

PRIMARY PRODUCTION OF TWO SMALL LAKES IN ATLANTIC CANADA

G.D. HOWELL
Environment Canada
Water Quality Branch
P.O. Box 861
Moncton, N.B.
E1C 8N6

and

J.J. KERKES
Environment Canada
Canadian Wildlife Service
Department of Biology
Dalhousie University
Halifax, Nova Scotia
B3H 4J1

At Layton's Lake, Nova Scotia, the total annual primary production was estimated to be $182 \text{ gC m}^{-2} \text{ y}^{-1}$ of which $87 \text{ gC m}^{-2} \text{ y}^{-1}$ was planktonic production. Macrophyte production accounted for the additional $95 \text{ gC m}^{-2} \text{ y}^{-1}$. The macrophytes appeared to be inhibitory to the phytoplankton during the summer growing season, as indicated by the low chlorophyll-a concentrations. Total phosphorus and maximum chlorophyll-a concentrations were the best trophic indicators, suggesting that Layton's lake is eutrophic. Long Lake, New Brunswick, had an estimated annual primary production of $36.4 \text{ gC m}^{-2} \text{ y}^{-1}$ due solely to phytoplanktonic production. Variations in daily areal production values could be explained largely by variations in surface insolation and flow rate. Neither total phosphorus concentration or chlorophyll-a concentration were good trophic indicators. It is suggested that peak chlorophyll-a concentration is the best trophic indicator for Long Lake, resulting in borderline oligotrophic-mesotrophic classification.

Au lac Layton en Nouvelle Ecosse, la production totale annuelle primaire a été évalué à $182 \text{ gC m}^{-2} \text{ a}^{-1}$ dont $87 \text{ gC m}^{-2} \text{ a}^{-1}$ a été la production planktonique. La production macrophytique explique la $95 \text{ gC m}^{-2} \text{ a}^{-1}$ de production en plus. Les macrophytes paraissent être inhibitoires aux phytoplanktons pendant la période de croissance estival, comme indiqué par le bas niveau de la chlorophylle-a. Le taux de phosphore totale et la concentration maximale de la chlorophylle-a ont été les meilleurs indices trophiques et suggèrent que le lac Layton est eutrophique. La production annuelle primaire du lac Long au Nouveau Brunswick a été évalué à $36.4 \text{ gC m}^{-2} \text{ a}^{-1}$ attribuable entièrement à la production phytoplanktonique. Les variations journalières dans les valeurs de productions d'aire peuvent être expliquées par les variations dans l'ensoleillement de la surface du lac et dans le débit d'eau. Ni les taux totales de phosphore ni la concentration en chlorophylle-a sont de bons indices trophiques. On suggère que la concentration maximale en chlorophylle-a est le meilleur indice trophique pour le lac Long et mène a une classification oligotrophique-mésotrophique.

Introduction

There has been little consideration of the primary productivity of the Atlantic province lakes with only values from five Newfoundland lakes presented in the literature (Kerekes, 1975). This paper presents primary productivity data for two lakes (Layton's Lake, N.S. and Long Lake, N.B.) sampled between June 14, 1977 and August 28, 1978. These two lakes lie approximately 18 km apart and exhibit different chemical and physical features.

Layton's Lake is located in the Amherst Point Bird Sanctuary, a section of the Chignecto National Wildlife Area near Amherst, Nova Scotia ($45^{\circ}47'40'' \text{ N}$; $65^{\circ}15'20'' \text{ W}$) and is ectogenically meromictic, having prior to the 1950's received

periodic intrusions of seawater from the Cumberland Basin (Howell and Kerekes, 1982). It is both small and shallow (surface area = 11.4 ha, \bar{z} = 2.1 m, z_{\max} = 10.5 m) and as the consequence of a small drainage basin (63 ha) has a water residence time of 104 days. The soils of this region are considered to be among the best agricultural soils of the province (Nowland and MacDougall, 1973) and thus the waters of Layton's Lake have high total phosphorus (44 mgP m^{-3}) and total nitrogen concentrations (300 mgN L^{-1}). The waters are clear (15 Hazen units) with the 1% light level found 4-6 meters below the surface.

Long Lake ($45^{\circ}37'40'' \text{ N}$; $64^{\circ}14'15'' \text{ W}$) is partially located within the Tintamarre National Wildlife Area near Sackville, New Brunswick. The lake is divided into two basins by a causeway and only the southern part is considered in this study. The south basin is small (20 ha), extremely shallow (\bar{z} = 1.36 m, z_{\max} = 2.0 m) and due to the relatively large drainage basin (13.5 km^2) has a water residence time of 6 days. This lake has high water colour (110 Hazen units) which reduces light penetration with the 1% light level usually less than 1.5 m below the surface. Due to the short water residence time, concentrations of chemical constituents can fluctuate rapidly (e.g. $8.5\text{-}65 \text{ mgP m}^{-3}$).

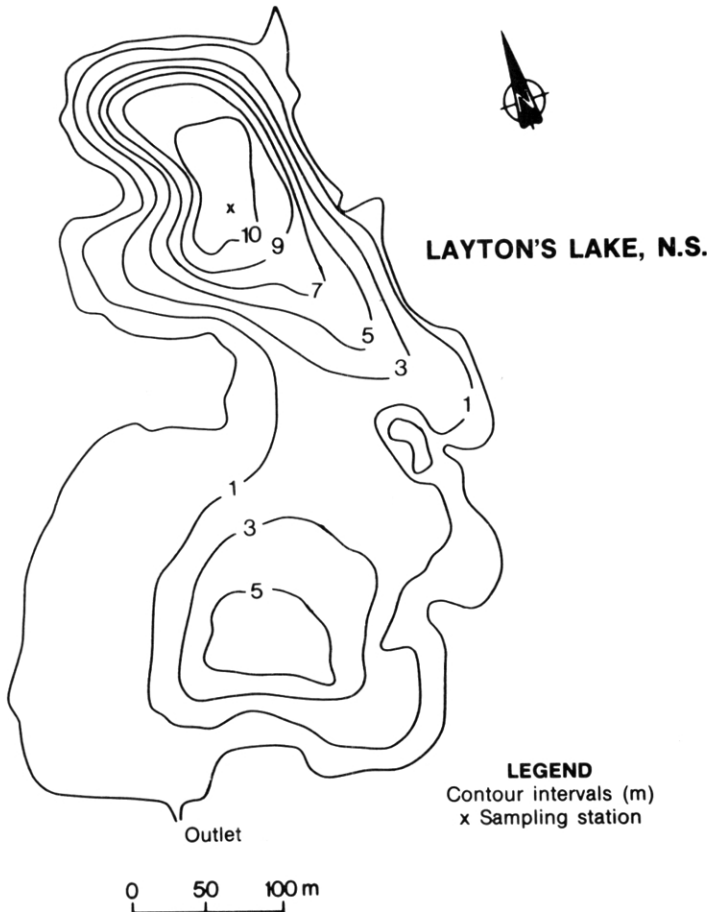


Fig 1 Bathymetric map of Layton's Lake, Nova Scotia.

