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Phosphorus Budget in Natural Population of *Corbicula japonica* Prime in Poikilohaline Lagoon, Zyusan-ko

Akira Fuji*

Abstract

The phosphorus flow through the natural population of *Corbicula japonica* Prime and the lagoon water surrounding them, in the poikilohaline lagoon of Zyusan-ko, Aomori Prefecture, was studied from Aug. 1974 to Aug. 1975. The average discharge of the Iwaki River, which has been assumed to be the major contributor for the river water flowing into the lagoon, was estimated at 19.3×10^8 m^3 yr^{-1}. The annual input of phosphorus from the river amounted to 2900, 1700 and 2600 mg m^{-2} in dissolved inorganic, dissolved organic and particulate phosphorus. A rough estimation of water exchange between lagoon water and coastal water is equivalent to 370×10^4 m^3 day^{-1}, and the tentative rate of mixing between both water masses is calculated at approximately 70%. Quantitative values of phosphorus added by the coastal water (mg P m^{-2} yr^{-1}) were: phosphate 700; dissolved organic 400; particulate 400. Phosphorus utilization by photosynthesis reaches about 1500 mg m^{-2} yr^{-1} and this value is the representation of the amount of particulate phosphorus produced by phosphorus uptake for the annual production of phytoplankton from the lagoon water. The clam population removed 681 mg P m^{-2} yr^{-1} of particulate phosphorus, of which 520 mg P m^{-2} yr^{-1} was ingested as food and 401 mg P m^{-2} yr^{-1} was deposited as biodeposits. The turnover time of phosphorus in the clam population was 83 days. The major effect of the population on the lagoon ecosystem was the removal of particulate matter from lagoon water; the turnover time of the particulate phosphorus inflowed to the lagoon was 6.6 days under the supposition that the clam population was the only agent involved.

Phosphorus is indispensable in organisms, and there is available to them only a limited amount of the phosphorus which is necessary for their life process. In nature, phosphorus moves from the environment to the plants during their growth, and passes from organism to organism by grazing and/or predation, and lastly returns to the environment through the processes of excretion or decomposition which contain many chemical transformations. Up to the present, on the phosphorus cycle in aquatic environment, Barnes1) reviewed current knowledge of the cycles and regional distribution of phosphorus in the sea, and Pomeroy2) reported the residence times and turnover rates of phosphorus in estuarine, coastal, and off-shore waters. Moreover, Corner & Davies3) reviewed the phosphorus cycle in the sea in terms of the sea water – plankton organisms relationship, and McRoy et al.4), Patriquin5) gave a detailed survey of work on the phosphorus cycle in an eelgrass ecosystem. The outlines of phosphorus circulation in the sea and of the pathway to the phosphorus cycle for estuaries and lagoon containing vascular

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plants are now known, but mostly no one has investigated the phosphorus budget of animal population in a poikilohaline lagoon without any eelgrass beds.

Zyusan-ko is an unpolluted lagoon located near the apex of the Tsugaru Peninsula, Aomori Prefecture. The lagoon which is about 17.4×10^6 m^2 in area and is about 18.6×10^6 m^3 in tidal mean volume, connects with the Japan Sea through a narrow waterway which is about 300 m in length and about 100 m in width. The Iwaki River discharges itself into this lagoon at the southern coast, in addition to being the major contributor for freshwater flowing into the lagoon. The lagoon ecosystem, therefore, is poikilohaline, the chlorinity of water shows a wide variation in different seasons. During the summer season, the chlorinity of surface water varies between 1‰ and 15‰ with high chlorinity at the central area, while in the residual seasons it ranges from 1‰ to 5‰ in a almost all areas. Lagoon benthic invertibrates are intimately characterized by the burrowing community predominating the *Corbicula japonica* in terms of density (Table 1), and could, therefore, be expected to influence the rate at which phosphorus fluxes through the clam population, and to evaluate the effect on the ecosystem of this particular pathway. For this purpose, the author's approach has been to deal with the phosphorus budget in the lagoon in terms of (1) the river water – the lagoon water relationship, (2) the lagoon water – the coastal water relationship, and (3) the lagoon water – the clam population relationship.

Table 1. *Seasonal variations of benthic fauna (Number/0.1 m²) found in Zyusan-ko.*

Species	Aug.	Oct.	Dec.	Mar.	Apr.	July	Aug.
Lamellibranchs:							
Corbicula japonica	131.1	437.2	1173.2	67.2	87.7	85.1	111.7
Gastropods:	0.0	0.0	0.0	0.0	2.0	0.1	1.3
Isopods:							
Cyathura murominensis	6.8	8.0	6.5	6.4	6.9	6.9	10.5
Amphipods:	0.3	2.8	1.8	0.2	0.0	0.3	0.1
Polychaetes:							
Prionospio japonicus	1.5	111.6	30.5	56.2	72.0	8.6	6.9
Heteromastus similis	19.2	68.6	32.7	79.1	74.5	69.5	55.5
Notomastus lateriseus	12.0	14.1	0.0	3.3	0.0	10.5	0.0
Sigambra sp.	1.3	0.5	0.7	0.6	0.5	1.1	0.0
Neanthes diversicolor	1.4	3.6	4.0	3.3	2.6	4.1	2.3
Nemertea:	6.1	5.7	7.0	18.4	14.6	13.5	6.4

