ECOLOGY AND BIOLOGICAL PRODUCTION OF LAKE NAKA-UMI AND ADJACENT REGIONS

2. AN ATTEMPT OF COMPARING THE PRODUCTIVITY OF LAKE SHINJI-KO AND LAKE NAKA-UMI ON THE BASIS OF INPUT AND OUTPUT OF TOTAL PHOSPHORUS¹⁾

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With 2 Text-figures and 6 Tables

Introduction and General Principle

The process of circulation, together with input and output, of phosphorus in a lake as a whole may be illustrated as Fig. 1. The phosphorus transported into a lake by numbers of rivers or canals (the total amount of which during a month is designated as I in Fig. 1) will circulate in the following ways; one part will be used by growing organisms and assimilated into their bodies (the quantity is designated by G); the other part will directly or indirectly be deposited on the bottom (the quantity is designated by D), and a part or whole

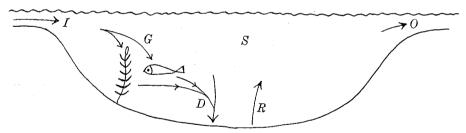


Fig. 1. Schematic representation showing of the process of circulation of phosphorus in a whole lake.

Abbreviations:

- I: Quantity of total phosphorus poured into the lake during a month.
- O: That poured out from the lake during a month.
- G: That assimilated by organisms (taken into organisms) during a month.
- D: That deposited on the bottom during a month.
- R: That resolved into water during a month.
- S: That dissolved or suspended in water at the definite day of a month.

¹⁾ Contributions from the Ôtsu Hydrobiological Station, No. 174.

of which in turn will, sooner or later, be resolved into water (the quantity is designated by R); and at last, the excess part is outpoured into a river (the quantity is designated by O). This must be a typical, somewhat simplified illustration of the destiny of inpoured phosphorus.

Now, the productivity of a lake as a whole will be measured by two ways. First, by measuring the states of organisms. This method seems to be better than the second one, which will be mentioned later, but the actual process is very complicated and laborious, because we have to measure the standing crop, growth and respiration rate, predation and decomposition rate and so on, with respect to each species, at least numbers of dominant species, composing the community.

The second method is rather simple, less laborious and so it seems to be adequate to gain a gross estimation of productivity of a lake as a whole. The general treatment is as follows.

Let us take the amount of total phosphorus in water, excluding that contained in living organisms, at the end of a definite month (X) as S_x , the amount of inpoured phosphorus to the lake during the next month (X+I) as I_{x+1} , that of outpoured phosphorus from the lake as O_{x+1} , the amount of phosphorus taken into all growing organisms during that month as G_{x+1} , that of deposited onto the bottom of the lake as D_{x+1} and that of resolved into water from the bottom as R_{x+1} , so the next equation may be introduced.

$$S_{x} + I_{x+1} + R_{x+1} - O_{x+1} - G_{x+1} - D_{x+1} = S_{x+1}$$
(1)

The same kind of equation can be considered in each month and total budget of a whole year may be,

From the equation (2) the next relation can be introduced.

$$(I_{x+i} + \dots + I_x) + (R_{x+i} + \dots + R_x) - (O_{x+i} + \dots + O_x) - (D_{x+i} + \dots + D_x) = (G_{x+i} + \dots + G_x) \qquad \dots$$
 (3)

Namely,

(total amount of input)+(total amount of resolution)

- -(total amount of output)-(total amount of deposition)
- =(total amount of net growth of organisms)

The total amount of net growth of organisms can be taken as a index of

productivity of the lake, and so the latter can theoretically be calculated in this way.

Unfortunately in the present case, we missed the exact measurement of the values of R and D. Although the value of D may generally exceed that of R, these two values may have not so remarkable difference year after year when the lake is in a state of equilibrium, and in this case the equations (1) and (3) may approximately become as;

$$S_{x} + I_{x+1} - O_{x+1} - G_{x+1} = S_{x+1}$$
 (4)

$$(I_{x+1}+\cdots+I_x)-(O_{x+1}+\cdots+O_x)=(G_{x+1}+\cdots+G_x) \qquad \cdots \cdots \cdots (5)$$

Lake Shinji-ko and Lake Naka-umi are both natural lakes, having the histories of more than thousands of years; so, when we especially attempt to get only relative estimation of productivity, it will not be unsuitable for using the equation 4 or 5.