Methods

Planktonic primary productivity was estimated using the technique of Steeman-Neilson (1952). Samples were collected from the surface and at various depths in the euphotic zone and combined to form an integrated sample. All collections were made with a non-metallic horizontal VanDorn sampler between 1100 and 1300, were taken to the field laboratory and were protected from light. Eight 68 mL light and two dark bottles were inoculated with $10 \mu\text{C}$ of radioactive sodium bicarbonate solution and incubated for 3h at 4 light levels in an incubator designed by Shearer (1976). Following incubation, a sample (5 mL) was transferred to a 25 mL scintillation vial, acidified with H_2SO_4 (0.5 mL, 2 N) and $^{14}\text{CO}_2$ was removed by aspiration with air for 15 min. (Schindler *et al.*, 1972; Theodorsson and Bjarnason, 1975). Scintiverse fluor (Fisher Chemical Co., 15 mL) was added and the radioactivity was determined using a Beckman LS100 Scintillation counter. Daily integral primary production was calculated as described by Fee (1973).

Results of the primary production experiments have been expressed in not only the usual areal (P-area) and volumetric (P-vol) units but also in two units (P-vol \bar{x} and P-area \bar{x}) which were presented by Kerekes (1975). These units correct the production estimates for the modifying effects of basin morphometry using the formulae: -

$$\text{P-vol } \bar{x} = \frac{1}{V} \int_0^{z_{eu}} A(z) p(z) dz \text{ mgC m}^{-3} \text{ day}^{-1}$$

$$\text{P-area } \bar{x} = \frac{1}{A} \int_0^{z_{eu}} A(z) p(z) dz \text{ mgC m}^{-2} \text{ day}^{-1}$$

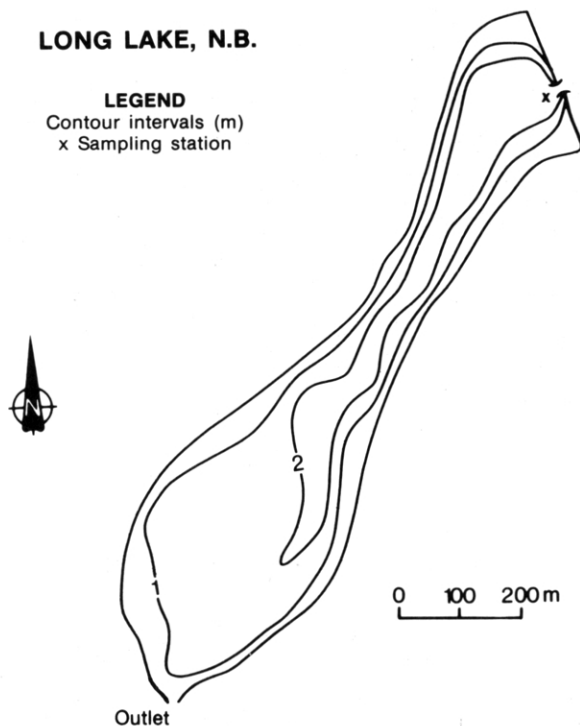


Fig 2 Bathymetric map of Long Lake, New Brunswick.

where A = area m^2 , V = volume m^3 , p = volumetric production $mgC\ m^{-3}\ day^{-1}$, Z_{eu} = depth of euphotic zone (m)

Areal rates of carbon assimilation (P -area \bar{x}) were converted to $g\text{-cal}\ m^{-2}$ using a conversion factor of $1\ gC = 11.25\ Kcal$ (Schindler and Nighswander, 1970) and were expressed as a percentage of $g\ cal$ of surface photosynthetic active radiation ($PAR\ m^{-2}$).

Surface and subsurface light intensities were measured with a submersible Li-Cor-LI-185 Quantum/Radiometer/Photometer. Daily surface irradiance was measured with a Belmont Pyrheliograph. All light measurements were converted to PAR using a factor of 0.45. Annual primary production was estimated by multiplying the production efficiency by the surface isolation for a given period and summing over the entire year.

Dissolved inorganic carbon (DIC) concentration was determined using a method of Stainton (1973). Total phosphorus concentration was measured by the molybdenum blue method (Murphy and Riley, 1962) after samples were digested by potassium persulphate (Menzel and Corwin, 1965). Total nitrogen and major ions were analyzed by the laboratory of Environment Canada, Inland Waters Directorate, Water Quality Branch, Moncton, New Brunswick. Chlorophyll-*a* concentration was determined on a Turner Model 110 Fluorometer using the method of Yentch and Menzel (1963) as modified by Holm-Hansen *et al.* (1965).

Macrophyte biomass was estimated for each sampling date by harvesting all plants lying within the boundaries of six randomly placed $0.5\ m^2$ quadrats. Fresh, dry and ash weights were determined for each sample. Organic weight (ash-free dry weight -AFDW) was converted to carbon using the factor of 0.48 given by Westlake (1965). In order to get an estimate of plant productivity 15 cm terminal macrophyte tips were incubated under constant light for 1 hour in 68 mL bottles. Water collected from the

Table I Representative chemical constituents of Layton's Lake, N.S. and Long Lake, N.B.

	Layton's Lake	Long Lake
pH	7.3	6.7
Total Alkalinity $mg\ L^{-1}$	30.5	5.6
Specific Conductance $umho\ cm^{-1}$	534	36
Water Colour (Hazen units)	15	110
Turbidity (NTU)	1.5	2.7
DIC $mg\ C\ L^{-1}$	9.2	3.3
TOC $mg\ C\ L^{-1}$	8.3	17.8
Total Phosphorus $mg\ P\ m^{-3}$	44	27
Chlorophyll- <i>a</i> $mg\ Chl\ m^{-3}$	4.4	3.8
Phaeophytin $mg\ m^{-3}$	2.2	2.3
Total Nitrogen $mg\ N\ m^{-3}$	300	280
Secchi Disc m	2.7	1.1
* $Ca^{++}\ mg\ L^{-1}$	50	4.4
$Mg^{++}\ mg\ L^{-1}$	5.5	0.9
$Na^{+}\ mg\ L^{-1}$	42	2.4
$K^{+}\ mg\ L^{-1}$	2.6	0.7
$Fe^{+++}\ mg\ L^{-1}$	0.3	0.5
$HCO_3^{-}\ mg\ L^{-1}$	37.2	6.8
$SO_4^{-}\ mg\ L^{-1}$	108	6.0
$Cl^{-}\ mg\ L^{-1}$	78	6.1

⁺ Layton's lake ion chemistry is for November 17, 1977. Long Lake ion chemistry is for September 30, 1977. Other values are annual means.

macrophyte region was filtered through 0.45μ GF/C glass fibre filters prior to use in the incubation bottles. Productivity was estimated using the oxygen light and dark method and expressed as $\text{mgC hr}^{-1} \text{g}^{-1}$ AFDW.

Results

Bathymetric maps of the two study lakes are presented in Figs 1 and 2, while Table I summarizes the water chemistry of the two lakes.