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Materials and Methods

From August 1974 to August 1975, a water column was bimonthly sampled using a 2-liter bottle sampler at routine stations (Fig. 1). Immediately after collection, these samples were filtered over a cellulosic membrane filter (Millipore) of 0.45 μ pore size and were stored in a deep-freezer at -20°C. The phosphorus present in the natural lagoon and river water was determined as three different fractions: the dissolved inorganic phosphorus (phosphate); the dissolved organic phosphorus; and the particulate phosphorus. Besides phosphate and total dissolved phosphorus, an analysis was made of particulate phosphorus. From these data, three fractions of phosphorus were determined. Phosphorus compounds were analyzed by Hansen & Robinson[6)] and Murphy & Riley[7)]. Bimonthly samples of the river water were collected at the mouth of the Iwaki River, and the phosphorus analyzed by the same procedures as those mentioned above.

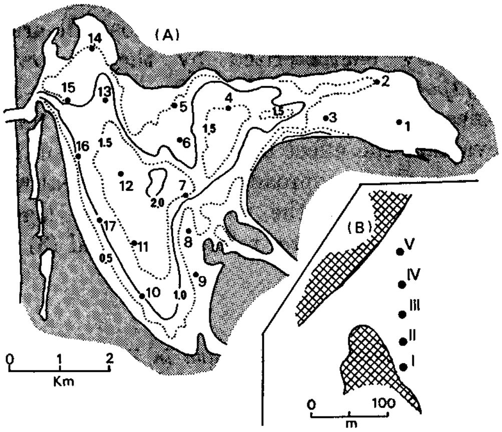


Fig. 1. Map of Lagoon Zyusan-ko showing positions of sampling sites (A). Depth contours coincide with the mean tidal low water line. Anchor stations situated at the outlet of the lagoon are numbered I to V (B).

Besides the samples for phosphorus, two liters of lagoon water was sampled, and filtered through a Whatman GF/C glass fiber paper for the determination of chlorophyll-a concentration by the trichromatic colourimetric method (SCOR/UNESCO procedure) using a Hitachi model 139 spectrophotometer. Light—photosynthesis experiments were done on the same water samples used in the chlorophyll-a determination. In these experiments, parts of photosynthesis in situ were measured from noon to sunset under light intensity corresponding to 100, 75, 50, 25 and 10% just below the surface. From the light—photosynthesis data obtained, the carbon assimilation per unit chlorophyll-a concentration gives hourly rate indications under any light intensity. To convert from hourly rate to daily rate, solar radiation was measured with a solarimeter at Station 15 during the entire course of the present study.

The clams were collected by means of a core sampler having a single sampling area of 0.1m^2, and were sorted out from sediments immediately after the sampling by a sieve with a 1 mm-mesh. Besides the sampling for a census of the clam, several samples for clarifying the phosphorus contents were taken at each station. Phosphorus in clam tissue was determined by the method outlined by Lindner[8)]. This method consisted of wet oxidation of the material in sulphuric acid and hydrogen peroxide, followed by a colourimetric determination of phosphorus based on the formation of the blue phospho-molybdate ion. In the present study, light absorbance was measured by a Hitachi model 139 spectrophotometer at 650 mμ. Samples of clam shells required an addition of hydrochloric acid after oxidation in order to dissolve the calcium salts. The remaining hydrochloric acid was neutralized before bringing the solution to its final volume.

The rate at which *Corbicula* feeds was estimated from the rate of decrease in concentration as the clam filtered a suspended particulate matter. Natural lagoon water was passed through a 95 μ screen in order to remove coarse particles, and then through a tared cellulosic membrane filter (Millipore) of 0.45 μ pore size. Then the filter was washed with a small quantity of filtered lagoon water, and it gave particulate matter in the 0.45 μ to 95 μ in size range. Suspension used in the feeding experiments was prepared from the above stock suspension. A group of 20 clams taken as a unit was placed in 3 liters of filtered lagoon water in an aquarium for several hours so that it might become acclimated and filted this water free of suspended matter. After acclimation, accumulated faeces and pseudofaeces were completely siphoned from around the clams, and the known volume of the stock suspension was added. The suspended matter was mixed by means of continuous air bubbles for aeration to form a stable suspension within the experimental period. The feeding rate was calculated by a formula similar to that used by Jorgensen[9]: $C_t=C_0 \exp[-M\cdot t/m]$, where m is the rate when the suspension is swept clear of particles; M is the volume of suspension; and C_0 and C_t are the concentrations of the suspended material at the beginning and after t hours respectively. The concentrations of suspension were determined colourimetrically by means of a spectrophotometer. It was found that the light absorbance, expressed as a function of the concentrations of the suspension, followed Beer's law. In these experiments, therefore, the proportion of particles removed from suspension could be directly determined from the corresponding decrease in light absorbance.

Biodeposits were siphoned from the bottom, briefly washed in distilled water, dried at 60°C, and weighed. These dried substances were stored in a desicator for the measurement of the phosphorus analysis. The particles settled out by gravity in a control aquarium were collected, and treated the same way as biodeposits.

