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ESTIMATION OF THE STATE OF THREE ESTONIAN SMALL LAKES ON THE BASIS OF BIOPRODUCTIVITY

Abstract. Plankton and fish productivity of three Estonian small lakes (Nohipalu Valgjärv, Uljaste, Korijärv) of different trophic states were investigated during the vegetation period of 1991. The water chemistry, underwater light climate, and species composition of the groups of biota studied are characterized as background. The phosphorus content is the main factor limiting primary production in all three lakes. In soft-water lakes Nohipalu Valgjärv and Uljaste photosynthesis may be temporarily restrained by poor availability of mineral carbon. In L. Nohipalu Valgjärv, which recently was oligotrophic, eutrophication results in big fluctuations of bioproduction. A large stock of phytoplankton biomass, formed in the metalimnion in spring, serves as further food for heterotrophs. The grazing type of food chain, which dominates in spring and summer, turns into the detrital type in autumn when bacteria obtain an intermediate position in the transformation of primary organic matter to zooplankton. At present the nutrient cycle in L. Nohipalu Valgjärv proceeds mainly at greater depths than the mixing depth, and the uppermost 5-metre layer retains its oligotrophic character. In the semidystrophic L. Uljaste the stability of primary production and its utilization in heterotrophic links are the main characteristics of the ecosystem. Smaller biomass and production of filter-feeding zooplankton together with the great share of predatory zooplankton in this lake result in a scanty food supply for the dominating fishes, peled and roach. The ecosystem of L. Korijärv belongs to the hypertrophic type. As the trophic state of this lake is higher, all production processes in it are much more intensive than in the other two lakes. In the temporal pattern of 1991 the maxima of primary and secondary productions did not coincide. In summer the production of bacteria exceeded primary production nearly twofold. This gives evidence of a steady domination of the detrital food chain.

Key words: water chemistry, light conditions, phytoplankton, zooplankton. bacterioplankton, fishes, species composition, production, trophic relations.

1. Introduction

Regardless of the small territory of Estonia, its natural conditions vary widely in different regions. This diversity is reflected also in lakes, which differ in size and depth, in the concentration of mineral and organic substances, as well as in the composition and productivity of biota. So far mainly static indices such as the composition (ionic, species) and concentration (chemical compounds, biomass) have been used as basis for the description and evaluation of lakes. The productivity of some single group of biota has been studied in Estonian small lakes only in a few cases. Production as a function of time offers a better understanding of the processes going on in lakes, especially in case the production of different trophic levels is measured simultaneously.

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The productivity of four trophic levels — phytoplankton, bacterioplankton, herbivorous, and predatory zooplankton — in a recently oligotrophic (L. Nohipalu Valgjärv), a semidystrophic (L. Uljaste), and a eutrophic lake (L. Korijärv) is discussed in this paper. In addition, an attempt was made to evaluate the fish production of these lakes. Our aim was to determine the productivity of these lakes, estimate the type-specific individuality of production processes in different lakes, and analyse the principles of lake management and protection and the prospects of restoring the ecosystems.

2. General Description of the Lakes

Lake Nohipalu Valgjärv, which recently was oligotrophic, is situated in moorland pine woods in Põlva County 2.5 km from the settlement of Veriora. Some decades ago it was considered the cleanest lake in Estonia. It is a closed lake, where direct precipitation forms the main water input. The drainage area is very small (Table 1). In the 1960s the water level dropped about 0.8 m due to the draining of the neighbouring peat-bog of Meenikunno. As the lake is isolated from cultivated lands, the main causes of its eutrophication can be atmospheric pollution, the influence of bathers and tourists, and also the rich-in-clay sand which has been brought on the beach (Mäemets, 1987).

Table 1

The main morphometric and hydrological parameters of the lakes studied (according to Kask, 1964, and Loopmann, 1984)

Parameter	Lake		
	Nohipalu Valgjärv	Uljaste	Korijärv
Area, ha	6.3	63	36.4
Mean depth, m	6.2	2.2	3.5
Maximum depth, m	11.7	6.4	5.1
Volume, 10^6 m^3	0.39	1.38	1.28
Drainage area, ha	<20	110	860
Water exchange, $year^{-1}$	~ 0	0.2	1.7

Lake Uljaste belongs according to the typology of Estonian lakes (Mäemets, 1977) to the semidystrophic type, i. e. to the transitional type between oligo- and dystrophic lakes, whose main characteristics are soft water and a rather high concentration of humic substances. This lake is located in Ida-Viru County, 4.3 km west of Sonda. The moor of Uljaste forms the drainage area of the lake. Sublacustrine springs make up a minor portion of the total water input. The lake is surrounded by a high ridge in the north and east and by a moor in the south-west, west, and north-west. The chiefly sandy bottom is covered with mud in the western part of the lake. The direct human impact is expressed by pollution caused by holiday-makers and fishermen, though most pollutants probably reach the lake as atmospheric precipitation from a large industrial area in the neighbourhood.

The highly eutrophic Lake Korijärv is situated on a moraine landscape in Valga County 7.5 km from Antsla. Its mostly agricultural drainage area exceeds the area of the lake more than 20-fold. Koosa Stream, the largest of the three main inflows, comes from a neighbouring reservoir, which acts as an oxidation pond. Numerous shore springs are characteristic of L. Korijärv.

The lake was strongly polluted by a pig-farm till the 1970s and is still polluted by a cattle-farm. The nutrient load caused by the latter is 4.3 kg P ha^{-1} and 147 kg N ha^{-1} calculated according to Velner and Loigu (Вельнер and Лойгу, 1985).

The last years with their warm winters and abundant rain have improved the ecological state of most of our lakes, while the more consistent use of nutrients during the long vegetation period and the diluting effect of rainwater prevent extensive fluctuations in biota. That is why several typical features of the investigated lakes did not necessarily appear in 1991. Unfortunately, this improvement is evidently of a temporary character.

3. Materials and Methods

The material for the present paper was collected during three expeditions in June, August, and September/October 1991. Data on fish date partially from 1990.

Hydrochemical and plankton samples were taken from the surface, at a depth of one metre, from thermocline in case it existed, and from the near-bottom layer at one station. Underwater light measurements by means of a spectral radiometer ИПО-2 were carried out in lakes Korijärv and Nohipalu Valgjärv in August. Values at 4 wavelengths within PhAR were registered with a discretion of 0.5 m. Two indices were calculated:

underwater illumination coefficient

$$\eta = I(z_i)/I(z_0), \text{ and}$$

light extinction coefficient

$$k_e = \frac{1}{z_2 - z_1} \cdot \ln \frac{I(z_1)}{I(z_2)},$$

where z_i — depth;
$I(z_i)$ — irradiance at depth z_i;
$I(z_0)$ — irradiance at the lake surface.

The first coefficient enables to estimate how many times the light reaching the depth z has weakened in comparison with the light at the surface. The light extinction coefficient, i. e. attenuation of light in a 1-metre water layer, characterizes the depth distribution of optically active substances (mostly particulate matter) and gives essential information especially in stratified lakes.

Hydrochemical samples were analysed using standard methods (Golterman, 1971). Pigment concentrations were measured spectrophotometrically and calculated for chlorophylls by means of the equations of Jeffrey and Humphrey (1975) and for carotenoids using those by Strickland and Parsons (1972).