Nutrient Concentrations

Mixolimnetic total phosphorus at Layton's Lake (Fig 3) were relatively high throughout the entire study period (range $30\text{-}90 \text{ mgP m}^{-3}$). Concentrations observed during late autumn, winter and the summer of 1978 were higher than during other periods.

At Long Lake phosphorus concentrations were generally highest during the summer and early fall and gradually declined throughout the autumn to minimum levels during periods of ice cover (Fig 4). Like Layton's Lake, total phosphorus concentrations were higher during the summer of 1978 than in the previous summer. The limited amount of total nitrogen data suggests that both lakes have similar levels (range $200\text{-}400 \text{ mgN m}^{-3}$). At Long Lake, N:P ratios were consistently above 10, while those at Layton's Lake ranged from 6 to 16.

Chlorophyll-a

The lowest ice-free season chlorophyll-a concentrations at Layton's Lake were observed during the summer months in the epilimnetic waters (Fig 5). This pattern was more pronounced in the summer of 1977 than in 1978. Conspicuously high chlorophyll-a concentrations developed in the hypolimnion during the latter part (July and August) of both summers. With the onset of autumnal circulation chlorophyll-a concentrations increased significantly and remained high throughout the early winter. On April 4, 1978, a chlorophyll-a concentration of 39.2 mg m^{-3} was found immediately under the surface of 0.39 m of snow-free transparent ice. Subsequent phytoplankton analysis revealed large numbers ($9.35 \times 10^5 \text{ cells L}^{-1}$) of the chlorophyte *Chlamydomonas*. Chlorophyll-a concentrations at Long Lake (Fig 6)

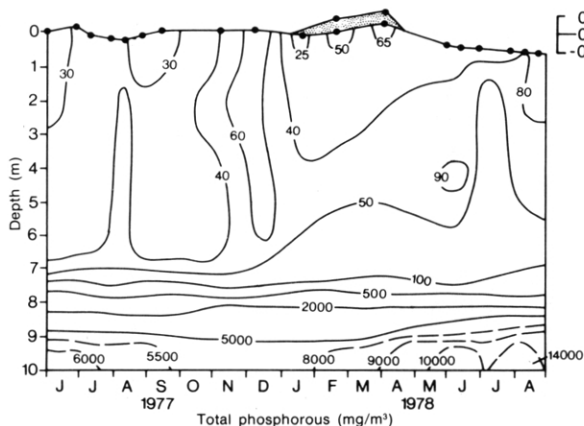


Fig 3 Isoleths of total phosphorus concentration for Layton's Lake, 1977 and 1978. Broken lines represent sampling uncertainty. Hatched area indicates ice cover.

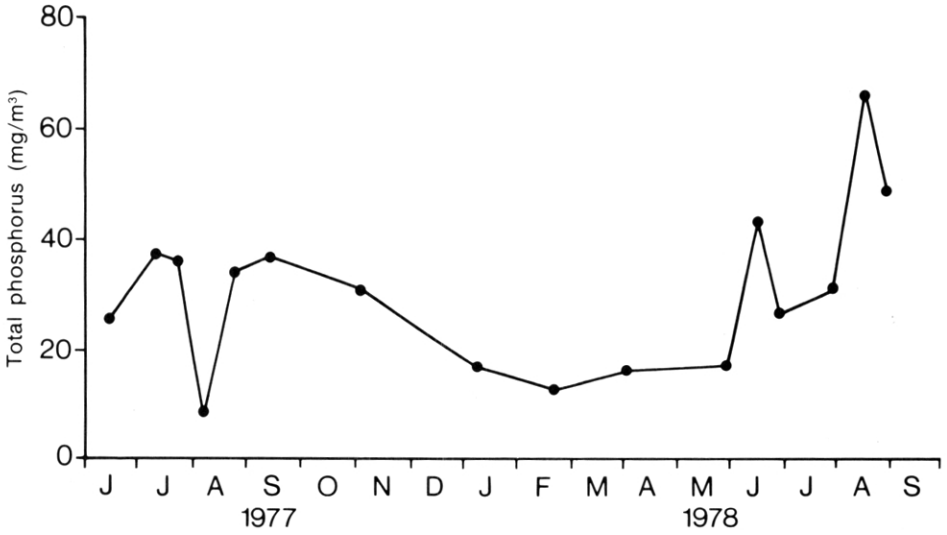


Fig 4 Seasonal variation of total phosphorus concentration in surface waters of Long Lake during 1977 and 1978.

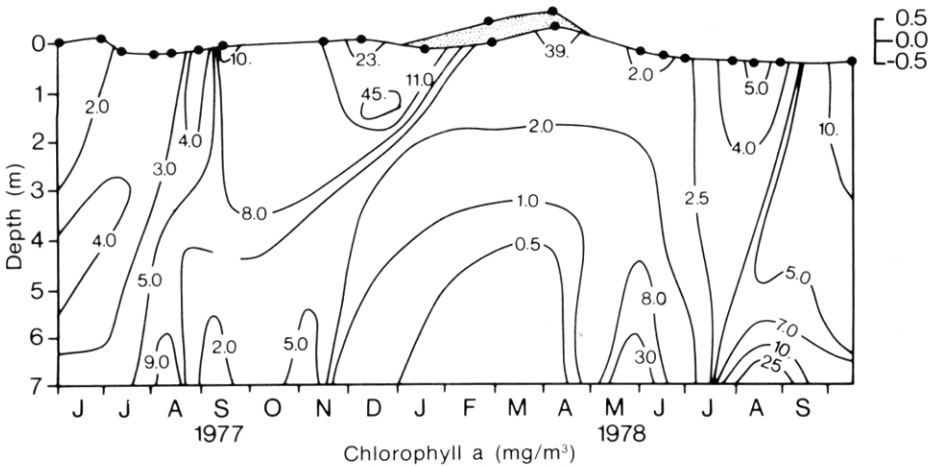


Fig 5 Isopleths of chlorophyll-a concentration for the mixolimnion of Layton's Lake, 1977 and 1978. Hatched areas indicate ice cover.

were the highest during the summer and declined rapidly during the late autumn to extremely low winter minima. Summer chlorophyll-a concentrations tended to be equal to or greater than epilimnetic values at Layton's lake while the fall and winter values were considerably lower.

Plankton Primary Production

Rates of planktonic primary production for Layton's and Long Lakes are presented in Table II and III respectively. At Layton's Lake, areal production values representative of the entire lake ($P\text{-area } \bar{x}$) range from 24 to 98% of the deep station areal production ($P\text{-area}$). $P\text{-area } \bar{x}$ and $P\text{-max}$ values tended to be the highest during the summer and fall with very low values found during the winter. The exception to this was the high $P\text{-area } \bar{x}$ ($173 \text{ mgC m}^{-2} \text{ day}^{-1}$) and $P\text{-max}$ ($414 \text{ mgC m}^{-3} \text{ day}^{-1}$) found under ice on April 4, 1978.