From July 21, 20 h until July 22, 21 h, the survey was made to calculate the water exchange between the lagoon and the coastal water. Anchor stations were set at 5 places in the cross section of the waterway, and numbered I to V (Fig. 1). A Tohodentan model CM-2 S current meter was suspended at the following depths: 0.5, 1.5, 2.5, 3.5 m. The 3.5 m sample was always within 0.5 m of the bottom. Both current velocity and direction were continuously measured at 1.5-hour intervals during the whole survey period. From the current measurements at anchor stations I to V, the tidal discharge was calculated by taking the product of measured current velocity and the area of the waterway cross section, corrected for differences at water level during the tidal cycle. The water level was obtained from a tidal gauge situated in the right coast of the waterway. Moreover, water temperature and salinity were simultaneously measured by means of a Salinity and Temperature Measuring Bridge Type MC 5/2 (Electric Switchgear).

Results

Phosphorus compounds in the lagoon water

The information obtained for phosphorus is presented in a series of graphs shoiwng the seasonal changes of dissolved inorganic, dissolved organic, and particulate phosphorus for a number of selected stations and maps of distribution (Fig. 2). In the fractions of phosphorus, a downward gradient in concentration is noticeable from the river-mouth to the outlet of the lagoon. It is assumed from the above data that the annual changes of phosphorus concentration in the lagoon water has been largely influenced by the phosphorus compound in the river water flowing into the lagoon.

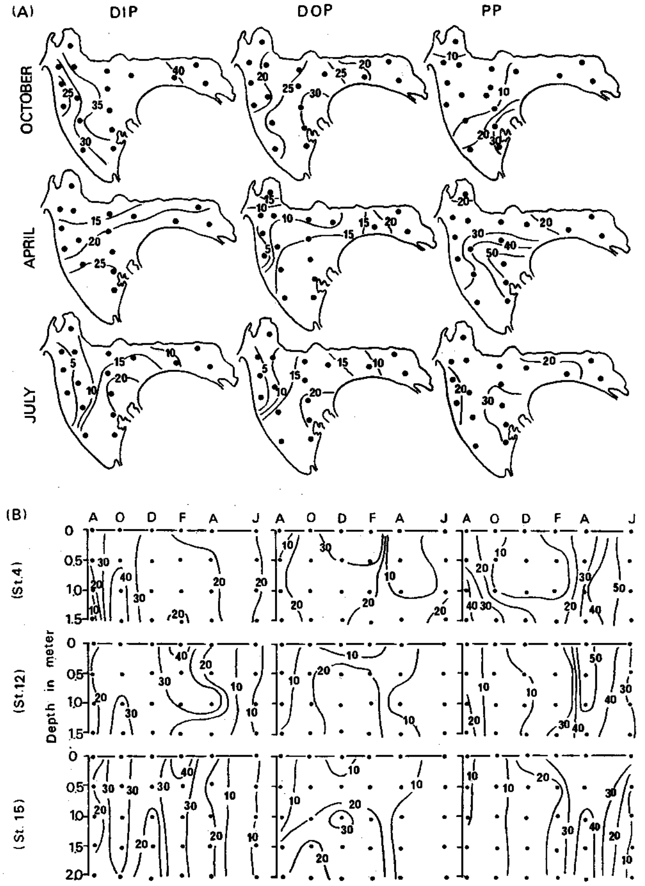


Fig. 2. Horizontal (A) and vertical (B) distributions of phosphorus at several selected stations. Phosphorus concentrations are $\mu g/l$.

The phosphorus concentrations in the lagoon water, together with the concentrations of the river water and the mixohaline water in the waterway are shown in Table 2 as the expression of monthly average. Since the average discharge of the Iwaki River, which has been assumed to be the major contributor for the phosphorus compounds in river water flowing into the lagoon, was estimated at 61.4 m^3/sec. (Table 3). This means that $61.4 \times 315.4 \times 10^5 = 19.3 \times 10^8$ m^3 of river water is added to the lagoon by the Iwaki River every year. Using the figure of 19.3 $\times 10^8$ m^3/yr as the inflowing water from the river, the mean incoming water volume per unit area, defined as the volume of inflowing water divided by the surface area of the lagoon at the mean tidal level, is $(19.3\times 10^8)/(17.4\times 10^6)=110.9$ $m^3/m^2/yr$. Then, the annual input value of phosphorus from the river is calculated by multiplying the mean volume of river water entering the lagoon by the concentrations of phosphorus in the water. At a mean volume of 110.9 $m^3/m^2/yr$ the annual input gives the value of 2900, 1700 and 2600 $mg/m^2/yr$ present in the three fractions, dissolved inorganic, dissolved organic and particulate phosphorus, on the mean tide.

Table 2. *Monthly average values for phosphorus fractions in the waters of the lagoon and the river* ($\mu g/l$).

