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EXAMINATION OF SILICATE LIMITATION OF PRIMARY PRODUCTION IN JIAOZHOU BAY, CHINA

I. SILICATE BEING A LIMITING FACTOR OF PHYTOPLANKTON PRIMARY PRODUCTION[*]

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Abstract Jiaozhou Bay data collected from May 1991 to February 1994, in 12 seasonal investigations, and provided the authors by the Ecological Station of Jiaozhou Bay, were analyzed to determine the spatiotemporal variations in temperature, light, nutrients (NO_3^--N, NO_2^--N, NH_4^+-N, SiO_3^{2-}-Si, PO_4^{3-}-P), phytoplankton, and primary production in Jiaozhou Bay. The results indicated that only silicate correlated well in time and space with, and had important effects on, the characteristics, dynamic cycles and trends of, primary production in Jiaozhou Bay. The authors developed a corresponding dynamic model of primary production and silicate and water temperature. Eq.(1) of the model shows that the primary production variation is controlled by the nutrient Si and affected by water temperature; that the main factor controlling the primary production is Si; that water temperature affects the composition of the structure of phytoplankton assemblage; that the different populations of the phytoplankton assemblage occupy different ecological niches for C, the apparent ratio of conversion of silicate in seawater into phytoplankton biomas and D, the coefficient of water temperature's effect on phytoplankton biomass. The authors researched the silicon source of Jiaozhou Bay, the biogeochemical sediment process of the silicon, the phytoplankton predominant species and the phytoplankton structure. The authors considered silicate a limiting factor of primary production in Jiaozhou Bay, whose decreasing concentration of silicate from terrestrial source is supposedly due to dilution by current and uptake by phytoplankton; quantified the silicate assimilated by phytoplankton, the intrinsic ratio of conversion of silicon into phytoplankton biomass, the proportion of silicate uptaken by phytoplankton and diluted by current; and found that the primary production of the phytoplankton is determined by the quantity of the silicate assimilated by them. The phenomenon of apparently high plant-nutrient concentrations but low phytoplankton biomass in some waters is reasonably explained in this paper.

Key words: phytoplankton, silicon, limiting factor, Jiaozhou Bay

INTRODUCTION

The production of phytoplankton is the first tache in the production by marine organisms and in the marine food chain. Knowledge of primary production in marine waters is prerequisite for exploi-

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tation and management of the ocean's living resources. The primary production in marine environment is one of the basic parameters for forecasting and estimating the fishery production. Studying the controlling factors of primary production is of important significance for sustainable use of marine living resources.

There were a number of studies dealing with the nutrients, and the growth of phytoplankton, in Jiaozhou Bay. Shen (1995) thought that nitrogen and phosphorous are limiting factors for phytoplankton growth in Jiaozhou Bay, where silicate concentration is a limiting factor for diatom growth. Wu and Zhang (1995) pointed out that inorganic phosphorous and total inorganic nitrogen are abundant enough to meet the requirement for growth and reproduction of Jiaozhou Bay phytoplankton; and other researchers (Wang et al., 1995) also considered N and P of Jiaozhou Bay are not limiting nutrients for phytoplankton growth. Zhang and Shen (1997)'s analysis of the proportion of the nutrients indicated that the probability of dissolved inorganic nitrogen and phosphorous as the limiting factors of phytophlankton growth is very small, or close to zero, at the surface layer of Jiaozhou Bay; while the probability of dissolved inorganic silicon as the limiting factor increases rapidly. However, the potential importance of silicate as a limiting factor for phytoplankton growth is still poorly known. This work yielded important data on the spatiotemporal variations in temperature, light, nutrients (NO_3^--N, NO_2^--N, NH_4^+-N, SiO_3^{2-}-Si, PO_4^{3-}-P) phytoplankton, and primary production in Jiaozhou Bay in 1992 - 1994 to serve as basic background for understanding the relationship of nutrients and phytoplankton and for understanding the impact of Si on the growth of phytoplankton.

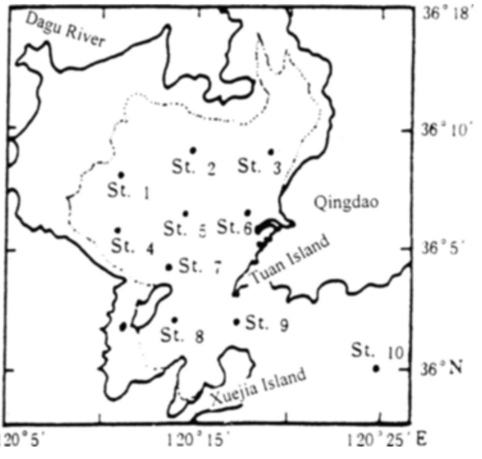

Fig.1 Investigation sites in Jiaozhou Bay

STUDY AREA AND DATA SOURCE

Jiaozhou Bay (35°55' - 36°18'N, 120°04' - 120°23'E) is a small partly-closed coastal waterbody surrounded by Qingdao, Jiaozhou and Jiaonan (Fig.1); is 390 km^2 in area, and 7 meter in depth (maximum of 50 m). The economic advance of industry and agriculture in the watershed has led to the inputting of a large amount of sewage from point and non-point sources (nutrients) to Jiaozhou Bay. In the 1980s, the quantity of industrial wastewater from Qingdao reached to 70 million t/a, and domestic sewage was 1.5 million t/a (Shen, 1995).