Phytoplankton was concentrated on Synpor membrane filters with a pore size 1.5 μm and counted in a Fuchs-Rosenthal chamber up to at least 400 units to achieve a reasonable accuracy of ±10% (Recommendations . . . , 1979).

Primary production (PP) was measured using the ^{14}C method (Steemann Nielsen, 1952). Samples were incubated *in situ* during 2 hours around noon. To derive daily production (PP_d) from the hourly production at noon (PP_h), an empirical relationship between these values and the day length (L_d) calculated on the basis of data on Lake Võrtsjärv was used:

$$PP_h/PP_d = -8.899 \cdot 10^{-3} \cdot L_d + 0.2297 \quad (n = 14;\ r = -0.81).$$

The total number of bacteria was counted on Synpor membrane filters with a pore size 0.2 μm. The production of bacterioplankton was measured using tritium-labelled dimethylthymidin (Guidelines . . . , 1988).

Integral zooplankton samples were taken with a quantitative Juday net. In addition integral bathometer samples were taken to catch small rotifers. The production (P) and ration (C) of zooplankton were calculated on the basis of the physiological method (Винберг, 1968; Waters, 1977; Методические . . . , 1984; Иванова, 1985). In the trophological sense, zooplankton represents a heterogeneous group, filter-feeding species belonging to herbivores and predatory species to the next trophic level. Therefore, the production of total zooplankton (P_{zp}), which is left over for fish, must be calculated as

$$P_{zp} = P_{filt} + P_{pred} - C_{pred},$$

where P_{filt} and P_{pred} are respectively the production of filtrative and predatory zooplankton and C_{pred} the ration of predatory zooplankton.

Thus, during some periods of the low activity of filter-feeding zooplankton P_{zp} may obtain negative values.

Experimental catches for fish fauna analysis with the use of gill nets were carried out in L. Korijärv in November 1991, in L. Uljaste in August 1990 and November 1991, and in L. Nohipalu Valgjärv in July 1990. For the sake of comparability the results were recalculated to the daily catch per 30-metre net, the so-called CPUE (catch per unit effort) index. In order to get an approximate estimation of the fish biomass, an empirical model relating the maximum sustained yield ($kg \cdot ha^{-1} \cdot y^{-1}$) to the summer average concentration of chlorophyll *a* ($mg \cdot m^{-3}$) in lakes of the north-temperate zone (Oglesby, 1977) was applied:

$$Y = -1.047 + 1.349 \text{ Chl } a.$$

As the maximum sustained yield makes up on an average a quarter of the biomass (Steffens, 1979), these values were multiplied by 4. The potential fish production was calculated according to Chapmann (Bagenal, 1978) by multiplying the fish biomass by the average growth rate. As the weight increment from the 3rd to the 4th year allows the best assessment of the population growth rate of most of our common species (Хаберман et al., 1991), the annual average rate of increase in weight (G) was calculated as:

$$G = \ln W_3 - \ln W_4,$$

where W_3 and W_4 are the average weights of the individuals of the 3rd and 4th year age groups.

The level of knowledge about the lakes is different: considering the number of the expeditions by the Võrtsjärv Limnological Station, L. Nohipalu Valgjärv has been investigated 23, L. Uljaste 12, and L. Korijärv 8 times, mostly in summer. In order to characterize long-term changes in the lakes unpublished data from earlier expeditions were partially used.

4. Results

4.1. Hydrochemical variables

Tables 2 and 3 present the values of the main hydrochemical variables of the lakes.

Lake Nohipalu Valgjärv is characterized by an extremely low concentration of salts. Under such conditions the concentration of HCO_3^- as the main source of inorganic carbon is greatly influenced by the metabolism of algae and varies on a relatively wide scale. As a result of human impact the concentration of sulphates and chlorides has grown

3.5 to 4 times as compared with the 1960s, while the highest values were registered in 1990—1991. The first data on nutrients in L. Nohipalu Valgjärv from July 1976 refer to its oligo-mesotrophic state (N_{tot} 260—300; P_{tot} 10). The vertical distribution of nutrients in the last years (Table 3) indicates strong stratification. The surface layer has retained its oligo-mesotrophic features, whereas the concentration of nutrients in the near-bottom water corresponds to that of the eu-hypertrophic state (Table 4).

Table 2

Average and absolute range of the concentration of major ions ($mg \cdot l^{-1}$), amount of organic matter (as permanganate (P_{ox}) and bichromate (D_{ox}) oxygen consumption, $mg\ O_2 \cdot l^{-1}$), and pH of the lakes since the 1950s

Variable	Lake		
	Nohipalu Valgjärv	Uljaste	Korijärv
HCO_3^-	3 (0—30)	11 (2—18)	205 (131—268)
SO_4^{2-}	16 (3—40)	8 (3—18)	36 (9—81)
Cl^-	3 (0.1—4.8)	3 (1.7—4.9)	10 (3.2—13)
Ca^{2+}	2 (1.6—2.8)	9 (6.0—12.0)	70 (48—116)
Mg^{2+}	3 (1.2—6.2)	3 (1.9—5.0)	17 (12—28)
P_{ox}	6 (0.9—13.8)	9 (4.5—16.0)	13 (7.9—18.2)
D_{ox}	12 (7—18)	25 (16—38)	33 (27—49)
pH	6.2 (5.0—7.2)	6.9 (6.0—7.6)	8.2 (7.6—8.9)

Table 3

Absolute range of total nutrient concentration ($mg \cdot m^{-3}$) of the lakes in 1989—1991

Lake, year	Layer	N_{tot}	P_{tot}	N : P
Nohipalu Valgjärv, 1990, 91	surface	380—430	7—21	20—54
	bottom	1150—1180	18—54	21—66
Uljaste, 1990, 91	surface	630—1370	20—35	33—39
	bottom	470—1760	18—35	49—52
Korijärv, 1989, 91	surface	860—2950	32—125	7—92
	bottom	1900—2770	32—125	15—87

Table 4

General ranges of primary production of phytoplankton and related characteristics of lakes of different trophic state*

Trophic state	PP, $mg\ C \cdot m^{-2} \cdot d^{-1}$	B_{php}, $g \cdot m^{-3}$	Chl *a*, $mg \cdot m^{-3}$	Light ext. coeff., m^{-1}	P_{tot}, $mg \cdot m^{-3}$	N_{tot}, $mg \cdot m^{-3}$
Ultraoligo-	<50	<1	0.01—0.5	0.03—0.8	<1—5	<1—250
Oligo-	50—300		0.3—3	0.05—1.0		
Oligo-meso-		1—3			5—10	250—600
Meso-	250—1000		2—15	0.1—2.0		
Meso-eu-		3—5			10—30	500—1100
Eu-	>1000		10—500	0.5—4.0		
Hypereu-		>10			30—>5000	500—>15000
Dys-	<50—500		0.1—10	1.0—4.0	<1—10	<1—500

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* Modified from Wetzel, 1975.