Month	Dissolved inorganic P			Dissolved organic P			Particulate P		
	Lagoon	Outlet of lagoon*	Iwaki River	Lagoon	Outlet of lagoon*	Iwaki River	Lagoon	Outlet of lagoon*	Iwaki River
Aug.	12	15	32	12	9	13	16	9	30
Oct.	34	—	21	21	—	12	32	—	10
Dec.	21	17	27	16	12	15	36	14	20
Feb.	29	—	38	18	—	19	13	—	38
Apr.	20	17	23	16	10	18	38	7	14
July	25	12	22	8	6	18	20	5	34
Aug.	37	—	27	28	—	17	24	—	30

*at high water

Table 3. *Monthly average volumes of the inflowing water from the Iwaki River* (m^3/sec).

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1971	33.0	35.7	94.1	127.1	44.7	28.9	33.2	24.0	29.5	35.1	42.6	67.4
1972	46.5	41.3	92.5	173.5	37.3	26.6	91.1	63.1	48.5	34.1	60.8	66.3
1973	84.1	71.8	68.4	197.0	44.5	13.9	5.5	54.5	81.7	62.0	82.0	71.1
Mean	54.5	49.6	85.0	165.9	42.2	23.1	43.3	47.2	53.1	43.7	61.8	68.3

A tidal flow may carry significant quantities of phosphorus originating from coastal waters. Although material fluxes vary both in time and in space in the tidal waterway cross section, total water transports of measured parameters can be obtained by integrating the product of water velocity and mass concentration vs. time. Figure 3 shows the results obtained for the diurnal variation of water volume flowing in and out over a period of tidal cycle (24.5 hours). The amount of water flowing through the cross section over a tidal cycle gives the values of 338.7×10^4 m^3 in flood water volume and 404.9×10^4 m^3 in ebb water volume. Therefore, a rough estimation of water exchange is equivalent to 370.0×10^4 m^3/day. To calculate the mixing between two water masses one needs to know at least one property of the water masses concerned, that can act as a tracer. Moreover, there must be a measurable difference in concentration between the two water masses. In many coastal areas where rivers are supplying freshwater, salinity and temperature can be used as such. In the present study, it is convenient to make use of the temperature — salinity (chlorinity) characteristics. The inflowing water is, of course, denser than the lagoon water mass, but it can able be expected that a portion of the inflowing water mixes with the lagoon water when these two water masses take place in confrontation, and that it is dispersed here. It is said, in general, that the temperature — salinity relationship in the lateral mixing takes place along σ_t surface, and that the diagram in the vertical mixing shows crossing σ_t surface[10]. Figure 4 shows the temperature — chlorinity relationship of water masses passing through the waterway. The inflowing water mixes well vertically with the lagoon water over 2 meters in depth, and this process leads to the formation of a water mass. On the other hand, since the water mass under 2 meters in depth remains stationary without mixing, the outflowing water mass has not a large difference to the inflowing water just before a turnover period. The tentative rate of mixing between the inflowing coastal water and the lagoon water is calculated at approximately 70% of the total inflowing water. Therefore, the mean inflowing coastal water per unit area of the lagoon is equivalent to $(230\times10^4)\times365/(17.4\times10^6)=48\ \mathrm{m^3/m^2/yr}$. As shown in Table 2 the annual mean values of 15, 9 and 9 $\mu g/l$ in the waterway on the flood tide are representative of the amount of dissolved inorganic, dissolved organic, and particulate phosphorus respectively. At a mean volume of 48 $\mathrm{m^3/m^2/yr}$ these phosphorus added from the coastal waters are equivalent to 700, 400 and 400 $\mathrm{mg/m^2/yr}$.

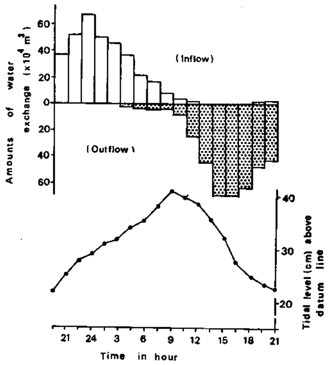
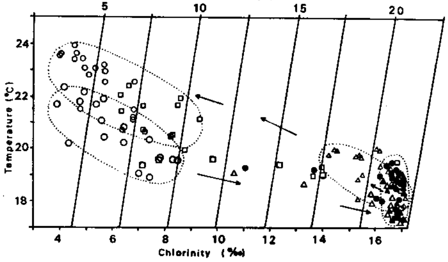


Fig. 3. Amount of water flowing through the cross section of the outlet per unit time.

A trophogenic zone was taken as 0.5 m on the basis of the direct measurements of underwater illumination at Station 11, 12 and 16 in July. From these findings, the bimonthly averages for chlorophyll-a in the trophogenic layer are shown in Table 4, and the overall range of chlorophyll-a was 1.4 to 19.4 $\mathrm{mg/m^2}$, with a distinct peak occurring late June or early July. A primary production is largely

Fig. 4. Temperature–chlorinity relationship at the outlet of the lagoon. In this figure, the symbols are ○; 1 m, □; 2 m, and △; 3 m in depth. Open small symbols show the values at 1st low water, and large ones are the values at 2nd low water. Closed symbols indicate the values at high water.



influenced by insolation, biomass of plant, and other environmental conditions of the lagoon. The mean monthly production showed that the variation of production was very seasonal with a marked bloom in early summer and an obvious slack in residual seasons. A bloom appeared in early summer, and the total production in the trophogenic layer was 550–920 mg C/m^2/ day. After August, the slack seasons, the total production decreased suddenly to the level of about 70 mg C/m^2/day. A poor production less than 10 mg C/m^2/day occurred in December. This low level of production was not necessarily attributed to low chlorophyll-a concentration only and the average intensity of insolation in the area was about 50 cal/cm^2/day, being nearly one sixth of the early summer. The total yearly (net) production was about 63 g C/m^2, and much lower than in an ordinary poikilohaline lagoon[11].