The dataset used in this work was provided by the Jiaozhou Bay Ecological Station which carried out May 1991 to February 1994 field surveys in 12 cruises. The water samples taken were collected at ten stations (Fig.1), each time in February, May, August, November, as representative of winter, spring, summer and autumn.

The raw data included NO_3^--N, NO_2^--N, NH_4^+-N, SiO_3^{2-}-Si, PO_4^{3-}-P (Shen, 1995). Nutrients were determined by a Technicon II Auto Analyzer; primary production was determined by ^{14}C method; chlorophyll-a was measured by fluorescence method (Jeffery and Humphery, 1975; Wu and Zhang, 1995). Nutrients data were accurate to two decimal places. The detection limit of silicate concentration was below 0.05 μmol/L. Water samples of the nutrients were collected with stainless steel water sampler (at surface, 5 m, 10 m, 15 m, …, and near bottom); and after the addition of 0.3% chloroform, were stored in polyethylene bottles and deepfreezed to below -25℃ in a refrigerator. The clear liquid at the upper layer was measured after thawing in laboratory (Shen, 1995). Water samples for chlorophyll-a measurement were taken at the surface and near bottom; and filtered immediately onboard through 0.45 μm pore-size sieve film.

RESULTS

Silicate and primary production

Seasonal variation The trends of seasonal variation of silicate concentration and primary production were very evident in Jiaozhou Bay. Every year there was only one peak of silicate concentration in summer. The silicate concentration in autumn, spring and winter was relatively lower, especially in winter, when it fell below detection limit, even to almost zero (silicate concentration below 0.05 μmol/L is termed zero). In May, the silicate concentration started to increase from 0 – 1 μmol/L and reached the highest value by August-September, then decreased to 0 – 1 μmol/L in the first few days of November, for example, at Stations 1 and 4 (Fig.2).

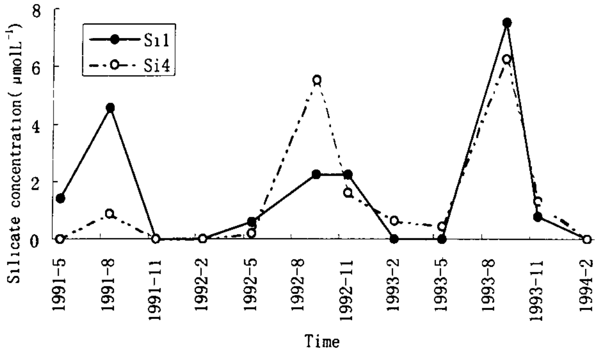

Fig.2 Seasonal variations of silicate concentration at Stations 1 and 4

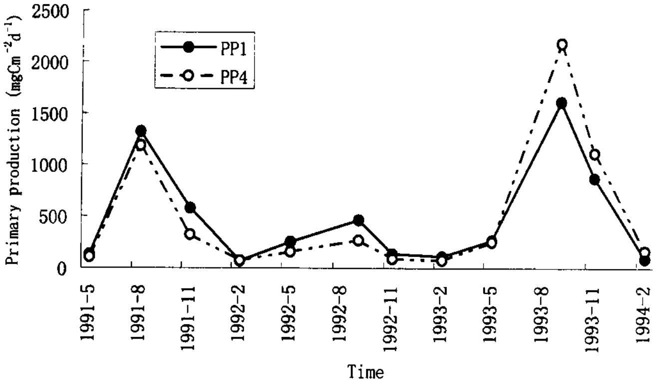

Fig.3 Seasonal variations of primary production at Stations 1 and 4

Similarly, there was only one peak of primary production in summer. Moreover, the peak of the primary production varied in time and space, with maximal values of 1600 – 2500 mgC/(m^2·d). Lowest primary production appeared only in winter, and ranged from 35 – 104 mgC/(m^2·d). The difference between summer and winter in primary production could be 20 – 50 times. From February to May, primary production slowly increased, but from May rapidly increased to a peak, then rapidly decreased until November. From November to February it slowly dropped to the lowest value.

From November to May, primary production remained very low; then recycled again, for instance, at Stations 1 and 4 (Fig.3).

A clear seasonal cycle could be identified for both silicate concentration and primary production, the seasonal variations in primary production and silicate concentration were similar and in phase.

Horizontal distribution The distributing features of silicate (Fig.4): In Jiaozhou Bay in summer, the silicate concentrations at Stations 1, 2 and 4 were higher than those at Stations 5, 6 and 7; and at Stations 8, 9 and 10 were lower than those at the other stations, especially Station 10, which was outside the Bay and showed much lower level of silicate concentration than that at the other stations. In winter the silicate concentrations were below 0.05μmol/L at all stations covered.