The principle mentioned above bears a resemblance to that used by Odum and Odum (1955) or Odum (1956). They measured the productivity of flowing water by measuring the oxygen content of water upstream and downstream simultaneously. They considered that the oxygen increase between stations during the day is the net photosynthetic production of the community and the oxygen decrease during the night is the total respiration of the community. Of course in the present case we are considering with phosphorus cycle and so there is naturally some different points.

Methods

Fig. 2 shows the topographical feature around Lake Shinji-ko and Lake Naka-umi (refer to Table 1), illustrating the main rivers pouring into the lakes. The water of Lake Shinji-ko outflows through the Ohashi-gawa River into Lake Naka-umi, and the water of the latter outflows through the Sakai Channel into Miho Bay.

	Surface area	Depth	Volume			
	(km²)	Largest	Mean	(m^3)		
Shinji-ko	82	6.4	4.0	3425×10 ⁵		
Naka-umi	102	9.0	4.6	5091×10^{5}		

Table 1. Some geophysical properties of Lake Shinji-ko and Lake Naka-umi.

The measurement of total phosphorus was performed once a month at the following rivers and channel.

Pouring into Lake Shinji-ko;

Hii and Tamanoyu

Pouring into Lake Naka-umi:

Iu, Iinashi, Yoshida, Hakuta and Ohashi

Pouring into Miho Bay:

Sakai Channel

Also the amount of total phosphorus in lake water was measured at three stations in Lake Shinji-ko (Si4, Si6 and Si10) and five stations in Lake Naka-umi (N3, N9, N16, N18 and N19), which are illustrated in Fig. 2. The depths of the lakes at these stations and the sampling depths at these stations are shown in Table 2.

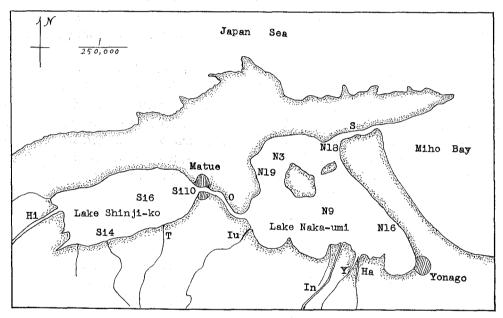


Fig. 2. General topographical features of Lake Shinji-ko and Lake Naka-umi together with pouring rivers and connecting canals. The research stations in the lakes where the measurement of phosphorus was performed are also shown (Si4, Si6, Si10 and N3, N9, N16, N18, N19). Hi: Hii River, T: Tamanoyu R., O: Ohashi R., Iu: Iu R., In: Iinashi R., Y: Yoshida R., Ha: Hakuta R., S: Sakai Channel, M: Miho Bay.

The values obtained from the same depth were averaged for each lake and by multiplying the volume of water of appropriate vertical strata of each lake, the total amount of phosphorus was calculated.

The water sample was collected by a ordinary water sampler, so it contained planktons as well as other organic matters. Practically, by this reason, the value of G in the said equation means the value of net growth of organisms larger than planktons (macroorganisms).

Lake	Stations	Depths (m)	Sampling depths (m)
-	Si4	5.0	0, 3, bottom
Shinji-ko	Si6	5.2	0, 3, 5, bottom
	Si10	6.0	0, 3, 5, bottom
	N3	6.3	0, 3, 5, bottom
	N9	6.5	0, 3, 5, bottom
Naka-umi	N16	2.3	0, bottom
	N18	7.9	0, 3, 5, bottom
	N19	2.4	0, bottom

Table 2. Depths of the lakes at the stations and the sampling depths.

The measurement of total phosphorus was performed by Mr. H. Okabayashi at the Shimane Hygienic Laboratory. The method is as follows. Acidifying 200 cc test water by HCl, evaporate, solidify, and after adding HCl boil and filter. Adding ammonia until some precipitation occurs, then solve the precipitation by adding HNO₃, furthermore add 10 cc of conc. HNO₃ and then add 500 cc of 5% NH₄NO₃ and shake strongly for few minutes. Leaving for a night, precipitate perfectly, filter with decantation, wash by 5% NH₄NO₃. When the filatrate does not assume a brown color by potassium ferrocianate (1%), put the precipitate into a crucible with filtering paper, burn to ash and weigh as $P_2O_5 \cdot 24$ MoO₃.