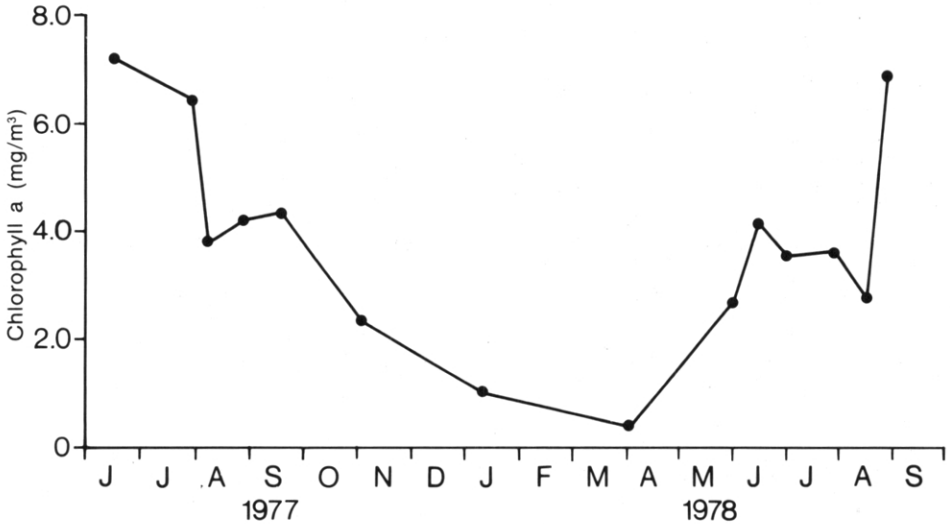


Fig 6 Seasonal variation of chlorophyll-a concentration in surface waters of Long Lake during 1977 and 1978.

At Long Lake $P\text{-area } \bar{x}$ production values were 76 to 88% of the corresponding $P\text{-area}$ values. The highest $P\text{-area } \bar{x}$ values were recorded during the summer with much lower levels found during the fall and winter.

On five occasions primary production incubations were conducted on Layton's Lake samples collected from the macrophyte region as well as at the deep station. The incubator uptake rates were similar (Table IV) with a paired difference ($\alpha = .05$) indicating no significant difference between the two sites. Production efficiencies at Layton's Lake were generally low during the summer with peak values observed during low light days (Table V). The winter efficiencies were similar to those found during the summer. As was observed for both total phosphorus and chlorophyll-a concentrations, production efficiencies were higher during the summer of 1978 than during the summer of 1977.

Long Lake production efficiencies followed a similar pattern to that observed at Layton's Lake, with the exception that the peak efficiencies observed during low light days were absent. Summer production efficiencies were slightly lower than those recorded at Layton's Lake.

Macrophytic Primary Production

Layton's Lake is a shallow clear-water lake and therefore ideally suited for the development of submergent macrophytes. A visual survey revealed that during the summer growing season approximately 68% of the lake's sediment surface was colonized by submergent macrophytes, dominated by *Myriophyllum exalbescens*

Table II Areal and volumetric primary production measurements at Layton's Lake, N.S. for thirteen sampling dates during 1977 and 1978.

Date	P-area mg C/m ² .day	P-vol \bar{x} mg C/m ³ .day	P-area \bar{x} mg C/m ² .day
1977			
June 15	142	33.2	61.1
July 11	463	86.5	159
August 9	448	115	211
August 23	546	109	201
November 4	343	100	185
1978			
January 12**	70.7	21.8	40.1
February 21***	15.7	8.5	15.4
April 4*	262	94.1	173
May 31	105	29.3	54
June 15	281	79.5	146
June 29	624	139	251
July 29	280	76.2	140.3
August 27	825	183	337.4

* Ice cover.

** Ice and light snow cover.

*** Ice and heavy snow cover.

and to a much lesser extent by *Potamogeton pectinatus*. Macrophyte biomass began increasing in late April or early May soon after loss of winter ice cover and reached a maximum biomass of 95.5 gC m⁻² of littoral zone in mid-August (Table VI). By the end of August the macrophyte communities began to senesce with biomass declining throughout the fall. Correcting the maximum biomass to give a value representative of the entire lake, the annual standing stock was approximately 61 gC m⁻².

Net photosynthetic capacity of both *Myriophyllum* and *Potamogeton* tips was low during June (0.5 - 1.5 mgC g-dry wt⁻¹ h⁻¹) however by late July when macrophyte

Table III Areal and volumetric primary production measurements at Long Lake, N.B. for thirteen sampling dates during 1977 and 1978

Date	P-area mg C/m ² .day	P-vol \bar{x} mg C/m ³ .day	P-area \bar{x} mg C/m ² .day
1977			
June 15	27.2	16.4	22
July 11	106.4	64.1	87.1
August 9	157	96.3	131
August 23	239	143	192
November 4	51.9	33	44.2
1978			
January 12	3.8	2.4	3.2
February 21	8.1	5.3	7.1
April 4	47.6	28	37.5
May 31	28.8	18.5	24.8
June 15	85.4	54.8	73.5
June 29	209	119	160
July 29	53.3	37.3	43.3
August 27	293	165	222

P-max mg C/m ³ .day	P-area \bar{x} / P-area	lo/day 1y	Euphotic Depth (m)
58.7	0.43	292	6.0
116	0.34	428	6.3
255	0.47	449	5.6
173	0.37	430	6.3
259	0.54	91.5	4.5
67.9	0.57	98.2	3.0
86	0.98	79.4	1.2
414	0.66	251	1.8
74.9	0.51	44.4	5.1
192	0.52	197	4.9
226	0.40	358	6.3
185	0.50	77.5	5.3
241	0.41	359	5.3

biomass was increasing at the greatest rate, photosynthetic activity was up to 2.5-3.5 mgC g-dry wt⁻¹ hr⁻¹. Due to the small number of macrophyte productivity experiments, it was not possible to calculate annual production by this method.

In contrast to the high degree of colonization by submergent macrophytes at Layton's Lake, Long Lake which has high water colour, short water residence time and a rocky bottom had insignificant macrophyte development.

P-max mg C/m ³ .day	P-area \bar{x} / P-area	lo/day 1y	Euphotic Depth (m)
42.8	0.81	292	1.75
252	0.82	428	0.90
339	0.83	449	1.50
291	0.80	430	1.35
136	0.85	91.5	1.30
7	0.84	98.2	1.10
36.5	0.88	79.4	0.80
58.3	0.79	251	0.85
89.6	0.86	44.4	1.70
166	0.86	197	1.10
272	0.77	358	2.00
84.9	0.81	77.5	1.80
299	0.76	359	1.90

Table IV Incubator uptake rates for two stations at Layton's Lake measured on five sampling dates.