Table 5

Changes in permanganate and bichromate consumption in L. Nohipalu Valgjärv

Index	1960s	1991
P_{ox}, mg $O_2 \cdot l^{-1}$	2 (0.9—3.5)	8 (6.5—13.8)
D_{ox}, mg $O_2 \cdot l^{-1}$	11 (7.1—13.7)	13 (10.6—18.0)
P_{ox}/D_{ox}, %	22 (7—42)	63 (49—81)

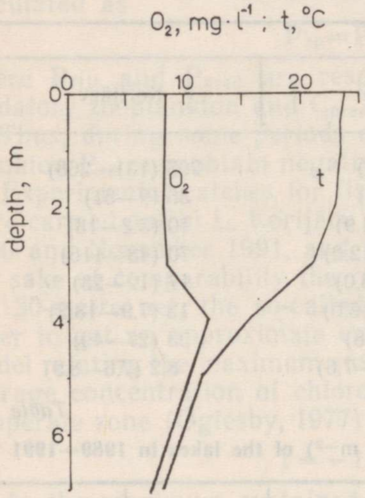


Fig. 1. Depth distribution of oxygen and temperature in L. Nohipalu Valgjärv on Aug. 8, 1991.

The amount of autochthonous organic matter as an evidence of considerable eutrophication has greatly increased, causing an about fourfold growth of permanganate consumption (Table 5). The summer oxygen profile (Fig. 1) shows a clear metalimnetic maximum with supersaturated values up to 100—120%. Below this a sharp decrease appears in the hypolimnion. While before the 1960s no oxygen deficit was reported even in winter, anaerobic conditions accompanied by the formation of H_2S in the hypolimnion have been recurrently registered since the early 1970s.

In Lake Uljaste the content of HCO_3^- and Ca^{2+} ions exceeds the average values of L. Nohipalu Valgjärv 3—4 times, but salinity remains still very low. The range of the seasonal changes of the SO_4^{2-} concentration has obviously increased since both the lowest and the highest values were registered in 1991. The estimation of the trophic state on the basis of nutrients leads to contradictory results: the N_{tot} content characterizes the lake as a hypertrophic one, while P_{tot} remains in the meso-eutrophic range (Table 4). The N:P ratio is relatively stable. The content of organic substances in L. Uljaste is somewhat higher than in L. Nohipalu Valgjärv, especially when expressed as the bichromate consumption, which takes into account the humic substances. The oxygen depth curve demonstrated a slight decrease in the oxygen concentration at a depth of 4 m up to 30% of saturation values in summer, but due to the shallowness of the lake these vertical differences are of a temporary nature.

Lake Korijärv is a well-buffered hard-water lake with neutral or slightly alkaline water common to eutrophic water-bodies. The content of sulphates and chlorides has increased 3—4 times like in L. Nohipalu Valgjärv reaching a high level. As to the nutrients concentration L. Korijärv belongs to hypertrophic water-bodies. In June 1991 the N : P ratio was about 90 in the lake and only 30 in the main inflow. The large phosphorus input has accelerated the eutrophication of the lake. The content of organic substances in L. Korijärv is moderate but still exceeds that in both other lakes. In spite of the shallow water a strong oxygen gradient appeared during a short stagnation. In August 1991 the oxygen concentration of 8.7 mg $\cdot l^{-1}$ in the surface layer decreased to 1 mg $\cdot l^{-1}$ at a depth of 2 m and fell to zero at a depth of 3 m.

4.2. Water transparency and distribution of light

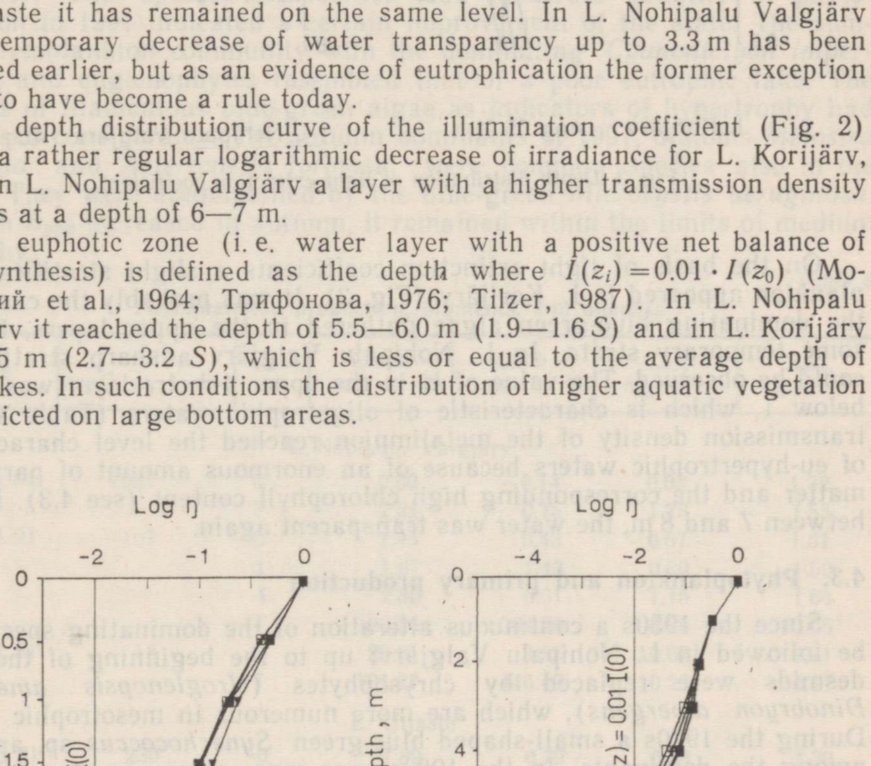
Owing to its simplicity Secchi disk transparency (*S*) continues to be widely used in the approximate evaluation of the optical qualities of water. In unstratified lakes this method gives a rather good picture of the prevailing light conditions and the amount of suspended matter. In stratified lakes, however, no information can be obtained about the stratification type and the optical qualities of deeper layers. According to water transparency in 1991 the lakes were arranged in the following order:

1. L. Nohipalu Valgjärv	3.5—4.0 m
2. L. Uljaste	1.6—2.3 m
3. L. Korijärv	1.05—1.1 m

In comparison with the 1950s the average water transparency has decreased twice in L. Nohipalu Valgjärv and L. Korijärv, while in L. Uljaste it has remained on the same level. In L. Nohipalu Valgjärv some temporary decrease of water transparency up to 3.3 m has been observed earlier, but as an evidence of eutrophication the former exception seems to have become a rule today.

The depth distribution curve of the illumination coefficient (Fig. 2) shows a rather regular logarithmic decrease of irradiance for L. Korijärv, while in L. Nohipalu Valgjärv a layer with a higher transmission density appears at a depth of 6—7 m.

The euphotic zone (i. e. water layer with a positive net balance of photosynthesis) is defined as the depth where $I(z_i) = 0.01 \cdot I(z_0)$ (Мокиевский et al., 1964; Трифонова, 1976; Tilzer, 1987). In L. Nohipalu Valgjärv it reached the depth of 5.5—6.0 m (1.9—1.6 *S*) and in L. Korijärv 3.0—3.5 m (2.7—3.2 *S*), which is less or equal to the average depth of both lakes. In such conditions the distribution of higher aquatic vegetation is restricted on large bottom areas.



L. Korijärv Aug. 05.91. L. Nohipalu Valgjärv Aug. 06.91.

Fig. 2. Depth distribution of underwater illumination coefficient.