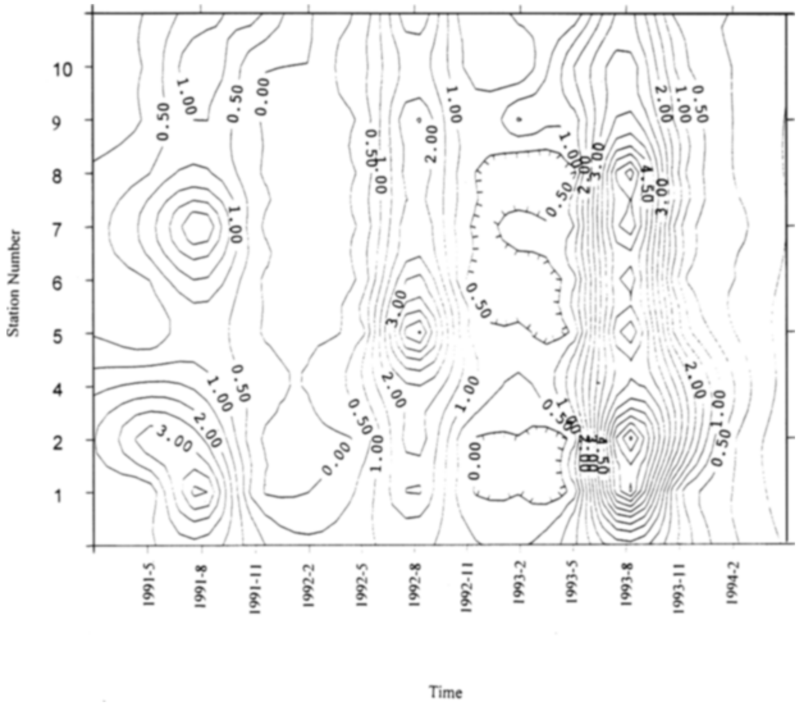

Fig.4 Spatiotemporal distribution of silicate concentration at 9 Stations (μmol/L)

The variation of vertical distribution of silicate: At Stations 1 and 2, the vertical distributions of silicate concentrations were uniform. The annual peak value of silicate concentration at the surface layer at Stations 4, 5 and 6 increased from 1991 to 1994, from 1.56 μmol/L in August, 1991 to 3.35 μmol/L in September, 1992 to 5.55 μmol/L in August, 1993 at Station 5; while the annual peak of silicate concentration in the near-bottom layer was almost stable, and from the bottom to surface became higher. At Station 7, the silicate concentrations at the surface and bottom layers were horizontally distributed uniformly, but the peak concentration increased from 1991 to 1994 (Fig.5). The annual peak of silicate concentration at the surface layer at Stations 8 and 10 was stable and the silicate concentration at the bottom layer increased from < 0.05 μmol/L to > 0.05 μmol/L. At Station 9, the silicate concentration at the surface layer was higher than that at the bottom layer at the beginning of May, 1991, then became lower than that at the bottom layer.

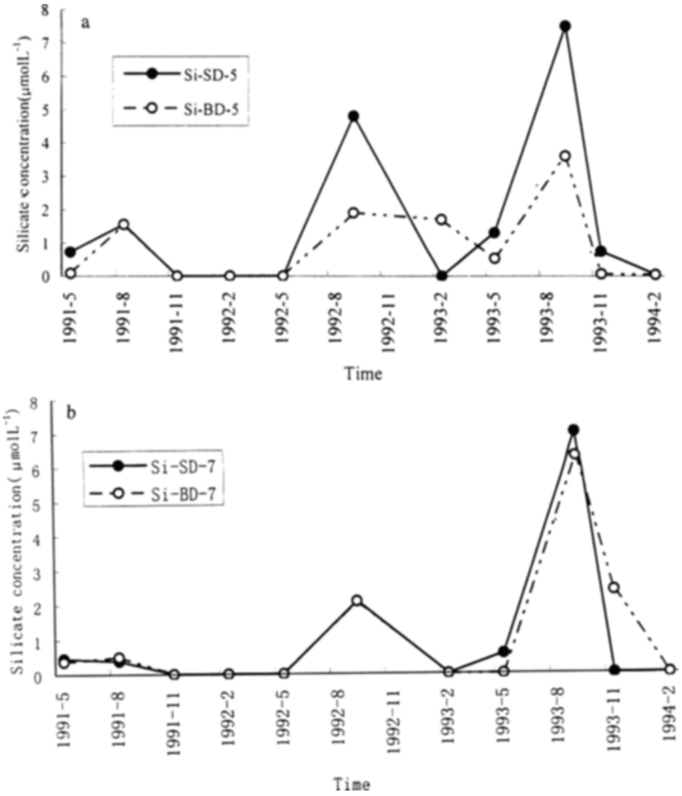

Fig.5 Depth profile of silicate concentration at the surface (SD) and bottom (BD) at Stations 5(a) and 7(b)

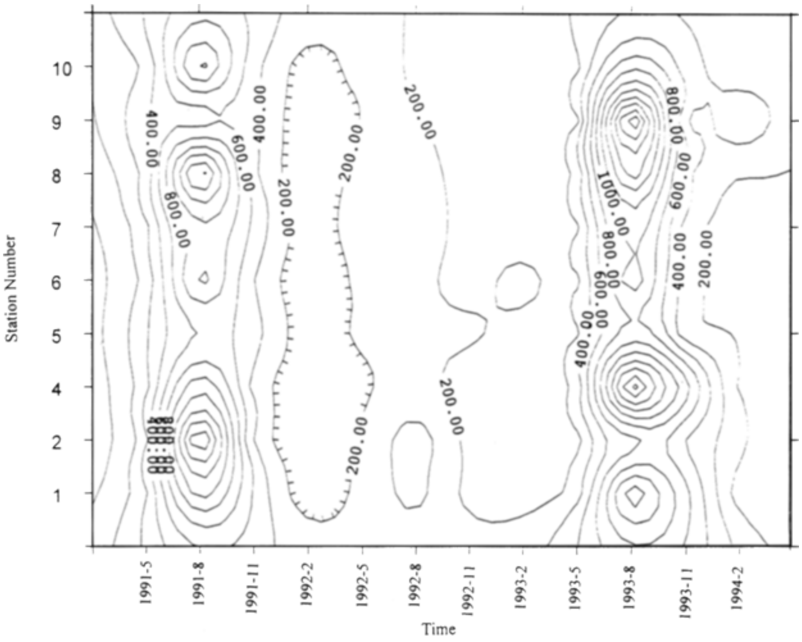

Fig.6 Spatiotemporal distribution of primary production at 9 stations (mgC/(m^2·d))