Date	Light	¹⁴ C Uptake mg C m ⁻³ h ⁻¹	
		Macrophytic Zone	Limnetic Zone
1977			
November 4	.392	33.1	37.3
	.084	32.9	34.2
	.028	12.2	13.4
	.006	3.2	2.9
1978			
June 15	.519	16.9	17.1
	.046	16.9	16.1
	.029	8.2	6.9
	.007	2.0	1.8
June 28	.337	31.0	24.2
	.084	25.2	20.0
	.021	6.7	6.0
	.004	1.6	1.8
July 29	.571	33.7	31.7
	.129	31.3	31.2
	.029	13.9	14.7
	.006	2.7	4.0
August 27	.359	50.4	49.2
	.084	53.3	43.0
	.024	20.1	14.5
	.006	3.5	6.9

Table V P-area and P-area \bar{x} production efficiencies at Layton's Lake, N.S. and Long Lake, N.B. for thirteen sampling dates during 1977 and 1978.

Date	Layton's Lake		Long Lake	
	P-area	P-area \bar{x}	P-area	P-area \bar{x}
1977				
June 15	0.12	0.05	0.02	0.02
July 11	0.27	0.09	0.05	0.05
August 9	0.15	0.12	0.09	0.07
August 23	0.32	0.12	0.14	0.11
November 4	0.94	0.51	0.14	0.12
1978				
January 12	0.18	0.10	0.01	0.01
February 21	0.05	0.05	0.03	0.02
April 4	0.26	0.17	0.05	0.04
May 31	0.59	0.30	0.16	0.14
June 15	0.36	0.19	0.11	0.09
June 29	0.44	0.17	0.15	0.11
July 29	0.90	0.45	0.17	0.14
August 17	0.57	0.24	0.20	0.15

Table VI Macrophyte biomass* estimates at Layton's Lake for seven sampling dates during the summer of 1978.

Date	Macrophyte Biomass				Dry Wt. g C m ⁻²
	Fresh Wt. g m ⁻²	Dry Wt. g m ⁻²	Ash Wt. g m ⁻²	Ash-Free	
1978					
May 31	1016	168	90.7	77.6	37.3
June 14	691	90.7	42.2	48.5	23.3
June 28	1124	150	50.8	98.8	47.4
July 28	2318	263	74.1	189	90.7
August 14	2222	251	59.7	199	95.5
August 28	1437	149	36	113	54.3
October 10	454	47	11.3	35.7	17.1

* Biomass estimates are expressed on a per m² littoral zone basis.

Discussion

In lakes where the ratio of $\bar{z}:z_{eu}$ (z_{eu} = euphotic zone depth) is much less than unity, P-area production estimates from the deep station will greatly overestimate areal production, as the euphotic zone is restricted due to the shallowness of the lake. To overcome this, Kerekes (1975) proposed the use of a volume corrected P-area value which he termed P-area \bar{x} . Fee (1980) observed that use of P-area overestimates actual lake production by approximately 20%. However, as this overestimation of production is a function of both basin morphometry and transparency, clearwater lakes such as Layton's which have a large littoral zone and a small area of deep water (i.e., low $\bar{z}:z_{eu}$), may have errors much greater than 20%. At Layton's Lake, where the $\bar{z}:z_{eu}$ ratio

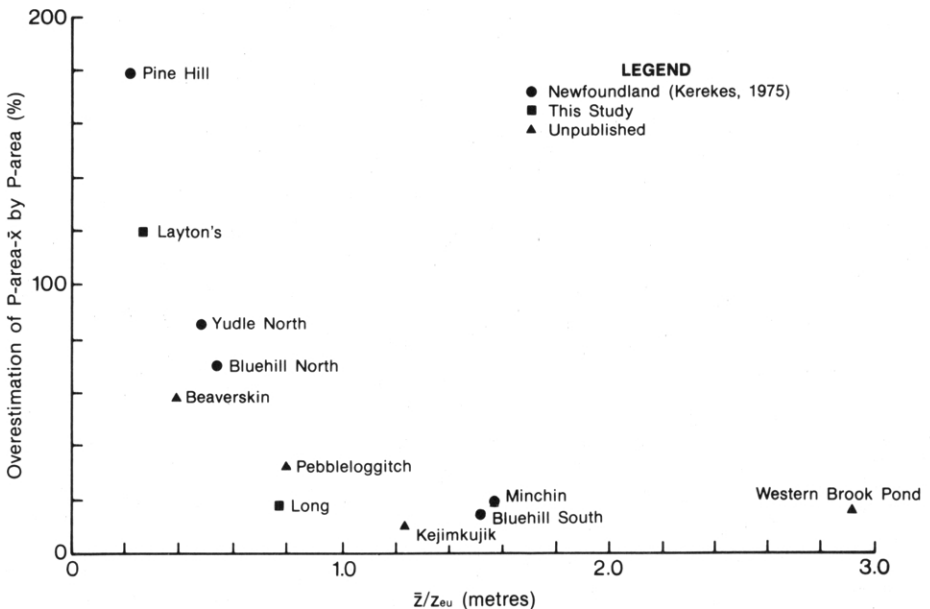


Fig 7 Relationship between the percent overestimation of areal production and the $\bar{z}:z_{eu}$ ratio for several lakes.

Table VII Results of the linear regression analysis relating Layton's Lake and Long Lake phytoplankton production (P-area \bar{x}) to environmental factors during the ice-free season and the summer season.

Layton's Lake (summer 1977 and 1978)			
P-area \bar{x} = 0.251 I ₀ + 107.	r ² = 0.16	F = 1.10	NS
T-values \bar{x} 1.59 NS			
P-area \bar{x} = 0.356 + 5.81 TP - 167	r ² = 0.48	F = 4.2	NS
T-values \bar{x} 1.99 NS 2.52 NS			
P-area \bar{x} = 0.320 I ₀ + 5.54 TP + 33.9 Chl-a	r ² = 0.92	F = 26.56	HS
T-values \bar{x} 4.45 HS 5.99 HS 5.21 HS			
Layton's Lake (Ice-free)			
P-area \bar{x} = 0.272 I ₀ + 100	r ² = 0.17	F = 2.79	NS
T-values \bar{x} 1.67 NS			
P-area \bar{x} = 0.354 + 5.67 TP - 160	r ² = 0.48	F = 5.19	S
T-values \bar{x} 2.67 S 2.43 S			
P-area \bar{x} = 0.487 I ₀ + 5.82 TP + 18.8 Chl-a-284	r ² = 0.73	F = 9.07	S
T-values \bar{x} 4.52 HS 3.44 HS 2.71 S			
Long Lake (Ice-free)			
P-area \bar{x} = 0.323 I ₀ + 11.8	r ² = 0.44	F = 8.56	S
T-values \bar{x} 2.93 S			
P-area \bar{x} = 0.253 I ₀ + 190 WL - 110	r ² = 0.62	F = 11.5	S
T-values \bar{x} 3.36 HS 2.66 S			

NS - not significant S - significant ($\leq .05$) HS - significant ($\leq .01$)

I₀ - incident solar radiation (PAR) Langley's day⁻¹

TP - total phosphorus concentration mg P m⁻³

Chl-a - chlorophyll-a concentration mg m⁻³

WL - water level (recorded as m below reference)

NOTE: all correlation co-efficients have been corrected for low degrees of freedom.

is low (0.35), the use of P-area will on an annual basis overestimate actual production (P-area \bar{x}) by 120%. At Long Lake, where the $\bar{z}:z_{eu}$ is larger (.78), P-area production overestimates P-area \bar{x} production by 17%.