Results

Table 3 shows the concentration and total amount of phosphorus in Lake Shinji-ko and Lake Naka-umi, and Table 4 shows the concentration and total amount of phosphorus together with the volume of discharge of the rivers.

When these values are applied to the equation (4), Table 5 for Lake Shinji-ko and Table 6 for Lake Naka-umi can be obtained.

In these tables, on the assumption that the amount of phosphorus depositing on the bottom is nearly equal to that of resolving into water (i.e. D=R), + of G means that the "positive growth" of organisms (in this case, macroorganisms) in excess of death or disintegration has taken place during the month designated, and - of G means that the "negative growth" (death or disintegration) has taken place in excess of positive growth during the month designated. Concerning with this point, the "negative growth" has occured in both lakes in the year investigated; namely, in Lake Shinji-ko -144.3 tons and in Lake Naka-umi -243.7 tons for the year respectively. At first sight of these tables the "negative growth" is larger in Lake Naka-umi and so it will be considered as if being less productive than Lake Shinji-ko. However,

Table 3*. Concentration and total amount of phosphorus in Lake Shinji-ko and Lake Naka-umi.

Lake			4	1960 Sept.	Oct.	Nov.	Dec.	1961 Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
		0~2 m	Concentration (7/L)	345.6	500.0	695.0	294.0	182.0	180.0	69.0	67.5	66.0	154.0	150.2	168.7
	th	0~2 m	Total amount (ton)	52.8	76.6	106.4	45.1	27.8	27.6	10.6	10.4	10.2	23.6	23.0	25.8
Shinji-ko	Depth	2~bottom	Concentration (7/L)	740.1	426.0	1045.0	260.0	239.0	232.0	133.0	93.0	53.0	223.0	109.6	191.6
Shinji-ko		Z~bottom	Total amount (ton)	139.5	80.3	197.0	49.1	45.1	43.8	25.1	17.6	10.1	42.0	20.7	36.1
	average of concentration (γ/L)			632.5	448.0	940.0	270.0	232.0	216.0	114.0	81.0	58.0	204.0	129.9	180.1
	Sum (ton)			192.3	156.9	303.4	94.2	72.9	71.4	35.7	28.0	20.3	65.6	43.7	61.9
		0~3 m	Concentration (7/L)	489.0	415.0	1839.0	173.0	131.0	277.0	291.0	246.5	202.0	171.0	97.1	182.9
			Total amount (ton)	137.0	117.4	514.3	47.5	36.3	78.2	81.0	68.8	56.6	47.7	27.1	51.1
	Depth	3~5 m	Concentration (7/L)	597.0	749.0	2860.0	195.0	140.0	275.0	330.0	254.5	179.0	170.0	122.2	169.1
Naka-umi	Del		Total amount (ton)	86.3	107.8	411.3	28.7	20.1	40.2	47.4	36.6	25.8	24.4	17.6	24.3
Ivaka-uiii		5~bottom	Concentration (7/L)	605.0	1003.0	2360.0	215.0	200.0	273.0	355.0	258.0	161.0	200.0	167.1	194.9
		5~bottom	Total amount (ton)	52.2	85.7	202.2	18.8	17.1	23.1	30.8	22.3	13.8	17.1	14.3	16.7
	То1	average of concentration (γ/L)			665.0	2249.0	183.0	148.0	275.0	320.0	253.0	186.0	173.0	128.8	182.3
	10	Total Sum (ton)			310.9	1127.8	95.0	73.5	141.5	159.2	127.7	96.2	89.2	59.0	92.1

^{*} The volume of water of each strata are as follows:

5~bottom 85716×10³ m³

Table 4. Concentration and total amount of phosphorus together with the volume of discharge of the rivers.