The distributing features of primary production (Fig.6): Primary production in the outer part (except Station 8) of Jiaozhou Bay was higher than that in the southwest part (Station 8), where primary production was higher than that outside Jiaozhou Bay (Station 10). Between May, 1991 and November, 1994, the annual peak of primary production at Stations 8 and 10 decreased, but increased at Stations 5 and 6. The variations of the annual peak of primary production at Stations 1, 4, 7 and 10 were more significant than those at Station 9.

The primary production had the same horizontal distribution as that of silicate concentration.

Regarding the distributing features of silicate and primary production in the study area, three points should be emphasized.

1. Owing to weather conditions and the difficulty of techniques, every time there was data error from the voyage investigation as the observations data from some stations were not obtained at the same time.

2. The observational dataset obtained four times per year could not be used to simulate natural monthly variations. As the temporal scale of observation was different, the data depicted pattern of natural change in different temporal scale.

3. The monthly observation data in 1984, after being collated and converted to quarterly data, corroborated the results obtained by the use of these quarterly observation data above. Therefore, the results of the analyses of the distributing features of silicate and primary production are considered correct.

Relationship of primary production with silicate concentration and water temperature

(1) Correlation of primary production and silicate concentration

Among the 116 species of phytoplankton identified in Jiaozhou Bay, 100 species of 35 genera were diatoms, 15 species of 3 genera were dinoflagellates and 1 species of 1 genus belonged to Chrysophyta (Guo and Yang, 1992). The predominant species included *Skeletonema costatum* (Grev.) Cl., *Nitzschia pungens* Grun., *Ch. curvisetus* Cl., *Eucampia zoodiacus* Her., *Asterionella japonica* Cl., etc., and were all diatoms (average abundance of about 10^6 individual m^{-3}). In this study, one single species of diatom could reach to more than 50% of the total biomass of phytoplankton in the area. The non-diatomaceous predominant species appeared only in small number in July, August, September and accounted for < 5% of total biomass (Guo and Yang, 1992). So, total biomass of diatoms was almost the total biomass of phytoplankton of Jiaozhou Bay. On the other hand, primary production of non-diatomaceous species accounted for < 5% of total primary production of Jiaozhou Bay (Guo and Yang, 1992).

Although nutrient nitrogen and phosphorous were ample for phytoplankton growth and primary production, Wang and Jiao's (1995) analysis of the spatiotemporal variations of predominantly chemical factors such as NO_3^--N, NO_2^--N, NH_4^+-N, SiO_3^{2-}-Si, PO_4^{3-}-P in Jiaozhou Bay showed that they affected the level of primary production (PP) of the phytoplankton there. During the reproduction process of diatoms, silicon is absolutely necessary. So, the correlation was considered. It was found that there was notable correlation of only silicate concentration with primary production in terms of the time series at all the stations (excluding Stations 2 and 10) in Jiaozhou Bay; and that the variation in the primary production was almost entirely consistent with that of the silicate concentration. But, because of the differences between the variation cycle of nitrogen, phosphorus and primary production, there was no correlation between them (Table 1).

Table 1 Correlation of silicate and primary production

Station	1	2	4	5	6	7	8	9	10
Correlation Coefficient	0.87	0.36	0.62	0.70	0.83	0.74	0.54	0.75	0.34

(2) A dynamic model

To understand the impact of silicate concentration on primary production, a simple model was developed to link silicate and primary production. The model of primary production elucidates the dependence of primary production variation on silicate concentration and water temperature; and quantifies the relation of the dynamic variations in primary production to silicate, and water temperature, in terms of time series, based on which this model was developed with differential equation and statistical data (Fig.7).

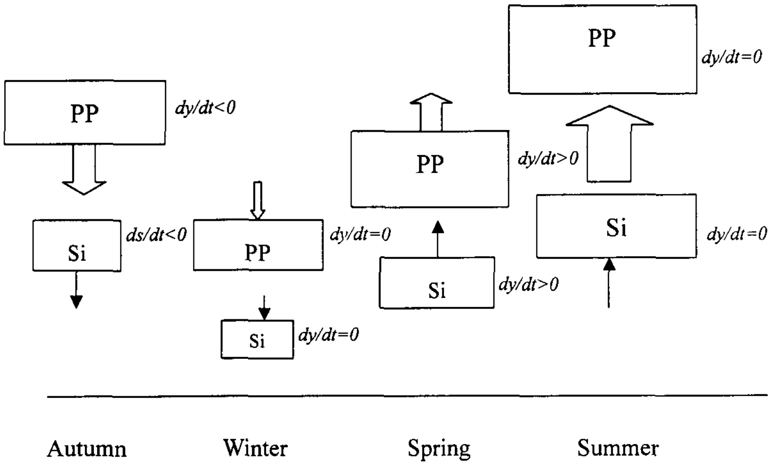

Fig.7 Schematic diagram of the primary production-silicate concentration in the model

The dynamic model describing the primary production and silicate concentration relationship is

$$dy/dt = C\,ds/dt + \pi/6\,D\,\mathrm{Sin}(\pi/6\,t - \pi/3) \qquad (1)$$

The two terms on the right hand side of Eq.(1) stand for the limitation of silicate and water temperature on primary production respectively. The model variables and parameters are, t: variable of time, month; $y(t)$: function of primary production, 33.60 – 2518 mgC/(m^2·d); $s(t)$: function of silicate concentration, 0 – 14.9μmol/L; C: apparent ratio of conversion of silicate in seawater into phytoplankton biomass, 62.92 – 474.85; D: coefficient of water temperature's effect on the primary production of phytoplankton, – 66 – 384.