Table 4. *Primary production, chlorophyll-a occurring within the photic layer* (0–0.5 *m in depth*), *and solar radiation at the surface.*

Duration	Chlorophyll-a content within photic layer (μg/l)	Monthly average of solar radiation (cal/cm^2/day)	Primary (net) production	
			(g C/m^2 /month)	(mg P/m^2 /month)
Oct. – Nov.	4.48	170	1.34	32.2
Nov. – Dec.	4.48	58	0.56	13.6
Dec. – Jan.	3.83	41	0.32	7.6
Jan. – Feb.	3.80	47	0.37	9.0
Feb. – Mar.	3.83	48	0.34	8.3
Mar. – Apr.	2.82	192	1.00	24.1
Apr. – May	3.57	324	2.69	64.6
May – June	17.77	381	7.84	188.3
June – July	36.71	395	16.67	400.2
July – Aug.	38.85	261	28.05	673.2
Aug. – Sept.	5.22	325	2.36	56.8
Sept. – Oct.	5.20	273	2.10	50.5

Phosphorus utilization by phytoplankton was converted using the atomic ratio of C/P=106/1 from monthly mean net production illustrated in the third column of Table 4. This value becomes about 1500 mg P/m^2/yr. Since the phytoplankton has shown a capacity of growth utilizing the phosphorus of inorganic and organic compounds[12,13,14], this value of 1500 mg P/m^2/yr is representative of the amount of particulate phosphorus produced by two dissolved fractions of phosphorus uptaken for the annual production of phytoplankton from the lagoon water.

Phosphorus budget of the clam population

The age structure of the clam population is estimated on the basis of size distribution, which is a graphical analysis making use of the probability paper derived by Harding[15]. From this treatment, the mean shell height in each of the age-group and the age structure in percentage occupancy is possible to determine. Although the density of the clam varies markedly at the habitats within the lagoon, the population size for the entire lagoon is possible to calculate on the basis of the average density at various habitats and the age structure in percentage occupancy (Table 5). There is good correlation between the shell height and the dry weight of body components (viz., shell and flesh). It is possible, therefore, without measuring each of the body components, to make an accurate estimate of shell and flesh weight by the use of shell height — shell weight regression and of shell height — flesh weight regression. The mean weight of the body components of the individuals belonging to the various groups is enumerated in Table 6 according to various times of the year.

Table 5. *Population sizes in number per square meter for Corbicula japonica living on the entire lagoon of Zyusan-ko.*

Month	Age-class			
	0	I	II	III
Aug.	—	146.8	142.0	76.4
Oct.	—	140.0	149.6	70.8
Dec.	—	113.1	100.8	57.2
Feb.	—	102.5	85.1	53.2
Apr.	—	78.9	64.0	49.9
July	85.6	89.9	49.3	34.8
Aug.	106.2	96.0	41.6	30.8

Table 6. *Seasonal changes in the average dry weight of body components (mg/ind.).*

Month	Shell				Flesh			
	0	I	II	III	0	I	II	III
Aug.	—	24.1	308.2	1414.0	—	0.3	7.2	44.5
Oct.	—	37.5	396.1	1558.1	—	0.8	13.6	69.3
Dec.	—	70.0	658.8	1677.3	—	1.4	22.8	74.0
Feb.	—	177.4	809.7	1920.0	—	3.9	23.8	66.7
Apr.	—	266.5	998.6	2065.6	—	13.9	58.1	127.2
July	10.2	400.5	1560.0	2811.0	0.3	18.5	88.0	172.8
Aug.	19.1	448.2	1556.1	2969.3	0.5	13.1	57.3	123.3

It is considered that the logarithm of phosphorus content, P, is linearly related to the logarithm of an individual shell weight, S, and flesh weight, F. These exponential equations are: $P=aS^b$ and $P=aF^b$, where a is a constant, and b is a regression coefficient. The parameters of regression formulae are illustrated in Table 7. The above equations were used to estimate the phosphorus content of the individuals belonging to the various age-groups as a function of dry weight of body component. This estimation is shown in Table 8. The amount of population increment attributed to the individual growth is taken to be the difference between the initial and final phosphorus content multiplied by the arithmetrical mean of the

Table 7. *Regression formulae for computing phosphorus content (P, μg) of the body components from measurements of dry weight of shell (S, gr) and flesh (F, mg).*

Month	$P=aS^b$		$P=aF^b$	
	a	b	a	b
Aug.	18.09	0.701	18.05	0.800
Oct.	23.90	0.803	9.39	0.840
Dec.	26.87	0.766	14.79	0.800
Feb.	33.52	0.748	15.16	0.819
Apr.	33.51	0.748	20.74	0.751
July	27.73	0.847	18.69	0.842

