność niż w pozostałych strefach zbiornika.

W pobrażu badanych jezior wyróżniono trzy źródła materii organicznej: 1) Materia produkowana w pobrażu przez zamieszkujący to środowisko zespół producentów; 2) Materia pochodzenia jeziornego – produkowana w innych częściach zbiornika – gromadząca się w pobrażu w wyniku falowania; 3) Materia pochodzenia lądowego.

Produkcja pierwotna w pobrażu charakteryzuje się okresowo dużą intensywnością, nie notowaną w innych środowiskach jeziornych (tab. VI). Znacznie częściej niż w pozostałych strefach spotkać tu można masowe jednogatunkowe pojawy różnych glonów. Czynnikiem sprzyjającym intensywnej produkcji jest niewątpliwie bogactwo soli mineralnych. Z drugiej strony, w pobrażu działa wiele czynników ograniczających produkcję pierwotną. Są to niekorzystne warunki świetlne, okresowe osuszanie środowiska, całkowite przemarzanie w okresie zimy itp. W wyniku tego, mimo tak dużej okresowej intensywności procesów produkcji, średnie wartości rocznej produkcji pierwotnej w pobrażu są niższe niż w pozostałych strefach jeziora.

We wszystkich badanych zbiornikach materia pochodzenia jeziornego, gromadząca się w pobrażu, reprezentowana jest głównie przez makrofity, które stanowią ponad 90% kumulującej się masy tego rodzaju materii. Poza makrofitami obserwuje się też gromadzenie się planktonu, perifitonu i różnego rodzaju detrytus.

Wśród materii pochodzenia lądowego znaczną rolę odgrywają: opadające do zbiornika części roślinności lądowej, materia erodowana z terenu bezpośredniej zlewni na skutek opadów deszczu oraz erodowana z brzegów na skutek falowania. W niektórych jeziorach duże znaczenie mają ścieki miejskie.

Akumulujący się w pobrażu materiał pochodzenia jeziornego i lądowego jest źródłem nie tylko materii organicznej, ale również mineralnej, co niewątpliwie wpływa na znaczną koncentrację biogenów w tym środowisku.

Udział wyróżnionych źródeł materii organicznej w pobrażu kształtuje się bardzo różnie. W Jeziorze Mikołajskim porównanie takie w skali rocznej, w przeliczeniu na 1 m² powierzchni pobraża, przedstawia się następująco: produkcja pierwotna – 2100 kcal, akumulująca się materia pochodzenia jeziornego – 4860 kcal i akumulująca się materia pochodzenia lądowego – 1940 kcal.

Materia organiczna w pobrażu użytkowana jest w rozmaity sposób. Wykorzystują ją miejscowi konsumenci oraz organizmy zamieszkujące środowiska sąsiednie, penetrujące okresowo pobraże. Wśród tych ostatnich główną rolę odgrywają ryby. Na skutek ruchu wody materia produkowana i gromadząca się w pobrażu dostaje się (na różnym etapie rozkładu) do innych części zbiornika, gdzie może być wykorzystywana przez przedstawicieli różnych poziomów troficznych.

Podstawowe znaczenie mają w pobrażu procesy użytkowania materii przez mikroorganizmy. Wiąże się to z wyraźną dominacją materii, która w niewielkim tylko stopniu może stanowić bezpośredni pokarm fauny (makrofity, liście drzew). Intensywność procesów destrukcji w pobrażu jest znacznie większa niż w środowiskach sąsiednich – na lądzie i w litoralu. Najintensywniejsze procesy destrukcji stwierdzono w bagnistym terenie przybrzeżnym, na którym tworzą się małe zbiorniki (fig. 29). W środowiskach tych notowano również największą liczebność bakterii (Godlewska-Lipowa, materiały nie publikowane), wielokrotnie przekraczającą liczebność bakterii w innych środowiskach jeziornych.

Różna dostępność dla konsumentów, jak też różna podatność na rozkład bakteryjny materii organicznej pobraża sprawia, że w poszczególnych częściach pobraża lub

w różnych okresach realizuje się w krańcowej swojej postaci łańcuch troficzny roślino-żerców lub detrytusożerców.

Można wyróżnić dwa zasadnicze aspekty roli pobraża w obiegu materii w zbiornikach wodnych:

1) Pobraże jest strefą charakteryzującą się okresowo intensywną produkcją pierwotną. O znaczeniu tej produkcji dla jeziora w dużym stopniu decyduje obszar jaki zajmuje pobraże w stosunku do powierzchni zbiornika.

2) Pobraże jest „magazynem” wielu rodzajów materii pochodzenia lądowego i jeziornego, kumulującej się tutaj na skutek falowania. Jest to najczęściej materia trudno rozkładalna, w małym stopniu wykorzystywana jako bezpośredni pokarm fauny (liście drzew, makrofity). Duża intensywność destrukcji w pobrażu sprawia, że może być ona włączona w obieg materii w zbiorniku znacznie szybciej niż materia gromadząca się w innych strefach jeziora. Materia ta po częściowym rozkładzie, przy zmianie warunków hydrologicznych, dostaje się do pozostałych stref jeziora, wprawdzie w zredukowanej ilości, ale w postaci dostępnej dla konsumentów tych stref.

Okres, w którym materia organiczna pobraża zostanie wykorzystana przez zbiornik i postać, w jakiej dostaje się do innych części jeziora (stopień jej zmineralizowania), zależne są od zmian poziomu wody w zbiorniku. Zmiany te, powodujące okresową izolację lub przyłączanie przybrzeżnych partii, nie tylko utrudniają lub umożliwiają kumulację materii allochtonicznej, wynoszenie materii pobraża do zbiornika i penetrację tego środowiska przez ryby, lecz również stwarzają zasadnicze różnice w warunkach mineralizacji.

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