				1960 Sept.	Oct.	Nov.	Dec.	1961 Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
		Discharge ((m³/month)	114,825,600	82,226,880	49,196,160	67,308,192	13,566,096	115,057,152	115,037,280	109,848,960	77,352,192	79,056,000	193,487,616	73,682,784
	Hii	Total	Concentration (\gamma/L)	434	270	241	241	561	269	54	121	308	90	228	70
		Phosphorus	Total amount (ton/month)	49.830	22.199	11.856	16.221	7.610	30.961	6.235	13.292	23.824	7.115	44.115	5.600
Rivers		Discharge ((m³/month)	440,640	535,680	311,040	374,976	857,088	653,184	669,600	648,000	428,544	466,560	1,392,768	455,328
inflowing to Lake	Tamanoyu	Total	Concentration (\gamma/L)	1,510	127	364	15	355	222	144	64	297	1,119	113	43
Sinji-ko		Phosphorus	Total amount (ton/month)	0.665	0.065	0.113	0.006	0.304	0.145	0.096	0.041	0.127	0.522	0.157	0.020
		Discharge ((m³/month)	25,401,600	30,265,920	18,480,960	24,266,304	48,077,280	41,223,168	41,220,576	39,216,960	28,605,312	27,216,000	58,415,904	25,016,256
	Other rivers	Total	Concentration (\gamma/L)	576	142	200	28	264	234	104	79	273	289	149	60
		Phosphorus	Total amount (ton/month)	14.610	4.297	3.696	0.689	12.682	9.658	4.291	3.098	7.809	7.865	8.704	1.501
River connecting		Discharge (m³/month)		150,336,000	120,528,000	76,412,160	104,458,000	198,202,000	166,925,000	163,382,000	158,112,000	115,171,000	111,456,000	273,197,000	107,136,000
Lake Shinji-ko	Oohashi		Concentration (\gamma/L)	527	232	1,424	192	352	256	104	75	45	234	142	161
and Lake Naka-umi			Total amount (ton/month)	79.227	27.962	108.800	20.055	69.767	42.732	16.991	11.858	5.183	26.080	38.794	17.249
		Discharge (m³/month)		1,814,400	2,142,720	1,296,000	1,740,960	4,231,872	3,386,880	3,294,432	3,188,160	2,062,368	2,073,600	6,294,240	1,821,312
	Iu	Total	Concentration (\(\gamma/L\)	846	51	196	195	196	244	80	89	218	22	176	34
		Phosphorus	Total amount (ton/month)	1.530	0.109	0.254	0.339	0.829	0.826	0.265	0.284	0.449	0.046	1.108	0.062
		Discharge ((m³/month)	1,814,400	19,820,160	12,363,840	12,775,968	31,364,064	26,611,200	27,132,192	25,712,640	18,909,504	19,051,200	40,711,680	19,900,512
	Iinashi	Total	Concentration (\gamma/L)	25	251	124	23	113	224	139	93	289	53	70	86
		Phosphorus	Total amount (ton/month)	0.450	4.972	1.533	0.291	3.547	5.972	3.768	2.391	5.465	1.010	2.850	1.711
Rivers		Discharge (m³/month)	3,888,000	4,017,600	2,540,160	2,437,344	6,428,160	5,322,240	5,571,072	5,287,680	3,883,680	3,888,000	7,231,680	3,749,760
inflowing to Lake	Yoshida	Total	Concentration (7/L)	497	88	179	36	141	228	93	54	249	349	180	53
Naka-umi		Phosphorus	Total amount (ton/month)	1.932	0.353	0.454	0.088	0.903	1.213	0.520	0.286	0.967	1.357	1.301	0.199
		Discharge (m³/month)	6,998,400	8,303,040	5,391,360	5,571,072	12,856,320	11,128,320	11,195,712	10,679,040	7,981,632	7,905,600	14,999,040	6,963,840
	Hakuta	Total	Concentration (\gamma/L)	141	65	124	39	150	218	114	51	281	102	132	68
		Phosphorus	Total amount (ton/month)	0.960	0.539	0.668	0.221	1.931	2.430	1.281	0.545	2.243	0.806	1.980	0.474
		Discharge (m ³ /month)	28,252,800	29,462,400	18,014,410	23,569,920	46,604,160	40,061,952	39,801,024	38,102,400	27,828,576	28,252,800	62,058,528	32,060,448
	Other rivers	Total	Concentration (\gamma/L)	576	142	200	28	264	234	104	79	273	289	149	60
		Phosphorus	Total amount (ton/month)	16.260	4.182	3.602	0.669	12.294	9.386	4.143	3.010	7.597	8.165	9.247	1.924
Channel		Discharge (1	m³/month)	222,912,000	192,845,000	124,416,000	171,418,000	316,052,000	263,692,000	257,126,000	251,424,000	184,809,000	178,848,000	425,866,000	179,453,000
outflowing from Lake	Sakai	Total	Concentration (m³/month)	347	966	1,499	154	116	366	293	214	136	76	141	199
Naka-umi		Phosphorus	Total amount (ton/month)	77.350	186.288	186.499	26.398	36.662	96.511	75.337	53.804	25.134	13.592	60.047	35.711

Table 5. Balance sheet of total phosphorus (tons) of Lake Shinji-ko.