Jiaozhou Bay data collected every three months from May 1991 to February 1994 were used to calculate C and D, by Eq.(1). Samples taken from July 15 to September 15 were regarded as taken in August (Table 2).

Table 2 Values of the parameters *C* and *D* in Eq.(1)

Station parameter	1	4	5	6	7	8	9
C	154.27	120.02	62.92	173.61	90.46	89.77	474.85
D	187.34	278.61	96.41	-35.49	180.96	384.96	-66.84

The absence of data from Stations 3, 2 and 10 is irrelevant.

The critical value of the correlation coefficient and *F* test results

$$R_{0.05}(10) = 0.671,\ R_{0.01}(10) = 0.776,\ F_{0.05}(2,9) = 4.26,\ F_{0.01}(2,9) = 8.02$$

Eq.(1) applied to Stations 1, 6, 7 is meaningful for $\alpha = 0.01$ and applied to Stations 4, 5, 8, 9 is meaningful for $\alpha = 0.05$ (Table 3).

Table 3 Correlation coefficients of Eq.(1)

Station parameter	1	4	5	6	7	8	9
Correlation efficient	0.88	0.68	0.74	0.82	0.81	0.70	0.69
F value	18.41	4.353	6.377	11.036	9.868	4.863	4.771

(3) Application of the model

The simulated curves for the 7 stations (1, 6, 7, 4, 5, 8, 9) were obtained with the dynamic model of primary production and silicate concentration. The model showed that silicate regulated primary production. The predicted values compared well with measured values. Stations 1 and 7 were randomly selected for comparison between the measured curve PP1, PP7 of primary production at Stations 1 and 7 and the simulated curve PB1, PB7 of primary production at these stations (Fig.8).

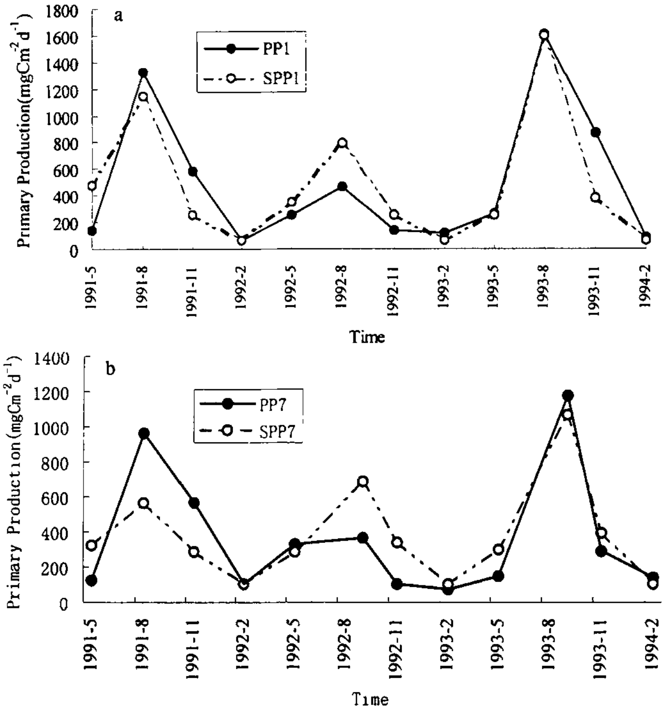

Fig.8 Comparison between curve of measured primary production and simulated curve of Eq.(1) at Stations 1(a) and 7(b)

Curve of measured primary production: PP1 at Station 1, PP7 at Station 7 Simulated curve of Eq.(1): SPP1 at Station 1, SPP7 at Station 7

DISCUSSION

1. Source of silicate

Stations 1, 2 and 4 were close to the Dagu River and Yang River (Fig.1). The seasonal variation curves of the silicate in Jiaozhou bay, the rainfall in its drainage basin, and the runoff of the Dagu River and Yang River corresponded well in cycle, peak value and trend. Moreover, analysis of the features of the horizontal and vertical distribution of silicate indicated further that the variation of the silicate concentration in Jiaozhou Bay was related with the runoff of the Dagu River and Yang River; and that the runoff into the bay provided abundant amount of silicate.