Table 8. *Changes in phosphorus content of an individual clam (μg P/ind.).*

Month	Shell				Flesh			
	0	I	II	III	0	I	II	III
Aug.	—	1.33	7.92	40.85	—	6.9	87.6	376.7
Oct.	—	1.71	11.36	34.13	—	7.8	84.2	330.6
Dec.	—	3.50	19.52	39.94	—	19.3	179.7	459.9
Feb.	—	9.21	28.63	54.59	—	46.2	203.6	473.7
Apr.	—	12.47	33.47	57.61	—	165.1	438.7	790.7
July	0.57	12.77	40.41	66.56	6.8	218.3	811.7	1433.0
Aug.	1.11	10.31	24.67	38.82	10.4	141.6	461.0	851.3

initial and final population density. The negative value in the above computation indicates an approximation of the magnitude for ejected gametes. If it is positive, the above computation corresponds to the magnitude for the phosphorus attributed to the newly born individuals. On the other hand, if it is negative, it is taken to be the population loss attributed to natural mortality and yield. The rates of change of the phosphorus in four fractions of the clam population in the lagoon may now be calculated (Fig. 5). The annual phosphorus accumulation for the population during the study period was estimated to be 134 mg P/m^2, and the amount of lost phosphorus from the population amounted to 117 mg P/m^2/yr. Therefore, it is pointed out that the final phosphorus content of the population is estimated to be 63 mg P/m^2 by adding 17 mg P/m^2 to the phosphorus content of the initial population.

The deposition of true faeces and pseudofaeces always greatly exceeded the deposition of solids by gravity (control) which averaged 6.2% of the combined weight of faeces and pseudofaeces. The data from the feeding rate and biodeposi-

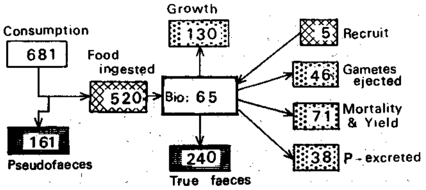


Fig. 5. Diagram of phosphorus flow through the clam population. Biomass (Bio.) of the clam population is mg P/m^2. The flux rate of phosphorus excreted by the clam population is a calculated value necessary to balance the other, measured flux rates, and is mg P/m^2/yr.

tion (true faeces plus pseudofaeces) rate experiments show a tendency for a larger rate at high temperatures. Furthermore, at the same temperatures, there was some tendency for the larger clams to ingest and to excrete at a higher rate than the smaller ones. There is a good correlation between the heights of a clam shell and the logarithmic value of the rate of ingestion and of biodeposition. The rates of ingestion and of biodeposition for each size class of the clams were computed by the application of the following equations:

log $I=aH+b$ and log $E=aH+b$, where I and E are the rates of ingestion and of biodeposition, H is the shell height (Table 9). These equations lead the rates of ingestion and of biodeposition for an individual clam of mean shell height in each of the age-groups belonging to the population under the given temperatures of their habitats. Since the feeding rate and the egesting rate of biodeposits for the individual clam estimated by the above equations is linearly related to the logarithm of total seston, the rate of ingestion and of biodeposition with quantities of seston which they met in the lagoon now can be calculated as an expression of mg per individual per day. The magnitude for population ingestion and biodeposition is taken to be the arithmetic mean of the initial and final population density multiplied by the arithmetic mean of the initial and final value of feeding rate and the egesting rate of biodeposits.

Table 9. *Regression formulae for computing food intake (I) and biodeposits egested (E) as the unit of mg/ind./day for measurements of shell height (H, mm).*

Month & Temp. (°C)	Seston (mg/l)	log I=aH+b		log E=aH+b	
		a	b	a	b
Aug. (25.0-26.0)	42	0.0407	0.7839	0.0516	0.3124
	33	0.0421	0.7109	0.0466	0.3263
	22	0.0426	0.6040	0.0425	0.2815
	17	0.0425	0.5500	0.0450	0.1074
	12	0.0416	0.4899	0.0427	−0.0830
July (22.5-23.7)	42	0.0432	0.7156	0.0478	0.3622
	33	0.0426	0.6620	0.0511	0.2167
	22	0.0444	0.5243	0.0475	0.1326
	17	0.0429	0.4738	0.0455	0.0182
	12	0.0422	0.3670	0.0489	−0.3443
Oct. (10.5-11.3)	42	0.0465	0.4231	0.0497	0.1466
	33	0.0451	0.3649	0.0501	0.0028
	22	0.0493	0.1056	0.0586	−0.4196
	17	0.0485	0.0129	0.0532	−0.6774
	12	0.0630	−0.7020	0.0589	−1.0477
Feb. (2.0-3.1)	42	0.0524	0.0140	0.0506	−0.0101
	33	0.0510	−0.0874	0.0477	−0.1134
	22	0.0550	−0.5555	0.0396	−0.4669

At a low concentration of seston pseudofaeces do not form. The minimum concentration which they form is estimated to be about 22 mg/l of suspension.