	Equation										
1960	S_{\aleph}	+	$I_{\chi+1}$		$O_{\chi+1}$	-	$S_{\chi+1}$	=	$G_{\chi+1}$		
Sept.	61.9*	+	65.2	_	79.2	_	192.3	-	-144.4		
Oct.	192.3	+	26.6	_	27.9		156.9	=	34.1		
Nov.	156.9	+	15.7		108.8	_	303.4	==	-239.6		
Dec. 1961	303.4	+	16.9		20.0		94.2	=	206.1		
Jan.	94.2	+	20.6		69.7	_	72.9		-27.8		
Feb.	72.9	+	40.7	_	42.7	_	71.4	=	- 0.5		
Mar.	71.4	+	10.6	—	16.9	_	35.7	=	29.4		
Apr.	35.7	+	16.4		11.9		28.0	=	12.2		
May	28.0	+	31.8	_	5.2		20.3	=	34.3		
June	20.3	+	15.5	_	26.1		65.6	=	-55.9		
July	65.6	+	53.0		38.8		43.7	=	36.1		
Aug.	43.7	+	7.1	-	17.2	-	61.9	=	-28.3		
Total	1146.3	+	352.2	-	496.5	_	1146.3	_	-144.3		

^{*} This value is quoted from the value observed at the end of August of 1961.

Table 6. Balance sheet of total phosphorus (tons) of Lake Naka-umi.

	Equation											
1960	S_{x}	+	$I_{\chi+I}$		O_{X+I}	_	S_{x+1}	=	G_{X+1}			
Sept.	92.1*	+	100.3		77.3		275.5		-160.4			
Oct.	275.5	+	38.1	_	186.3		310.9	=	-183.6			
Nov.	310.9	+	115.3	_	186.5		1127.8		-888.1			
Dec. 1961	1127.8	+	21.6	_	26.3	-	95.0	=	1028.1			
Jan.	95.0	+	89.3	_	36.6	—	73.5	=	74.2			
Feb.	73.5	+	64.7	_	96.5		141.5	=	-99.8			
Mar.	141.5	+	26.9	_	75.3	_	159.2	=	-66.1			
Apr.	159.2	+	18.4		53.8	_	127.7	=	- 3.9			
May	127.7	+	21.9	_	25.1	_	96.2	=	28.3			
June	96.2	+	37.5	-	13.6		89.2	=	30.9			
July	89.2	+	55.3	_	60.0	_	59.0	=	25.5			
Aug.	59.0	+	40.0		35.7	_	92.1	=	-28.8			
Total	2647.6	+	1187.0	_	1430.7		2647.6	=	-243.7			

^{*} This value is quoted from the value observed at the end of August of 1961.

when we consider the input and output balance, the reverse relation will become clear. The percent of the amount of phosphorus lost by death or disintegration of organisms from Lake Shinji-ko (144.3 tons) to the amount of phosphorus inpoured to the same Lake (352.2 tons) was about 41 (144.3/352.2 \times 100=40.9%), whereas the corresponding value was about 20% for Lake Naka-umi (243.7/1187.0 \times 100=20.5%); in other words, higher percent of phosphorus inpoured to the lake was retained by the organisms living in Lake Naka-umi than by the organisms living in Lake Shinji-ko. Furthermore, the amount of inpoured phosphorus per m³ of water mass through the year was 2.33 g for Lake Naka-umi (inpoured phosphorus/water volume of lake=1187 \times 106 g/5091 \times 105 m³=2.33 g), whereas it was 1.02 g for Lake Shinji-ko (352.2 \times 106 g/3425 \times 105 m³=1.02 g), which suggests greater activity of phosphorus cycle of the former than the latter.

Considerations

Several works have hitherto been published as for phosphorus metabolism in natural waters. Among them, using radioactive isotope is considered to be one of the most effective method to see the fate of phosphorus in lake waters. Coffin, Hayes, Jodrey and Whiteway (1949), Hutchinson and Bowen (1950) or Rigler (1956) had used this method and contributed to the knowledge about the exchange relation of phosphorus among higher plants, seston or mud. Generally speaking, the uptake of phosphorus by plants was conspicuous and the amount of radioactive phosphorus dissolved in water rapidly decreased after addition. It entered into plants and then passed through zooplankton to higher animals such as fish. After death of these organisms it resolved into water or deposited on the bottom. Einsele (1941) put a large amount of phosphate into Lake Schleinsee in 1938, but this abnormally high density decreased to the normal level after about one year, saying that some self-regulatory mechanism might have been working. Other several data are cited in the Hutchinson's book (1957).