In summer, silicate concentrations at Stations 1, 2 and 4 in the estuary were higher than those at the other stations in Jiaozhou Bay; and the silicate concentrations at the surface and bottom layer were horizontally uniformly distributed; which provided evidence that runoff carried abundant silicate into the bay; and that the silicate concentration was vertically well mixed near the shore. The silicate concentrations at Stations 5, 6 and 7 were lower than those at Stations 1, 2 and 4. And the silicate concentrations at the surface layer at Stations 4, 5 and 6 being higher and bottom concentrations being constant showed that the silicate concentration decreased from the estuary nearshore to the bay center; and that there was abundant silicate at the surface in summer. Maximal Jiaozhou Bay tide velocity was observed (150 m/s – 170 m/s) at Station 7 at the inner bay mouth with silicate concentration vertically well mixed but gradually decreasing. Silicate concentrations at the bay mouth and outside it (Stations 8, 9 and 10) were much lower than those inside Jiaozhou Bay. Silicate concentrations at Station 10 outside the bay was lower than that of all stations inside the bay; and at the bottom layer was higher than that at the surface layer. So, it was obvious that biochemical action and water exchange transported silicon from the estuaries to the mouth of and then outside the bay and sedimented it there (Dugdale et al., 1995). After runoff brings abundant silicate into Jiaozhou Bay, because of its dilution by the bay's silicate-poor seawater, and uptake by diatoms, the silicate concentration trended to gradually decrease in the order estuary > bay center > bay mouth > outside bay.

2. Distribution features of primary production and silicate

Analysis of observation data obtained from May, 1991 to February, 1994 showed that in summer, Jiaozhou Bay silicate concentrations were in the order; the estuary (Stations 1, 2 and 4) > southwest part (Station 8) of Jiaozhou Bay > outside Jiaozhou Bay (Station 10). The horizontal distribution of primary production had the same trend as that of silicate concentration. The estuarine waters (Stations 1, 2 and 4) were areas of high primary production. In winter, the primary production of the whole of Jiaozhou Bay did not vary significantly; in estuarine waters (Station 1,2,4), primary production (63.32 – 103.96 $\mathrm{mgC/(m^2 \cdot d)}$) was the median of that in the Bay.

The spatiotemporal variation patterns in silicate concentration and primary production of all the nine stations were almost identical (Fig.4, Fig.6).

In the monthly investigations in Jiaozhou Bay in 1984, it was found that at the end of June, in the waters within the estuaries of the Dagu River and Yang River, the primary production reached the highest value [2177 $\mathrm{mgC/(m^2 \cdot d)}$] of Jiaozhou Bay (Guo and Yang, 1992). An important finding in this work was that the variation in the primary production in estuarine waters of the Dagu, Yang and Licun Rivers controlled the variation of the primary production of the whole bay. In addition, the trend of the variation in the primary production outside the bay was similar to that inside the bay in summer and slowed down one and half months earlier than that inside the bay in autumn. Also, at the end of January in 1984, the primary production throughout Jiaozhou Bay was 20 – 30 $\mathrm{mgC/(m^2 \cdot d)}$; the difference of the primary production in bay waters was small. These observations indicated that the horizontal distribution patterns of the primary production and silicate varied alsmost identically in all the seasons.

3. Ecological significance of the model

C and D in Eq.(1) are analyzed

From Table 2, with $C > 0$, it can be deduced that a prerequisite for phytoplankton primary production is their assimilation of available silicate.

The coefficient D is discussed below on the basis of Table 2.

When $D > 0$, the analysis is as given below:

The silicate concentration is lowest in February every year; $ds/dt = 0$, and the water temperature is lowest in February (Weng et al., 1992); $\pi/6\ D\ \mathrm{Sin}(\pi/6\ t - \pi/3) = 0$. So $dy/dt = 0$, which means that the primary production reaches minimum.

The time changes from February to August every year. On the right side of Equation (1), when $\pi/6\ D\ \mathrm{Sin}(\pi/6\ \mathrm{t} - \pi/3)$ is positive, this means that as the temperature rises, primary production increases. When the apparent conversion ratio $C > 0$ and silicate concentration increases, $ds/dt > 0$, which means that as the silicate concentration increases, the primary production increases. Hence, on the left hand side of Eq.(1), $dy/dt > 0$, which means that the primary production increases.

When the silicate concentration maximizes in August every year, $ds/dt = 0$; and when the water temperature maximizes in August (Weng et al., 1992), $\pi/6\ D\ \mathrm{Sin}(\pi/6\ t - \pi/3) = 0$. So, $dy/dt = 0$, which means that the primary production reaches maximum.

The time changes from August to February in the second year. On the right hand side of Eq.(1), when $\pi/6$ D $\mathrm{Sin}(\pi/6\ t - \pi/3)$ is negative, which means that as the temperature falls, the primary production decreases. When the apparent conversion ratio $C > 0$ and the silicate concentration decreases, $ds/dt < 0$, which means that the silicate concentration decreases, and that the primary production decreases. Hence, on the left hand side of Eq.(1), $dy/dt < 0$, which means that the primary production decreases.

Structure analysis of Eq.(1) showed that the predominant species of the phytoplankton assemblage at stations where $\mathrm{D} > 0$ tended to be oligothermal, and were made up of warm species.

When $D = 0$, the analysis is as given below:

Phytoplankton growth is adaptable to a very wide variation range of temperature or is little affected by the variation of temperature. In this case, the variation of phytoplankton is mostly determined by the variation of silicate.

The predominant species of the phytoplankton assemblage at stations where $D = 0$ tended to be eurythermal, and was composed mainly of eurythermal species.

When $D < 0$, the analysis is as given below:

The time changes from February to August every year. On the right hand side of Eq.(1), when $\pi/6\ D\ \mathrm{Sin}(\pi/6\ t - \pi/3)$ is negative, or as the temperature rises, the primary production decreases. When $C > 0$ and the silicate concentration increases, $ds/dt > 0$, which means that as the silicate concentration increases, the primary production increases. However, on the left hand side of Eq.(1), $dy/dt > 0$, which means that the primary production increases.