The relationship between the percent overestimation of annual P-area \bar{x} by P-area and the ratio $\bar{z}:z_{eu}$ for several lakes in the Atlantic Region is presented in Fig 7 and emphasizes the necessity of correcting station areal production, particularly in those lakes which have a ratio of $\bar{z}:z_{eu}$ much less than 1.0.

P-area \bar{x} at Layton's Lake was generally highest during the summer months when surface insolation was high. However, the linear relationship between summer (1977 and 1978) P-area \bar{x} and surface insolation was poor (Table VII), possibly due to improved nutrient concentrations in the mixolimnion during the dry summer of 1978 (Fig 3). Inclusion of total phosphorus concentration in the linear regression improved the co-efficient of determination ($r^2 = .48$) but as indicated by the low F value, these two variables (I₀ and TP) do not explain the variation in summer P-area \bar{x} values.

Many authors (Hasler and Jones, 1949, Goulder, 1969; Planas et al., 1981) have documented inhibitory effects of macrophytes on phytoplankton. This would explain why Layton's Lake summer chlorophyll-a concentrations and production efficiencies are relatively low. This was most pronounced during the summer of 1977 as higher nutrient concentrations in 1978 resulted in slightly higher chlorophyll-a and

production efficiencies. Metalimnetic and hypolimnetic chlorophyll-a concentrations were often greater than epilimnetic values which may be a response to higher nutrient concentrations below the thermocline. Similar findings have been documented by Kerekes (1974) and Fee (1976). Thus chlorophyll-a concentration may be useful as an indicator of not only the nutrient status of the lake but also any inhibitory effects caused by macrophytes. Inclusion of chlorophyll-a into the regression analysis improved the co-efficient of determination from 0.48 to 0.92.

It is interesting to consider Layton's Lake P-area \bar{x} values on the ice-free season basis (Table VII). The relationship between P-area \bar{x} and surface insolation is poor, but addition of total phosphorus concentrations to the regression analysis again improves the relationship ($r^2 = 0.48$). Inclusion of chlorophyll-a concentration into the regression analysis raises the coefficient of determination for the ice-free season from 0.48 to 0.73. During circulation periods in the spring and fall, mixolimnetic phosphorus concentrations increase slightly partially due to mixing of hypolimnetic waters, release from senescing macrophytes, and increased internal loading of nutrient rich monimolimnetic water (Howell and Kerekes, 1982). However, these slightly increased phosphorus concentrations cannot alone explain the large increases in chlorophyll-a concentration and production efficiency during these periods. One possible explanation is that a shift to more biologically available phosphorus is involved, rather than an actual increase in concentration. However, from the limited data available, there is no discernible increase in the percentage of total phosphorus found in the soluble reactive form during the circulation periods. With the onset of autumnal circulation

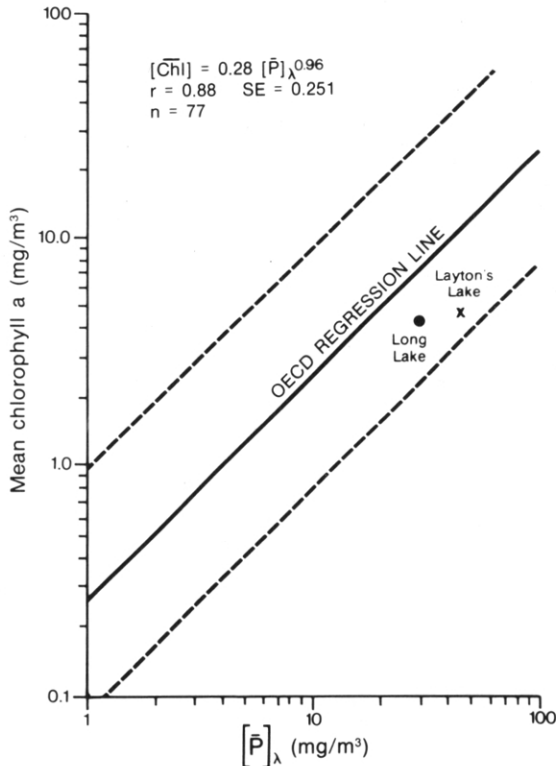


Fig 8 OECD relationship between mean chlorophyll-a concentration and mean in-lake total phosphorus concentration.

the macrophytes begin to senesce and thus, during the fall, winter and spring the phytoplankton have less competition for available nutrients. This reduction of competition or antagonism could account for the phytoplankton blooms during periods of circulation.

Similar to Layton's Lake, P-area \bar{x} at Long Lake was highest during the summer when surface insolation was also high. Linear regression analysis indicated a positive correlation between P-area \bar{x} and surface insolation ($r^2 = 0.44$) but unlike Layton's Lake, addition of total phosphorus concentration did not significantly improve the relationship ($r^2 = 0.42$). A large proportion of the total phosphorus in coloured waters is associated with clays and organic compounds (Hines and Barker, 1957; Fillos, 1976) and is not available to phytoplankton. This may explain the insignificant effect inclusion of total phosphorus has on the regression analysis.

In lakes such as Long Lake which have extremely high flushing rates, the phytoplankton are often susceptible to washout (Dickman, 1969; Wagner and Parker, 1973; Gorham *et al.*, 1974). Flow rate may also affect light extinction by changing organic carbon concentrations, water colour and turbidity. From Table VII, inclusion of water level into the regression analysis improved the coefficient of determination considerably from 0.49 to 0.62.

Using P-area \bar{x} production values for Layton's Lake, annual phytoplankton production was approximately $87 \text{ gC m}^{-2} \text{ y}^{-1}$. In order to estimate total annual primary production for Layton's Lake, it is necessary to include the macrophyte production component. However, the calculated maximum standing crop of $61 \text{ gC m}^{-2} \text{ y}^{-1}$ completely ignores any biomass loss by excretion, grazing and sloughing. As Layton's Lake had a maximum macrophyte biomass similar to Lake Wingra (Adams and McCracken, 1974) (AFDW Layton's Lake = 199 g/m^2 ; Lake Wingra = 222 g/m^2) and photosynthetic activity approximately 60% of that recorded at Lake Wingra, a produc-

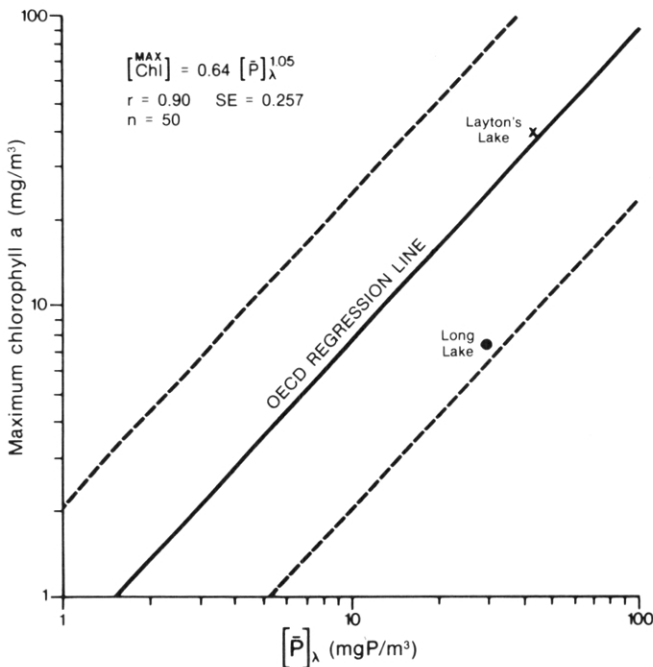


Fig 9 OECD relationship between peak chlorophyll-a concentration and mean in-lake total phosphorus concentration.