Upwards from this level, it shows a steady increase in the proportion of pseudofaeces rejected with increasing concentration. As to a same clam size, faeces production, however, keeps up a similar level, with no apparent relationship between faeces and total seston. Therefore, rates of pseudofaeces rejection were calculated by subtraction of the rate of biodeposition under the concentration of 22 mg/*l* in total seston from the rates of biodeposition. The annual food intake, faeces excretion, and pseudofaeces rejection by the natural clam population are summarized in Table 10. Phosphorus content of the seston and the biodeposits vary slightly from month to month. The maximum content of phosphorus from February to July may reflect a large biotic fraction of seston, since the bloom of phytoplankton appears during the period of late spring or early summer. Haven & Morale-Aloma16) reported that there were no discernible differences in the organic content of oyster faeces and pseudofaeces. If it is permissible to the phosphorus content of the clam faeces and pseudofaeces, the rate of phosphorus ingestion and elimination rates for biodeposits can be estimated by multiplying the rate of ingestion and the elimination rates for faeces and pseudofaeces times the phosphorus content of seston and biodeposits. These results are summarized in Tale 11. From the above data, the loss of phosphorus in true faeces gives values of 240 mg P/m^2/yr, and this result led to be about 161 mg P/m^2/yr. for the rejection rate of pseudofaeces. The rate of ingestion for particulate phosphorus is calculated by subtracting the rate of pseudofaeces rejection from the feeding rate of the clam population, and the rate of ingestion becomes 520 mg P/m^2/yr. Since a little under half the ingested phosphorus is released in faeces, the assimilation efficiency for phosphorus is estimated to be about 46% in nature.

Table 10. *Food consumed and biodeposits rejected by the clam population* (*g*/*m*^{2}).

Duration	Consumption				True faeces				Pseudofaeces			
	0	I	II	III	0	I	II	III	0	I	II	III
Aug.-Oct. (60)	—	45.47	87.17	87.37	—	15.19	23.53	22.65	—	5.48	16.36	21.68
Oct.-Dec. (60)	—	23.07	49.32	48.29	—	5.01	5.60	3.76	—	9.64	25.35	29.13
Dec.-Feb. (60)	—	6.05	13.65	14.85	—	4.07	6.32	6.01	—	1.49	5.75	6.95
Feb.-Apr. (60)	—	14.75	21.71	13.24	—	2.71	7.45	4.84	—	4.39	4.34	2.17
Apr.-July (90)	10.57	31.60	78.57	90.77	3.01	11.60	30.00	36.20	0.57	2.03	7.34	8.07
July-Aug. (30)	18.32	35.96	34.57	38.89	2.86	13.03	13.26	15.57	4.02	3.22	4.01	4.63

Table 11. *Phosphorus consumption and phosphorus rejection of the clam population* (*mg P*/*m*^{2}).

Duration	Consumption				True faeces				Pseudofaeces			
	0	I	II	III	0	I	II	III	0	I	II	III
Aug.-Oct. (60)	—	32.96	63.20	63.34	—	12.33	19.10	18.39	—	4.45	13.29	17.61
Oct.-Dec. (60)	—	19.61	41.92	41.04	—	4.77	5.33	3.58	—	9.18	24.13	27.73
Dec.-Feb. (60)	—	5.90	13.31	14.48	—	4.44	6.90	6.56	—	1.63	6.28	7.59
Feb.-Apr. (60)	—	17.03	25.07	15.29	—	3.51	9.64	6.26	—	5.68	5.62	2.81
Apr.-July (90)	11.41	34.13	84.85	98.03	4.73	14.04	36.30	43.80	0.69	2.45	8.88	9.77
July-Aug. (30)	14.29	28.05	26.96	30.33	2.50	11.39	11.59	15.16	3.51	2.81	3.50	4.04

The changes of population phosphorus given in Figure 5 show that the combined gains by flesh and shell due to recruitment and growth were 134 mg $P/m^2/yr$, whereas the loss due to mortality, yield and ejected gametes were 117 mg $P/m^2/yr$. It is possible that the population losses were slightly less than the gains during the study periods, and the amount of 17 mg P/m^2 is equal to the actual amount of phosphours which was added into the population during a whole year.

The rate of phosphorus input must equal the rate of its output from the population. The value of about 38 mg $P/m^2/yr$ is calculated as a difference between them. Pomeroy & Haskin17) reported a basal excretion rate of phosphorus by American oysters of 20 μg P per individual (ca. 10 g in dry weight) per day. If this is also permissible in the case of the clam, it is probably more nearly the estimated rate of phosphorus elimination from the average clam population. It has been reported that marine animals uptake dissolved inorganic and organic phosphorus from the water.12,17,18,19) Since the utilization of dissolved organic and inorganic phosphorus has not been proved in the present study, it is not shown in Figure 5.