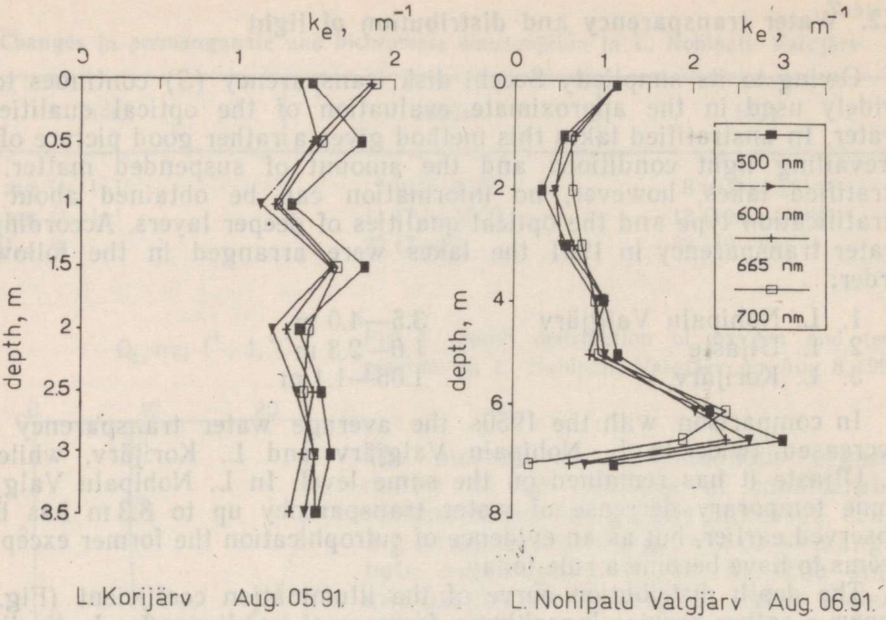


Fig. 3. Depth distribution of light extinction coefficient.

On the basis of light extinction coefficients a slight stratification of plankton appeared in L. Korijärv (Fig. 3). It was probably the case when the dominating blue-green algae gathered in the upper layers, forming some temporary strata. In L. Nohipalu Valgjärv a sharp stratification could be observed. The value of k_e in the upper 4-metre layer was mostly below 1, which is characteristic of oligotrophic waters (Table 4). The transmission density of the metalimnion reached the level characteristic of eu-hypertrophic waters because of an enormous amount of particulate matter and the corresponding high chlorophyll content (see 4.3). Deeper, between 7 and 8 m, the water was transparent again.

4.3. Phytoplankton and primary production

Since the 1950s a continuous alteration of the dominating species can be followed in L. Nohipalu Valgjärv: up to the beginning of the 1970s desmids were replaced by chrysophytes (*Uroglenopsis americana*, *Dinobryon divergens*), which are more numerous in mesotrophic waters. During the 1970s a small-shaped blue-green *Synechococcus* sp. appeared among the dominants. In the 1980s ever more chlorococcales (*Oocystis* spp., *Schisochlamys* sp.) and, during the last years, also pyrrophytes and euglenophytes appeared, which are characteristic of the lakes becoming poor in the species composition. In 1991 chrysophytes (*Dinobryon divergens*, *D. cylindricum*, *Uroglena proxima*) were among the dominants in June, the euglenophyte *Gonyostomum semen* in August and September. The biomass of phytoplankton (B_{php}) reached about $5\ g \cdot m^{-3}$ in the epilimnion and $20\ g \cdot m^{-3}$ in the metalimnion.

M. Pork reported weak annual blue-green blooms in L. Uljaste already in the 1950s (cited in Mäemets, 1977). In spite of this L. Uljaste had a rich species composition with a large number of desmids. The situation in which a number of species with very different indicator values occur among the dominating blue-greens has persisted up to now. Besides indicators of oligotrophy (*Staurodesmus dejectus*, *Botryococcus braunii*, *Staurastrum* spp., *Dinobryon* spp.) indicators of eutrophy and even hypertrophy (*Oscillatoria agardhii*) can be found. Such an eclectic algal community is typical of the semidystrophic lake type as an intermediate one. As an evidence of eutrophication the species diversity has decreased especially among desmids while the proportion of blue-greens in biomass has increased up to 70%. Most of the dominating species of blue-greens, *Aphanizomenon flos-aquae*, and four species of the genus *Anabaena* are N-fixing and thus independent of the concentration of this nutrient in water.

Annual spring water blooms in L. Korijärv in the 1950s were caused by diatoms and chrysophytes. In summer these groups were replaced by blue-green algae. This kind of a succession is characteristic of eutrophic water-bodies with a great species diversity and usually with the domination of large-cell species. In the 1970s and 1980s L. Korijärv was clearly hypertrophic (dominating blue-greens: *Oscillatoria agardhii*, *Aphanizomenon flos-aquae*, *A. gracile*, *Anabaena* spp.) with some features of dystrophication (appearance of numerous euglenophytes and chlorococcales). The species composition and moderate quantity of phytoplankton in 1991 indicated a certain improvement of the state. The summer phytoplankton community with the dominating *Cyanodictyon imperfectum* and euglenophytes resembled that of a poor eutrophic lake. The number of filamentous blue-green algae as indicators of hypertrophy had decreased considerably. The autumn dominants of 1991, diatoms *Melosira ambigua* and *Asterionella formosa*, were common species also in the 1950s. They were accompanied by the blue-green *Microcystis aeruginosa*. Though B_{php} increased in autumn, it remained within the limits of medium eutrophy.

Table 6

Phytoplankton production, pigments, and biomass

Date	PP, mg C · m^{-2} · d^{-1}	Depth, m	Chl *a*, mg · m^{-3}	Chl *b*, mg · m^{-3}	Car, mg · m^{-3}	B_{php}, g · m^{-3}
L. Nohipalu Valgjärv						
12.06.91	1051	0	0.60	−0.14	0.02	1.32
		7	2.21	0.75	1.73	1.55
06.08.91	107	0	1.95	0.43	0.67	1.51
		1	1.87	1.43	0.20	1.50
		4	2.80	0.61	1.15	1.64
		7	120.76	304.20	3.95	19.05
30.09.91	18	0	23.61	3.83	10.67	4.71
		7	101.27	446.42	10.23	16.17
L. Uljaste						
13.06.91	230	0	7.89	0.79	0.63	2.39
		4	9.59	0.90	3.27	2.64
08.08.91	554	0	22.57	2.27	6.57	4.56
		4	13.07	0.58	4.04	3.16
08.10.91	144	0	19.70	2.97	7.28	4.13
		4	17.92	3.78	6.51	3.87
L. Korijärv						
10.06.91	1325	0	11.80	1.91	4.99	2.97
		3	20.96	1.38	8.23	4.32
05.08.91	1247	0	18.59	2.33	5.61	3.97
		1	21.56	1.37	5.61	4.41
		3	15.63	3.69	4.49	3.53
01.10.91	483	0	44.04	12.83	11.51	7.73
		3	49.76	5.39	13.42	8.57

To characterize the pigment composition, the concentration of Chl *a*, Chl *b*, and carotenoids was measured (Table 6). The concentration of Chl *a* as the main photosynthetic pigment of all plants is in common use as a parameter of phytoplankton quantity. Chl *b* is an additional photosynthetic pigment in chlorophytes and euglenophytes. As the precision of measurement of Chl *b* is obviously much lower than this of Chl *a*, the determination of Chl *b* must be regarded as qualitative rather than quantitative (Recommendations . . . , 1979). Carotenoids (Car) have a protective function against excessive light intensities by shielding chlorophylls and by diverting excitation energy, which otherwise would lead to the photooxidation of photosynthetic pigments (Pearl et al., 1983). The concentration of carotenoids is in a strong correlation with the concentration of Chl *a* ($r=0.95$ in the present material), as both of them depend on the amount of plankton. The ratio Car/Chl *a* allows to estimate, within certain limits, the physiological state of a phytoplankton community. Since in dead cells Car are decomposed slowlier than Chl *a* (Давыдова, 1983), the ratio will increase together with the proportion of dead cells.