The time changes from August to February in the second year. On the right hand side of Eq.(1), when $\pi/6\ D\ \mathrm{Sin}(\pi/6\ t - \pi/3)$ is positive, or as the temperature falls, the primary production increases. When $C > 0$ and the silicate concentration decreases, $ds/dt < 0$, which means that as the silicate concentration decreases, the primary production decreases. However, on the left hand side of Eq.(1), when $dy/dt < 0$, the primary production decreases.

Similarly, the primary production minimizes in February and maximizes in August.

At stations where $D < 0$ the assemblage tended to be oligothermal and was mainly made up of cold species.

The above discussion of cases when $D > 0$, $D = 0$, especially $D < 0$ clearly shows that silicate concentration and water temperature in combination controlled the quantity of primary production and that the main controlling factor was still nutrient silicon. But when silicate tended to be exhausted, water temperature level controlled the variation of primary production, but at this time the variation of primary production was very minimal. Eq. (1) was differentiated to obtain

$$d^2y/dt^2 = C\,d^2s/dt^2 + \pi^2/36\,D\,Cos\,(\pi/6\,t - \pi/3) \tag{2}$$

When $D > 0$, it can be deduced from Eq.(2) that when the variation rate of silicate concentration fell from May to November every year, $d^2s/dt^2 < 0$, and Cos $(\pi/6\,t - \pi/3) < 0$. Hence, $d^2y/dt^2 < 0$, which means that the variation rate of primary production fell. When the variation rate of silicate concentration rose from November to May in the second year, $d^2s/dt^2 > 0$, and Cos $(\pi/6\,t - \pi/3) > 0$. Hence, $d^2y/dt^2 > 0$, which means that the variation rate of primary production rose. When the silicate concentration reached maximal rate of rise in May every year, $d^2s/dt^2 = 0$, and Cos $(\pi/6\,t - \pi/3) = 0$. Hence, $d^2y/dt^2 = 0$, which means that primary production reached the maximal rate of rise in May. When the silicate concentration reached the maximal rate of fall in November every year, $d^2s/dt^2 = 0$, and Cos $(\pi/6\,t - \pi/3) = 0$. Hence, $d^2y/dt^2 = 0$, which means that primary production reached the maximal rate of fall in November.

The case when $D = 0$ or $D < 0$ can be discussed in the same way and the result will be the same as that above.

Eq.(2) of the model shows that the maximum rate of rise (fall) rate of the PP (silicate concentration) was in the May (November) rainy season, when the Dagu and Yang rivers(the main rivers flowing into Jiaozhou Bay) bring abundant supply of silicate.

The relation of C, the apparent ratio of conversion of silicate in seawater into phytoplankton biomass and D, the coefficient of water temperature's effect on phytoplankton primary production.

When $D > 0$, D is termed as the coefficient of suitable temperature's effect on the growth of phytoplankton; C reached lowest value of 62.92 – 154.27.

When $D = 0$, C reached the median value.

When $D < 0$, D is termed as the coefficient of unsuitable temperature's effect on phytoplankton growth; C reached the highest value of 173.61 – 474.85.

The phytoplankton assemblage has different ecological niche for C and D (Fig.9). C and D divide

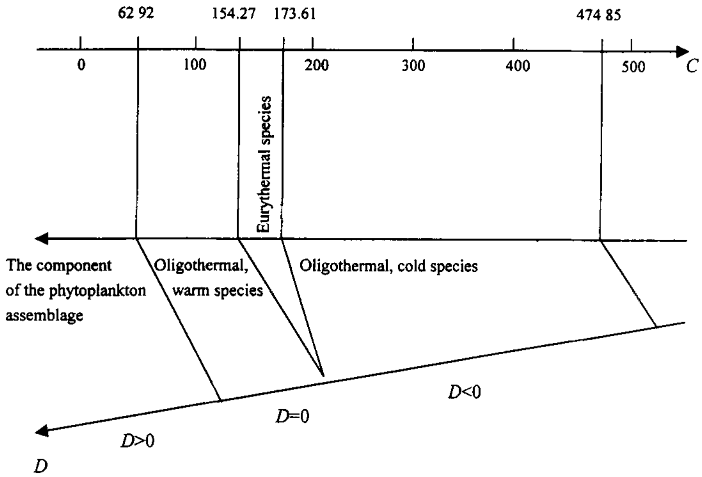

Fig.9 Different populations of the phytoplankton assemblage in Jiaozhou Bay occupy different ecological niches for C, the apparent ratio of conversion of silicate in seawater into phytoplankton biomass and D, the coefficient of water temperature's effect on primary production

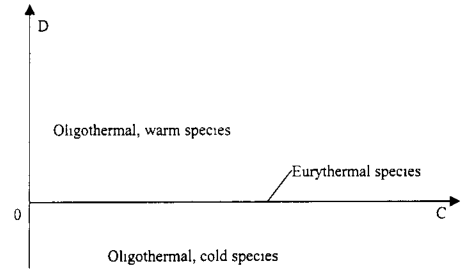

Fig. 10 The phytoplankton increasing primary production by assimilating silicon are divided into three parts: oligothermal, warm species; oligothermal, cold species; and eurythermal species

the phytoplankton assemblage into different components (Table 4). The different populations of the phytoplankton assemblage occupy different ecological niches for C and D, which keeps the stability of Jiaozhou Bay's ecological system.