tion to biomass (P/B) ratio of 1.56 (60% of the Lake wingra P/B (2.6)) was assumed. This P/B ratio is similar to values of 1.25 given by Winberg *et al.*, (1972) and 2.0 used Sorokin (1972). Using a P/B ratio of 1.56, annual macrophytic production is estimated to be approximately $95 \text{ gC m}^{-2} \text{ y}^{-1}$ which when summed with planktonic production gives a total production of $182. \text{ gC m}^{-2} \text{ y}^{-1}$ for Layton's Lake. This is similar to the value of $172 \text{ gC m}^{-2} \text{ y}^{-1}$ estimated for the eutrophic lake 227 in Ontario (Fee, 1980).

Long Lake, N.B., had an estimated annual P-area \bar{x} production of $36.4 \text{ gC m}^{-2} \text{ y}^{-1}$ which is slightly higher than values given by Fee (1980) for numerous coloured ELA lakes.

Janus and Vollenweider (1981) and Kerekes (1983) showed that the Organization for Economic Co-operation and Development (OECD) empirical relationships (Vollenweider and Kerekes, 1980; Vollenweider and Kerekes, 1981) may be used to analyse an individual lake response to nutrient status as it related to "average" lake behaviour. Given the annual mean total phosphorus concentration both Layton's Lake and Long Lake have annual mean chlorophyll-a concentrations which are below the OECD regression line (Fig 8). At Long Lake much of the measured total phosphorus is organically bound and is therefore not available to the phytoplankton. The Layton's Lake point is also below the OECD line due to the inhibitory effects the macrophytes have on the phytoplankton.

From the OECD relationship between peak chlorophyll-a concentration and mean annual in-lake phosphorus concentration (Fig 9), it is apparent that Long Lake falls below the regression line, but Layton's Lake is slightly above the OECD line. The peak chlorophyll-a concentration ($\approx 45 \text{ mg m}^{-3}$) was observed during the late fall when

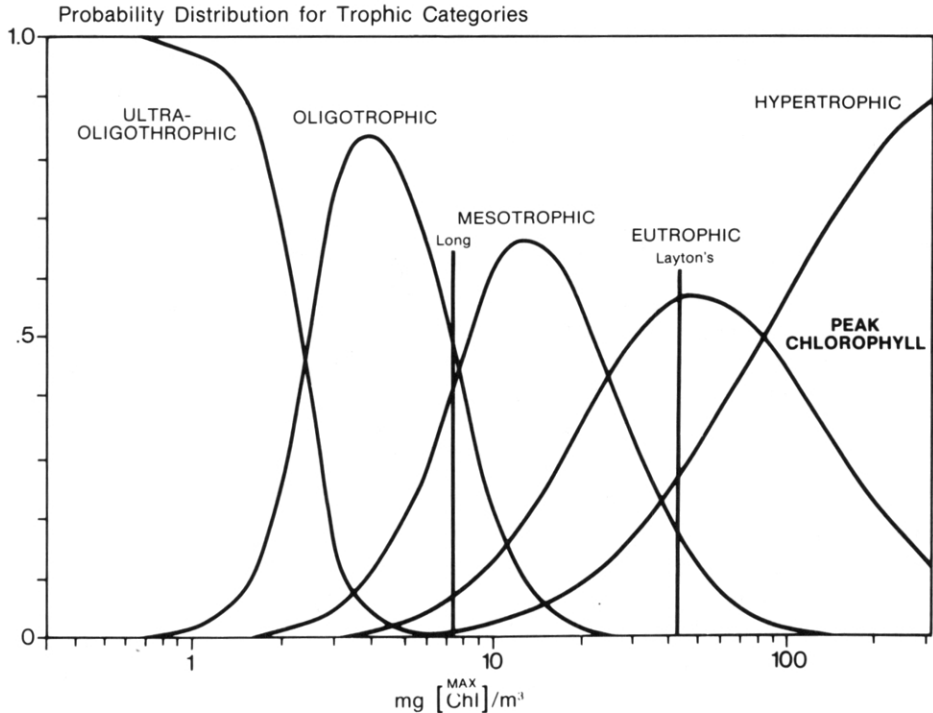


Fig 10 Predicted trophic conditions in terms of probability (five trophic categories) for annual peak chlorophyll-a concentration (after Vollenweider and Kerekes, 1981).

there was no macrophyte competition or inhibition. This would suggest that at Layton's Lake, both total phosphorus and maximum chlorophyll-a concentration would tend to overestimate planktonic primary productivity but would be good indicators of total (planktonic and macrophytic) primary productivity. From the OECD study it was found that on average, peak chlorophyll exceeds yearly average chlorophyll by a factor of 3. At Layton's Lake, the ratio of Chl_{max} : Chl is approximately 10, indicating the considerable effect that the macrophytes have on chlorophyll-a concentrations.

Thus it appears that total phosphorus concentration and peak chlorophyll-a concentration are the best trophic indicators for Layton's Lake. Using the probabilistic trophic category scheme for maximum chlorophyll-a concentration (Fig 10) given by Vollenweider and Kerekes (1980), Layton's Lake has a 17% chance of being mesotrophic, 58% chance of being eutrophic and a 25% chance of being hypertrophic. Using a similar scheme based on total phosphorus concentration Layton's Lake had a nearly equal probability of being mesotrophic or eutrophic. Therefore, it is concluded that Layton's Lake is presently eutrophic.

At Long Lake it is obvious that both mean chlorophyll-a and total phosphorus concentrations would tend to overestimate annual production. However, as the ratio of maximum chlorophyll-a concentration to mean chlorophyll-a (1.9) is less than the average value of 3.0, it appears that maximum chlorophyll-a is probably the best trophic indicator. From Fig 10 the probabilities of being oligotrophic, mesotrophic, eutrophic and hypertrophic are 51%, 42%, 5% and 2% respectively. Thus, Long Lake would appear to be in a borderline oligotrophic-mesotrophic condition.

Acknowledgements

The authors thank Dr. P. Schwinghamer, Dr. J.G. Ogden, S. Beauchamp, W. Prescott, A. Smith and J. Inder.