When analysing productivity, the concentration of pigments and the physiological state of phytoplankton are of the greatest interest. In all three lakes the Chl content increased during the vegetation period (Fig. 4). In lakes Uljaste and Nohipalu Valgjärv the ratio Car/Chl *a* also followed this trend (Fig. 5). In L. Korijärv the Chl *a* content reached the highest value — 44 $\mathrm{mg \cdot m^{-3}}$ — in autumn while the importance of Car decreased. This could have been the result of a radical transformation of the plankton community. Judging by chlorophyll data a strong stratification existed in L. Nohipalu Valgjärv in August and September. The high content of Chl *b* in the near bottom layer originated from the euglenophyte *Gonyostomum semen*. No essential differences occurred in the depth distribution of pigments in the other lakes.

The depth distribution curve of PP in lakes with a rather uniform plankton distribution, L. Uljaste and L. Korijärv, had a regular shape (Fig. 6). In most cases photosynthesis was inhibited at the surface due to excessive light, its maximum being located between 0.25—1 *S*. In the stratified L. Nohipalu Valgjärv the depth distribution of photosynthesis still depended on the plankton distribution. While in June and August a light-limited range of the PP vs. depth curve could be observed below 4 m, in September no photosynthesis occurred already at the depth equal to water transparency, where light cannot be a limiting factor. Consequently, other factors such as the lack of nutrients (N, P, C) could have been the cause on this.

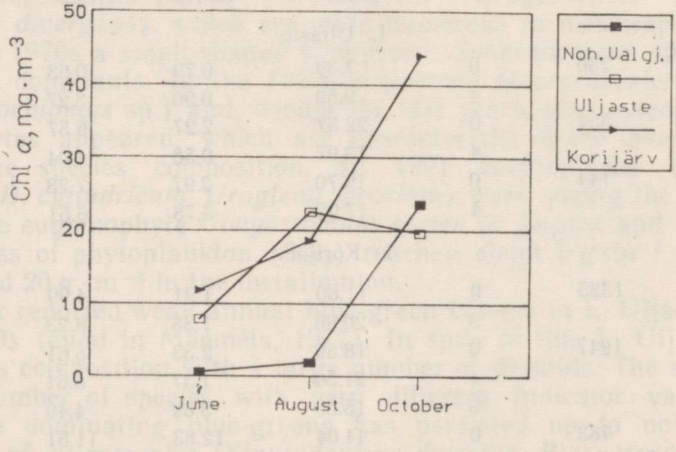


Fig. 4. Seasonal changes in chlorophyll *a* concentration in 1991.

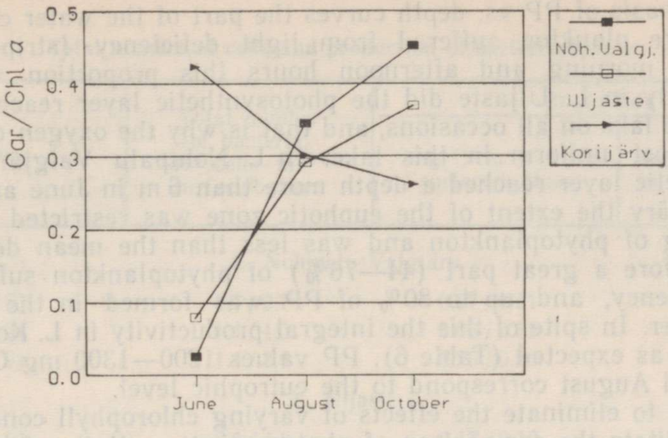


Fig. 5. Seasonal changes in carotenoid/chlorophyll *a* ratio in 1991.

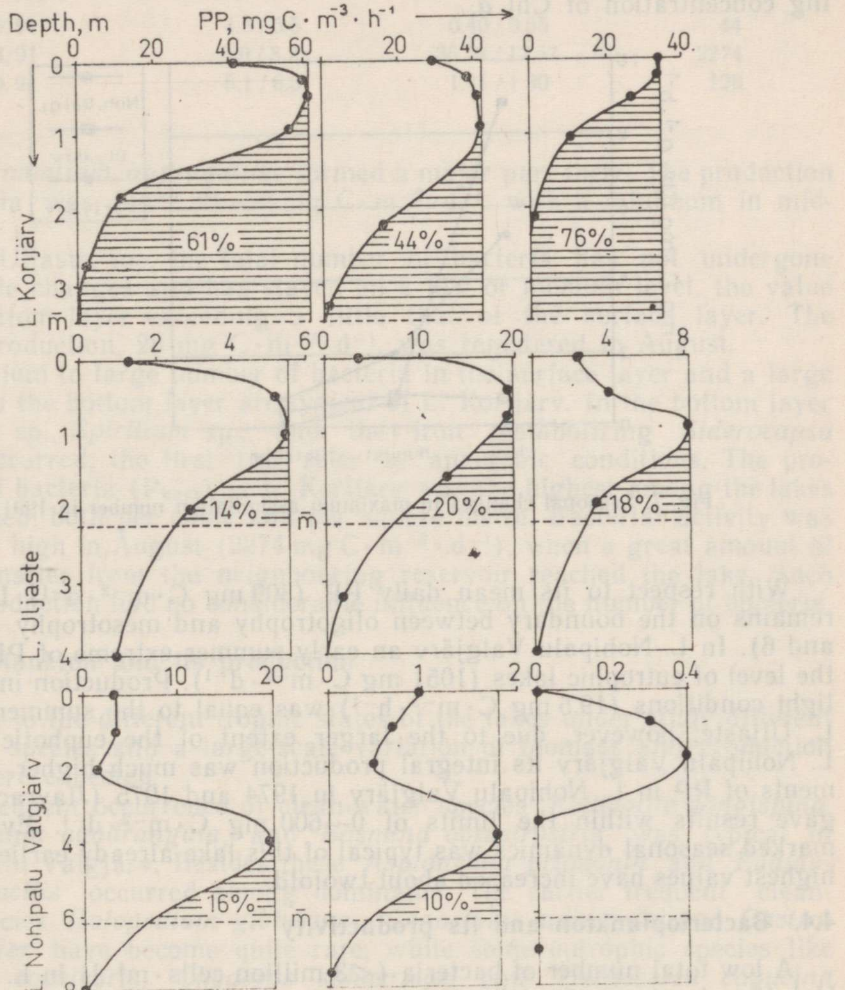


Fig. 6. Depth distribution of primary production and the part of the water column where plankton suffers from light deficiency (striped area); 1991.