Discussion

The productivity of poikilohaline and freshwater bivalve population has been little studied although more information is available for marine species. The productivity for the population of *Corbicula japonica* in Lagoon Zyusan-ko was 134 mg $P/m^2/yr$, it is about two times lower than that reported recently for the North Texas population of *Corbicula manilensis*20) at 250 mg $P/m^2/yr$, when converted from the author's carbon values. However, these values are the highest productivity rate ever reported for a freshwater bivalve species. Considerably lower annual productivity estimates have been reported for several *Corbicula africana* population in Africa21) which, when converted from values in kilocalories per meter square into phosphorus equivalents, are equal to annual productivity rates of 13, 25, 37, 46 and 114 mg P/m^2. The production values reported here also generally higher than those reported for many marine clams. Kilocaloric estimates of the annual productivity of *Modiolus demissus*, when converted into phosphorus equivalent were equal to 37 mg P/m^{2},19). Similarly, an English population of *Tellina tenuis* had an annual productivity rate of 77 mg $P/m.^{2}$,22)

Another measure of productivity is the turnover ratio, the average time it takes a population to produce new tissue growth equivalent to the average biomass23). The annual turnover ratio for the entire population was 2.7, equal to a turnover time of 135 days. Turnover ratios for other bivalves are generally still well within the range of 1.5 - 4.1. Aldridge & McMahon20) estimated an average annual turnover ratio of 4.1 for the North Central Texas population of *Corbicula manilensis*. Five populations of *Corbicula africana* in Lake Chad, Africa, had an annual turnover ratio of 2.6 21). Burke & Mann24) and Chamber & Milne25) reported that the annual turnover ratio for *Macoma balthica* ranged from 1.5 to 2.1 for Atlantic populations in Canada and Scotland.

Two sources of phosphorus are potentially available to filter feeders: the one combined in suspended particulate matter, such as plankton and detritus, and the other in solution in water in various chemical combinations. The latter may be divided into phosphate ions in equilibrium with various cations and dissolved organic compounds which include phosphorus in their make-up. In general, the budget of particulate phosphorus in the lagoon water may be represented by the following equation:

Standing crop=Primary production (net)+Inflow+Biodeposits – Consumption by the clam population – Outflow – Sinking

From the data obtained in the present study, the last item in the above equation is computed to be 22.6 ton/yr.

The exchange of phosphate between water and sediments may be enhanced by the movement of water up and down in the sediments as it evaporates during low tide and is replaced at high tide. For sediments budget into temporary suspension by moves, the exchange rate will vary with the time the sediments are in suspension. For exchange of the dissolved fractions between water and sediments in the lagoon Zyusan-ko may be estimated from the following equation:

Standing crop=Inflow+Excretion by the clam population – Photosynthesis – Outflow – Absorption+Release

Since the last two items, in the present study, are not revealed separately, they are clumped together as the value of –10.2 ton/yr.

The quantities of phosphorus in the clam population with the lagoon water over the population, the rate of river runoff, water exchange between the lagoon water and the coastal water, and the routes and rates of flow between these parts of the lagoon ecosystem may now be illustrated as shown in Figure 6. The above figure was based on the following hypothetical assumptions that the clam population constitutes the only route for particulate phosphorus to leave the lagoon. The decrease in particulate matter in the lagoon water has been already shown as 6.6 days of a participatory turnover time by the clam population (Fig. 5), and now the effect of the clams upon the clearing of the water appears evident. Very little study has been done on the phosphorus budget of poikilohaline and marine ecosystems by other workers. Bruce & Hood[26] studied shallow bays and reported the turnover rate to be 10 to 20 days, but it is not clear to which phosphorus fractions this turnover time applies. Pomeroy[2] used ^{32}P to study the phosphate flux between nature suspended matter and water, and found residence times of phosphorus to be from 1.7 to 7 days.

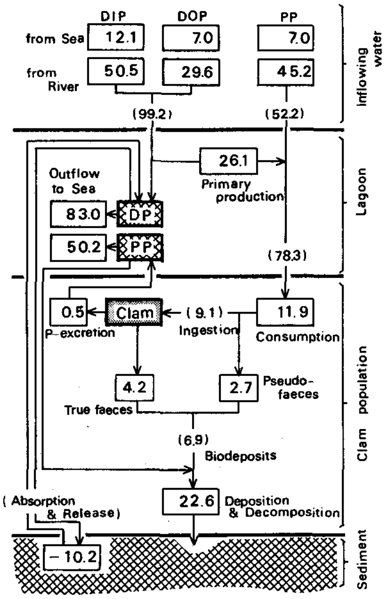


Fig. 6. A simplified box model of Lagoon Zyusan-ko showing the phosphorus budget. The flux rates of phosphorus are ton/yr.

The clam population has a relatively

long turnover time for phosphorus (83 days) in spite of an abundance of the element attributed to the inflowing water from the river. The major fractions of phosphorus present in the lagoon water are ineffectively used, the dissolved fractions being slightly utilized (about one fourth) by photosynthetic processes and the particulate phosphorus being largely wasted, even after the clams have utilized it out of suspension. The clam population, however, has a major effect on the lagoon water, annually removing one seventh of the particulate phosphorus from suspension. Certainly this is not a permanent loss of phosphorus from the water, but it may account for a significant part of the accumulation of phosphorus in the lagoon. They regenerate a small part of this into phosphate and reject the remainder in biodeposits which sink to the sediments. It is said, therefore, that the clam population may be important in this poikilohaline lagoon as a depositional agent, offering food materials to periphytal deposit-feeders (see Table 1), which regenerate the phosphate.

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