All these works are concerned the phosphorus circulation within a lake as a whole. Besides, some investigators studied the phosphorus metabolism of some special species population. For example, Vallentyne (1952) studied the phosphorus removal from lakes by insect emergence, and Kuenzler (1961) clarified the phosphorus budget of the ribbed mussel (*Modiolus demissus*) living in Georgia salt marsh.

On the other hand, only few knowledges are known as for the phosphorus balance sheet covering a wide range of a lake system together with inlet and outlet waters, which are the object of the present research. Curl (1959) studied the origin and distribution of phosphorus in western Lake Erie, and calculated the contribution of five tributaries to this lake. Notwithstanding of

the interesting planning, the measurement of phosphorus was done by taking the surface water only, so something like obscurity arose in the consideration. Namely, the amount of phosphorus fluctuates generally with increase or decrease of the amount of discharge of the Maumee River, but during October to February the correlation was not clear (viz. although the discharge increased during this season, the amount of phosphorus rather decreased), and he supposed the reason that the water from the Maumee River must have gone under the lake water unmixed with it. DUGDALE and DUGDALE (1961) investigated gains and losses of phosphorus and nitrogen in some lakes on Afognale Island of Alaska in summer by measuring the contents of these elements in inlet and outlet streams together with those in lake waters. By their data, a slight increase (ca. 0.02 g/L) must occur in lake water during July (so slight that it was nearly unmeasurable). He did not refer in what way this retention was used, but only said that a slight excess in lake water must have occured. His observation is restricted to only summer season and this may be another weak point.

When compared with those works mentioned above, the present research bases on the data of a whole year covering inlet and outlet waters together with lake waters of different depths. So relatively a wide view of phosphorus budget of lake system with tributaries can be obtained. Of course, there are several difficulties in the present work which must be overcomed in future works. One of which is that, a considerable amount of phosphorus fertilizers must have been poured into the lakes from surrounding rice fields through small creeks or streams. The other is that, polluted water from cities or towns situated on the lake side must also have been poured into the lakes. The phosphorus originated from these two sources are completely neglected in the present work, but they must have given influence on the phosphorus budget of the lakes. Also the author supposed the amount of deposition is equal to that of resolution, which seems to be unreal in the natural waters. After these difficulties are excluded, the exact description of phosphorus budget of a lake system can be made and the productivity will exactly be calculated.

Summary

Total phosphorus contents in the water of Lake Shinji-ko and Lake Nakaumi, and the inlet and outlet rivers, were measured throughout a year (from September of 1960 to August of 1961) and the productivities of these two lakes were compared.

In order to compare the productivity of a lake, the amount of phosphorus taken into organisms during a definite month $(G_{x+I}, x+I)$ means a definite month was calculated by the following equation:

$$G_{x+1} = S_x + I_{x+1} - O_{x+1} - S_{x+1}$$

where S_{x+1} : the amount of total phosphorus in water, excluding that contained in organisms, at the end of a definite month (X+I).

 S_x : the same at the end of the preceding month (X)

 I_{x+1} : the amount of inpoured phosphorus to the lake during the said month (X+1).

 O_{x+1} : the amount of outpoured phosphorus from the lake during the said month (x+1).

This equation is based on the assumption that the amount of phosphorus deposited on the bottom and that of resolved into water during a definite month are nearly equal, which will be true if the lake under consideration is attained to the stable state. As Lake Shinji-ko and Lake Naka-umi have histories of more than thousands of years, so the above equation was considered to be useful.

The total of the values of G of Lake Shinji-ko through September of 1960 to August of 1961 (-144.7 tons, which means "negative growth" had occured) was larger than that of Lake Naka-umi (-243.7 tons). But the amount of inpoured phosphorus per $\rm m^3$ of water mass through the year was 2.33 g for Lake Naka-umi, which was larger than the value ($1.02~\rm g$) for Lake Shinji-ko, suggesting higher productive activity of the former; furthermore, Lake Shinji-ko lost about 41% of inpoured phosphorus through outflowing water, whereas Lake Naka-umi about 20%, the rate of retention of the former was smaller than the latter.

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