On the basis of PP vs. depth curves the part of the water column was found where plankton suffered from light deficiency (striped area in Fig. 6). In morning and afternoon hours this proportion was surely greater. Only in L. Uljaste did the photosynthetic layer reach the mean depth of the lake on all occasions, and that is why the oxygen distribution was the most uniform in this lake. In L. Nohipalu Valgjärv, too, the photosynthetic layer reached a depth more than 6 m in June and August. In L. Korijärv the extent of the euphotic zone was restricted due to the self-shading of phytoplankton and was less than the mean depth of the lake. Therefore a great part (44—76%) of phytoplankton suffered from light deficiency, and up to 80% of PP was formed in the uppermost 1-metre layer. In spite of this the integral productivity in L. Korijärv was the highest as expected (Table 6). PP values 1200—1300 mg $C \cdot m^{-2} \cdot d^{-1}$ in June and August correspond to the eutrophic level.

In order to eliminate the effects of varying chlorophyll concentrations and to facilitate the comparison of photosynthetic activity of phytoplankton, the rate of maximum photosynthesis was expressed per unit weight of Chl *a*. This so-called assimilation number (AN_{max}) was the greatest in June (Fig. 7), further the specific productivity diminished with the increasing concentration of Chl *a*.

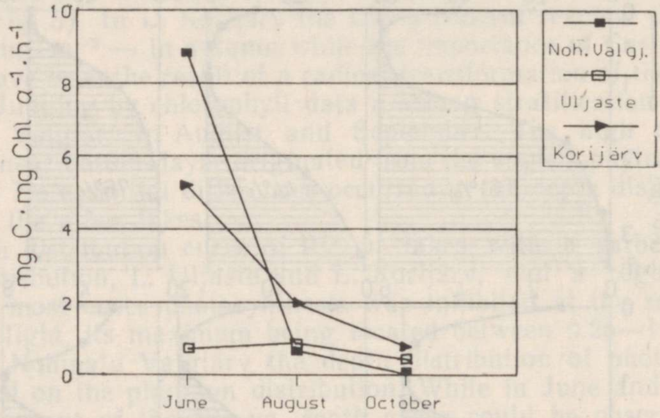


Fig. 7. Seasonal changes in maximum assimilation number in 1991.

With respect to its mean daily PP (309 mg $C \cdot m^{-2} \cdot d^{-1}$) L. Uljaste remains on the boundary between oligotrophy and mesotrophy (Tables 4 and 6). In L. Nohipalu Valgjärv an early summer extreme of PP reached the level of eutrophic lakes (1051 mg $C \cdot m^{-2} \cdot d^{-1}$). Production in optimum light conditions (19.5 mg $C \cdot m^{-3} \cdot h^{-1}$) was equal to the summer value of L. Uljaste; however, due to the larger extent of the euphotic layer in L. Nohipalu Valgjärv its integral production was much higher. Measurements of PP in L. Nohipalu Valgjärv in 1974 and 1975 (Лаугасте, 1980) gave results within the limits of 0—600 mg $C \cdot m^{-2} \cdot d^{-1}$. Evidently, a marked seasonal dynamics was typical of this lake already earlier, but the highest values have increased about twofold.

4.4. Bacterioplankton and its productivity

A low total number of bacteria (<3 million cells $\cdot ml^{-1}$) in L. Nohipalu Valgjärv in the surface layer has repeatedly been observed since 1975. In August and September 1991 the number of bacteria in the bottom layer had increased to the medium level (Table 7). As is common in the case of stratified lakes, photosynthetic bacteria *Chlorobium vibrioforme* and

Table 7

Total number of cells and production of bacterioplankton

Date	Total number of bacteria, 10^6 cells · ml^{-1} surface/bottom	Production	
		mg C · m^{-3} · h^{-1} surface/bottom	mg C · m^{-2} · d^{-1} in water column
L. Nohipalu Valgjärv			
12. 06. 91	1.7 / 2.7	0.27 / 0.21	35
06. 08. 91	1.4 / 4.5	0.03 / 0.32	26
30. 09. 91	1.4 / 3.9	0.26 / 0.26	38
L. Uljaste			
13. 06. 91	2.1 / 4.6	0.17 / 0.10	7
08. 08. 91	2.0 / 2.5	0.36 / 0.72	28
08. 10. 91	2.6 / 2.9	0.49 / 0.36	22
L. Korijärv			
10. 06. 91	4.5 / 5.5	0.40 / 0.65	44
05. 08. 91	6.0 / 8.2	36.58 / 17.57	2274
01. 10. 91	5.1 / 6.3	1.71 / 1.30	126

Chlorochromatium aggregatum formed a major part there. The production of bacteria was low: 26—38 mg C · m^{-2} · d^{-1} with a minimum in midsummer.

In L. Uljaste, too, the total number of bacteria has not undergone remarkable changes and has stayed on a low or medium level, the value in the bottom layer exceeding a little that of the surface layer. The highest production, 28 mg C · m^{-2} · d^{-1}, was registered in August.

A medium to large number of bacteria in the surface layer and a large number in the bottom layer are typical of L. Korijärv. In the bottom layer *Thiopedia* sp., *Spirillum* sp., and the iron metabolizing *Siderocapsa* species occurred; the first two refer to anaerobic conditions. The production of bacteria (P_{bact}) in L. Korijärv was the highest among the lakes investigated, both per cubic and per square metre. Bacterial activity was especially high in August (2274 mg C · m^{-2} · d^{-1}), when a great amount of organic matter from the neighbouring reservoir reached the lake. Such a high production had no considerable influence on the number of bacteria.

4.5. Zooplankton and its production

Owing to the different trophic states of the lakes under study different dominant species and a large-scale variation of biomass and production values were expected.

The frequent occurrence of clean-water species *Kellicottia longispina*, *Ceriodaphnia quadrangula*, and *Bosmina obtusirostris* was typical of L. Nohipalu Valgjärv. Besides these *Asplanchna priodonta* and *Eudiaptomus gracilis* occurred among dominants. The earlier frequent clean-water species *Holopedium gibberum*, *Conochilus unicornis*, and *Gastropus stylifer* have become quite rare, while some eutrophic species like *Keratella cochlearis*, *Chydorus sphaericus*, and *Trichocerca capucina* have appeared in plankton, which refers to the increase of the trophic state. The total number (N) of zooplankton was high due to the domination of the small rotifer *Kellicottia longispina.* The biomass (B) and production (P) values were medium (Table 8).