(Received 30 July, 1987)

References

- Adams, M.S. and McCracken, M.D.** 1974. Seasonal Production of the *Myriophyllum* component of the littoral of Lake Wingra, Wisconsin, *J. Ecol.* 62:457-465.
- Dickman, M.** 1969. Some Effects of Lake Renewal on Phytoplankton Productivity and Species Composition. *Limnol. and Oceanogr.* 14: 661-668.
- Fee, E.J.** 1973. A digital computer program for calculating integral primary production in vertically stratified water. Fisheries Research Board of Canada. Technical Report No. 376.
- Fee, E.J.** 1976. The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, Northwestern Ontario: Implication for primary production estimates. *Limnol. and Oceanogr.* 21: 767-683.
- Fee, E.J.** 1980. Important Factors for Estimating Annual Phytoplankton Production in the Experimental Lakes Area. *Can. J. Fish. Aquat. Sci.* 37: 513-522.
- Fillos, J.** 1976. Effect of Sediments on the Quality of the Overlying Water. In Junk and Pudoc (eds.) Interactions between sediments and freshwater. Amsterdam.
- Gorham, E., Lund, J.W.G., Sanger, J.E., and Dean, W.E.** 1974. Some Relationships between Algal Standing Crop and Water Chemistry in the English Lakes. *Limnol. and Oceanogr.* 19: 601-617.
- Goulder, R.** 1969. Interactions between the rates of production of a Freshwater macrophyte and plankton in a pond. *Oikos* 20: 300-309.
- Hasler, A.D. and Jones, E.** 1949. Demonstration of the Antagonistic Action of large Aquatic Plants and Algae and Rotifers. *Ecology* 28: 383-395.

- Hines, F.L. and Barkers, S.A.** 1957. Chelating Ability of soil organic matter. *American Soil Science Society Proceedings* 21: 368-373.
- Holm-Hansen, O., Lorensen, C.J., Holmes, R.W. and Strickland, J.D.M.** 1965. Fluorometric determination of chlorophyll. *J. Cons. Perm. Int. Explor. Mer.* 30: 3-15.
- Howell, G.D. and Kerekes, J.** 1982. Ectogenic meromixis at Layton's Lake, Nova Scotia, *J. Freshwater Ecol.* 1: 483-493.
- Janus, L.L. and Vollenweider, R.A.** 1981. Summary Report. The OECD Cooperative Programme on Eutrophication. Canadian contribution *Envir. Can. Nat. Water Res. Inst.*, Burlington, Ontario. Scient. Ser. No. 131.
- Kerekes, J.** 1974. Limnological conditions in five small oligotrophic lakes in Terra Nova National Park, Newfoundland. *J. Fish. Res. Bd. Can.* 31: 555-583.
- Kerekes, J.** 1975. The Relationship of Primary Production to Basin Morphometry in Five Small Oligotrophic Lakes in Terra Nova National Park in Newfoundland. *Symp. Biol. Hung.* 15: 35-48.
- Kerekes, J.** 1983. Predicting Trophic Response to Phosphorus Addition in a Cape Breton Island lake. *Proc. N.S. Inst. Sci.* 33: 7-18.
- Menzel, D.W. and Corwin, N.** 1965. The Measurement of Total Phosphorus in Seawater Based on the Liberation of Organically Bound Fractions by Persulphate Oxidation. *Limnol. and Oceanogr.* 10: 280-282.
- Murphy, J. and Riley, J.P.** 1962. A Modified Single Solution Method for the Determination of Phosphate in Natural Waters. *Anal. chim. Acta.* 27: 31-36.
- Nowland, J.L. and MacDougall, J.I.** 1973. Soils of Cumberland County, Nova Scotia. Canada Department of Agriculture Report No. 17.
- Planas, D., Sorhan, F., Duba, L., Godmaire, H. and Cadieux, C.** 1981. Ecological significance of phenolic compounds of *Myriophyllum spicatum*. *Verh. Internat. Verein. Limnol.*, 21: 1492-1496.
- Schindler, D.W. and Nighswander, J.E.** 1970. Nutrient supply and primary production in Clear Lake, Eastern Canada. *J. Fish. Res. Bd. Can.*, 27: 2009-2036.
- Schindler, D.W., Schmidt, R.V., and Reid, R.A.** 1972. Acidification and bubbling as an alternative to filtration in determining phytoplankton production by the ^{14}C method. *J. Fish. Res. Bd. Can.*, 29: 1627-1631.
- Shearer, J.A.** 1976. Construction and Operation of a Portable Incubator for Phytoplankton Primary Production Studies. Fisheries and Marine Service. Technical Report No. 638.
- Sorokin, Y.** 1972. Biological productivity of the Rybinsk reservoir. (Ed. by A. Kajak and A. Hillbricht-Ilkowska), PWN-Polish Scientific Publishers, Warszawa-Krakow. Pp. 493-503.
- Stainton, M.P.** 1973. A syringe CO_2 -stripping Procedure for gas chromatographic determination of dissolved inorganic and organic carbon in Fresh Water and Carbonates in Sediments. *J. Fish. Res. Bd. Can.*, 30: 1441-1445.
- Steeaman-Neilsen, E.** 1952. The use of radio-active carbon (^{14}C) for measuring organic production in the sea. *J. du Cans.*, 18: 117-140.
- Theodorsson, P. and Bjarnason, J.O.** 1975. The Acid Bubbling Method for Primary Productivity Measurements Modified and Tested. *Limnol. and Oceanogr.*, 20: 907-1070.
- Vollenweider, R.A. and Kerekes, J.J.** 1980. Synthesis Report Cooperative Program in monitoring of Inland Waters (Eutrophication Control). Report prepared on behalf of Technical Bureau, Water Management Sector Group, Organization for Economic Cooperation and Development (OECD), Paris. 290 p.
- Vollenweider, R.A. and Kerekes, J.** 1981. Background and summary results of the OECD Co-operative Program on Eutrophication. p. 25-36. In: Restoration of lakes and inland waters. Int. Sym. on Inland Waters and Lake Restoration. Sept. 8-12, 1980. Portland, Maine, U.S., EPS, Washington, D.C. EPA 440/5-81-110.

- Wagner, J.F. and Parker, M.** 1973. Primary Production and Limiting Nutrients in a small sub-alpine Wyoming Lake. *Trans. of Am. Fish. Soc.*, 102: 698-706.
- Westlake, D.F.** 1965. Some Basic Data for Investigations of the productivity of Aquatic Macrophytes. *Mem. Ist. Ital. Idrobiol.* 18 (suppl): 229-248.
- Winberg, G., Babitsky, V., Gavrieov, S., Gladky, G., Zakharenkov I., Kovalevskaya, R., Mikhieva, T., Nevyadomskaya, P., Ostapenya, A., Petrovich, P., Potaenko, J. and Yakushko, O.** 1972. Biological Productivity of different types of lakes. (Ed. by A. Kajak and A. Hillbricht-Ilkowska). PWN - Polish Scientific Publishers. Warszawa-Krakow. Pp. 383-404.
- Yetnsch, C.W. and Menzel, D.W.** 1963. Method for the determination of phytoplankton chlorophyll and pheophtin by fluorescence. *Deep Sea Research* 10: 221-231.