Table 8

Main zooplankton parameters

Date	Total number, $10^3 \text{ind} \cdot \text{m}^{-3}$	Biomass, $\text{g} \cdot \text{m}^{-3}$	P_{filt}	P_{pred}	P_{zp}	C_{filt}	C_{pred}
			$\text{mg C} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$				
			L. Nohipalu Valgjärv				
12. 06. 91	5084	1.4	51.0	4.7	35.5	245.4	20.3
06. 08. 91	1671	1.2	37.6	1.9	23.4	230.0	16.1
30. 09. 91	247	0.9	17.8	2.2	10.1	83.2	9.9
			L. Uljaste				
13. 06. 91	259	1.3	11.9	1.3	6.2	70.4	7.0
08. 08. 91	240	0.8	13.1	1.5	7.3	62.3	7.4
08. 10. 91	1004	0.5	2.9	1.0	−0.7	13.8	4.6
			L. Korijärv				
10. 06. 91	843	7.6	128.0	11.2	88.0	669.5	51.2
05. 08. 91	416	10.6	271.5	21.3	127.5	1623.8	165.2
01. 10. 91	4655	5.6	57.1	2.1	44.4	358.7	14.8

The simultaneous occurrence of the indicators of different trophic states was observed also in the zooplankton of L. Uljaste. Besides abundant clean-water species such as *Conochilus unicornis* and *Asplanchna herricki* the character species of eutrophic waters *Chydorus sphaericus* and *Bosmina longirostris* were frequent. The prevalence of small rotifers in the total number and larger copepods and cladocerans in the biomass is common knowledge. In Lake Uljaste, exceptionally, rotifers dominated both in the biomass and production, especially in August and October, due to the abundant occurrence of rather large species *Polyarthra euryptera* and *Asplancha* spp. In October when P_{filt} reached its minimum, a large proportion of the predatory *Asplanchna priodonta* (69% of the biomass) resulted in the decrease of the total zooplankton biomass. Generally, the total number of zooplankton in L. Uljaste can be regarded as medium, while the biomass and production were small. The values of quantitative indices were the lowest in L. Uljaste.

In L. Korijärv the character species of eutrophic water-bodies, *Daphnia cucullata*, was one of the most frequent species which dominated in the biomass and production during the whole vegetation period. It was followed by *Asplanchna priodonta* and *Eudiaptomus gracilis*, which were the common dominants in L. Korijärv and L. Nohipalu Valgjärv. In October the biomasses of rotifers, cladocerans, and copepods were almost uniform, while rotifers prevailed in the production. All quantitative indices of zooplankton, except for the total number, exceeded those of L. Uljaste by about one order of magnitude.

4.6. Fishes and fish production

In July 1990 only perch occurred in the experimental catch in L. Nohipalu Valgjärv (Table 9), though pike, too, has been caught in this lake during earlier expeditions. The growth rate of perch was in a good accordance with the average of Estonian lakes. The biomass and production values of fish were the lowest among the lakes investigated.

In L. Uljaste peled (northern whitefish), roach, and perch were dominating. Earlier data show an essential role of bream in this lake

Table 9

CPUE indices of the number of individuals (N) and weight of fishes (W); biomass (B), growth rate (G), and production of fish (P)

Species	N, ind · 30 m net^{-1} · d^{-1}	W, g · 30 m net^{-1} · d^{-1}	B, kg · ha^{-1}	G, y^{-1}	P, kg · ha^{-1} · y^{-1}
L. Nohipalu Valgjärv					
Perch (*Perca fluviatilis* L.)	77.0	1776	24.9	0.83	20.7
Total	77.0	1776	24.9		20.7
L. Uljaste					
Peled (*Coregonus peled* (Gmelin))	1.4	960	40.9	0.07	2.9
Roach (*Rutilus rutilus* (L.))	21.3	390	16.3	0.78	12.7
Perch (*Perca fluviatilis* L.)	2.2	360	14.7	0.83	12.2
Pike (*Esox lucius* L.)	0.1	100	3.9	0.37	1.4
Total	25.00	1810	75.8		29.2
L. Korijärv					
Roach (*Rutilus rutilus* (L.))	627.1	14364	155.0	0.78	120.9
Tench (*Tinca tinca* (L.))	10.3	4942	53.2	0.30	16.0
Bream (*Abramis brama* (L.))	17.5	2218	23.9	0.75	17.9
Perch (*Perca fluviatilis* L.)	50.4	2213	23.6	0.16	3.8
Carp (*Cyprinus carpio* L.)	1.4	653	6.8	0.30	2.0
Ruff (*Acerina cernua* (L.))	29.0	478	5.2	0.11	0.6
Crucian carp (*Carassius carassius* (L.))	1.4	228	2.4	0.32	0.8
Pike-perch (*Stizostedion lucioperca* (L.))	0.7	89	0.9	0.65	0.6
Total	737.8	25185	271.0		162.6

(Haberman et al., 1991). Feeding conditions ought to be favourable for bream, but the shortage of spawning places is a limiting factor. Perch, roach, and pike are the primeval inhabitants while bream was introduced in the last century and peled in 1978. The latter does not spawn in L. Uljaste. The growth rate and production of the 12-year-old population are rather small owing to the low zooplankton production. In 1990 the mean length of peled was 34.4 cm. The number of pikes is small due to the lack of spawning places on the one hand and the pressure of amateur fishermen on the other.

Roach is the main dominant in L. Korijärv, forming about 60% of the biomass and 75% of the fish production. The high trophic state of this lake resulted in the 3.5 times higher fish biomass and 5.5 times higher production in comparison with L. Uljaste.

5. Discussion

5.1. Type-specific individuality of the production processes of the lakes

A preliminary picture of trophic relations in the lakes and the type of the circulation of biological matter as a whole can be obtained by a simple juxtaposition of the productivity and rations of different trophic levels (Table 10).

Table 10

Percentage ratios of production and ration values in plankton communities; potential utilization of phytoplankton biomass by herbivorous zooplankton

Date	$\frac{P_{bact}}{PP}$	$\frac{P_{filt}}{PP}$	$\frac{P_{bact}}{P_{filt}}$	$\frac{C_{filt}}{PP}$	$\frac{C_{filt}}{PP+P_{bact}}$	$\frac{C_{pred}}{P_{filt}}$	$\frac{C_{filt}}{B_{php}}$ $(\% \cdot d^{-1})$
L. Nohipalu Valgjärv							
12. 06. 91	3	5	69	23	23	40	43
06. 08. 91	24	35	69	715	173	43	16
30. 09. 91	210	99	213	462	148	56	3
L. Uljaste							
13. 06. 91	3	5	59	31	30	59	18
08. 08. 91	5	2	214	11	11	56	10
08. 10. 91	16	2	759	10	8	160	2
L. Korijärv							
10. 06. 91	3	10	34	51	49	40	72
05. 08. 91	182	22	828	130	46	61	167
01. 10. 91	26	12	221	74	59	26	18

Ratios P_{bact}/PP and P_{filt}/PP characterize the transformation of primary production in herbivorous and decomposition links. The values exceeding 20% refer to the consumption of the biomass stock accumulated earlier.

The ratio P_{bact}/P_{filt} is an indicator of the food chain type. As bacteria and filter-feeding zooplankton are the main competitors for organic matter, their production ratio shows whether a detrital or grazing food chain prevails. From the point of view of fish production the efficiency of the latter is much higher, while in the detrital food chain bacteria form an additional link between algae and zooplankton, whose demand for the metabolic energy amounts to 90% of the energy consumed. If filamentous or other forms of algae, unedible for zooplankton, are prevailing or if excessive masses of phytoplankton have been developed, the detrital food chain will become dominating.

Ratios C_{filt}/PP and $C_{filt}/PP+P_{bact}$ illustrate the satisfaction of the food requirements of filtrative zooplankton by the instantaneous production of algae and bacteria. The values exceeding 100% indicate the major role of detritus or biomass produced earlier in the zooplankton ration.

The ratio C_{pred}/P_{filt} shows the proportion of the production of filter-feeding zooplankton consumed by predatory zooplankton, and thus the extent of competition between predatory zooplankton and plankton-feeding fish.

The ratio C_{filt}/B_{php} shows the percentage of the phytoplankton biomass which would be grazed by zooplankton per day if zooplankton fed only on phytoplankton. The values exceeding 100% indicate an essential part of other food in the zooplankton ration.

The ecosystem of L. Nohipalu Valgjärv as a lake which was recently oligotrophic can easily be thrown off its balance. Therefore, the eutrophication of this lake results in large fluctuations of bioproduction. During the first half of the vegetation period a great amount of the phytoplankton biomass is formed in the metalimnion; it serves as further food for heterotrophs. At present the nutrient cycle proceeds deeper than the mixing depth and the uppermost 5-metre layer retains its oligotrophic character. In the course of further eutrophication the PP maximum will move from the bottom upwards due to the self-shading effect of phytoplankton, and the water quality of the epilimnion will deteriorate rapidly. In the second half of the vegetation period PP is low or extremely low. As bacteria and zooplankton consume mainly the biomass stock formed earlier, the ratios P_{bact}/PP and P_{filt}/PP reached their highest values in September. Taking into account the efficiency of energy transformation in the food chain, these ratios cannot exceed 10—20% as an average for the vegetation period (Одум, 1975).

The ratios C_{filt}/PP and $C_{filt}/PP+P_{bact}$ in August and September (462—715% and 148—173%, respectively) show that the food requirements of filter-feeding zooplankton could not be satisfied even if all the instantaneous production of phyto- and bacterioplankton was consumed. Consequently, detritus or dissolved organic matter had to play an important role in the zooplankton ration. The grazing food chain type, which was predominant in spring and summer when the major part of the zooplankton ration was covered by living phytoplankton, was changed into the detrital type in September; in the latter bacteria obtained an intermediate position in the transformation of primary organic matter to zooplankton. The average ration of predatory zooplankton made up less than a half of the production of filtrative zooplankton. As young perch is the only consumer of the rather big zooplankton production, its feeding conditions ought to be favourable. The high Chl *a* concentration in September indicated that a great part of primary organic matter had remained unconsumed in the food chain. It would be mineralized during winter. The released nutrients are a precondition for high PP in spring.

In L. Uljaste a stable formation of PP and its utilization in heterotrophic links were the main characteristic features of the ecosystem. Because of the moderate eutrophication level and a rather good water circulation no accumulation of organic matter occurred. Low PP in June and the decrease of chlorophyll concentrations in autumn also gave proof of this. Examination of the ratio P_{bact}/P_{filt} shows the leading role of bacteria, especially in autumn. Filtrators consumed only 10—30% of PP. The dominance of the detrital food chain in L. Uljaste resulted in the small biomass and production of filtrative zooplankton. The role of predatory zooplankton was rather important, causing a rather scanty food supply for the dominating fish species, peled and roach, in L. Uljaste.

The ecosystem of L. Korijärv belongs to the hypertrophic type. Because of the higher trophic state of this lake all production processes in it were much more intensive than in the other lakes. The periods of maximum primary and secondary production did not coincide. The stock of released nutrients was utilized by phytoplankton in spring and early summer when water temperature was still too low for the mass development of bacteria and zooplankton. In August the production and biomass of bacteria and zooplankton reached their extreme values. The strikingly high P_{bact}, which exceeded PP nearly twice, might partially have been caused by allochthonous organic matter. The ratio P_{bact}/P_{filt} showed the firm domination of the detrital food chain in August. Its proportion diminished again in October. In autumn the biomass of phytoplankton continued increasing in spite of the decrease of PP. This was caused by the low grazing activity of zooplankton in cold water, by the domination of larger phytoplankters like *Melosira ambigua*, as well as by the wind-dependent resuspension of dead but still undestroyed algal material from the sediment. The accumulative type of matter recycling in L. Korijärv was reflected also in the fish fauna in which benthos-feeding species like roach, tench, bream, and carp played the leading role.

5.2. Principles of lake management and protection

Differing in their hydrochemical and biological nature, the lakes require a differentiated approach to the selection of measures for their management and protection.

The unique ecosystem of L. Nohipalu Valgjärv has already been strongly damaged by eutrophication, evidenced by high PP in spring and accumulation of organic matter. The low alkalinity of water restrains the rate of the formation of algal biomass by the poor availability of carbon, but cannot prevent the eutrophication of the lake. The low buffering capacity makes the lake highly sensitive to any kind of external impacts. As a first step in protecting the lake, the number of holiday-makers using it for swimming and recreation ought to be diminished. During the last years the local forestry enterprise has taken good care of the lake shore: a comfortable cottage with information tables, a fireplace, a ground for pitching tents, and a toilet have been built for tourists. Though these measures have undoubtedly had an educational effect on "wild" tourists, a well-organized recreation place attracts too many people to the lake. The only way to save and protect the unique ecosystem is the restoration of the lake and the establishment of the nature reserve regime. In order to select an appropriate restoration method, special investigations of the lake mud would be necessary. In summer a major part of nutrients is bound in organic compounds which are concentrated within a thin water layer in the metalimnion. One possible way to improve the state of the lake would be to pump water out of this layer and treat it on the shore using special purification equipment. No manipulation of the fish fauna would be recommended.

The ecological state of L. Uljaste is in general good. In spite of the high nitrogen concentration, PP remains on a moderate level as it is limited by the availability of phosphorus and/or mineral carbon compounds. The utilization of the scanty zooplankton by fish can be improved by the selective catch of peled, whose old and non-reproductive population feeds mainly on zooplankton and competes strongly with the fry of the other species. Peled can be caught only with gill nets and is therefore of no importance in sporting angle fishing.

The level of nature protection in the drainage area of L. Korijärv is low. Strong agricultural pollution has resulted in high productivity of all links in the ecosystem and in the accumulation of mud. Eutrophication has reached the level at which the mass development of N-fixing blue-green algae makes the system independent of the external amount of nitrogen compounds, while phosphorus remains the single factor limiting PP. Besides the decrease of the phosphorus input, the biomanipulation of the fish fauna may be a successful tool in improving the ecological state of this lake. According to Jeppesen et al. (1990) an essential decrease in B_{php} and the improvement of water transparency can be achieved by suppressing the biomass of plankton-feeding fish down to 8 $g \cdot m^{-2}$. The following mass development of zooplankton would control the B_{php} by intensive grazing. This measure would exert a temporary effect if the amount of plankton-feeding fish were suppressed artificially by selective catch (though it would be necessary as a first step). A steady state could be guaranteed by the introduction of predatory fishes, which would control the development of plankton-feeding small fishes. The turbid water of L. Korijärv is more favourable for the already existing pike-perch than for pike, which needs higher water transparency for hunting. A selective catch of roach for suppressing its biomass about twofold, followed by the introduction of young pike-perch and the improvement of its spawning conditions by making artificial spawning nests, would be highly desirable.

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