In Eq.(1), C (>0) and D are regarded as the horizontal axis and vertical axis respectively in the coordinates. Thus, the phytoplankton increasing primary production by assimilating silicon is divided into three parts (Fig.10).

Plane SW stands for oligothermal, warm species. Plane SC stands for oligothermal, cold species. The positive axis of C stands for eurythermal species. Then, by C, D, the area of the ecological niche occupied by the phytoplankton in Jiaozhou Bay is separated (Fig.11).

Table 4 The relation of C, the apparent ratio of conversion of silicate in seawater into phytoplankton biomass and D, the coefficient of water temperature's effect on phytoplankton primary production

C	$C > 0$ (62.92 - 154.27)	$C > 0$(154.27 - 173.61)$^{a)}$	$C > 0$ (173.61 - 474.85)
D	$D > 0$ (384.96 - 96.41)	$D = 0$	$D < 0$ (- 35.49 - - 66.84)
The component of the phytoplankton assemblage	Oligothermal, warm species	Eurythermal species	Oligothermal, cold species

a) Excluding the two values 154.27, 173.61.

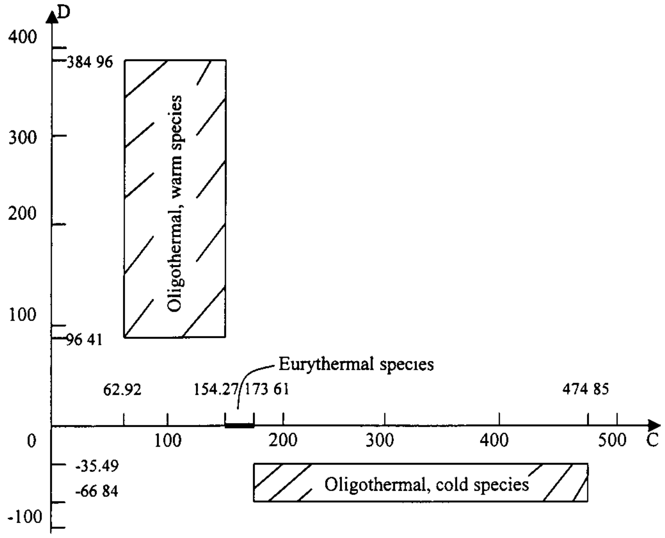

Fig. 11 The areas of the niches occupied by different populations of the phytoplankton assemblage in Jiaozhou Bay are separated by C, the apparent ratio of conversion of silicate in seawater into phytoplankton biomass and D, the coefficient of water temperature's effect on phytoplankton primary production

Study of Eq.(1) showed that the C values are spread over the whole range of real numbers.

The phytoplankton assemblage composed of plane COD (Fig.12).

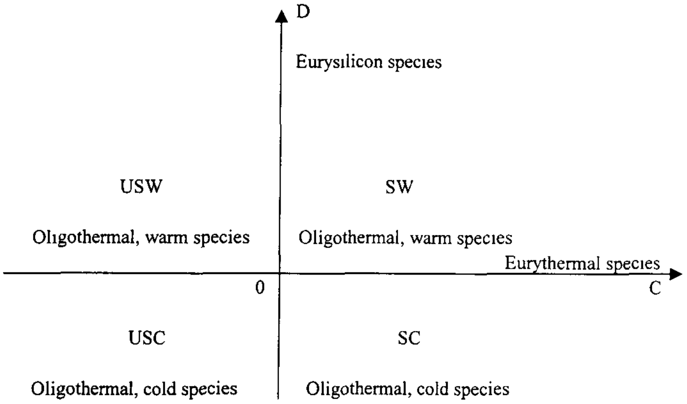

Fig.12 The phytoplankton assemblage is composed of plane COD in the range of the whole real numbers for C and D values

Plane $C > 0$ = plane SC + SW denotes the phytoplankton increasing primary production by assimilating silicon.

$C = 0$, namely axis D, denotes the phytoplankton whose growth is not affected by silicon.

Plane $C < 0$ = plane USC + USW denotes phytoplankton decreasing primary production by assimilating silicon.

Plane $D > 0$ = plane USW + SW denotes phytoplankton composed of oligothermal, warm species.

$D = 0$, namely axis C, denotes eurythermal phytoplankton with growth not affected by water temperature.

Plane $D > 0$ = plane USC + SC denotes phytoplankton composed of oligothermal, cold species.

After the range of C and D values is calculated with relevant data, the character of the phytoplankton assemblage may be known. Similarly, the range of C and D values is estimated by investigation of the component of the phytoplankton assemblage in the waters.

So, the results of the above analysis by Eqs (1) and (2) is generally consistent with that of the real case. It is known that the dynamic cycles, characteristics and trends of primary production and silicate concentration, have close relation with silicate and diatom structure and metabolism. Diatoms have an absolute requirement for silicon (Lewin, 1962), without which valves are not formed, and the cell cycle is not completed (Brzezinski et al., 1990; Brzezinski, 1992). Silicate may control phytoplankton processes in important regions of the ocean such as in coastal upwelling areas (Dugdale and Goering, 1967; Dugdale, 1972, 1985; Dugdale, et al., 1981; Dugdale and Wilkerson, 1998) and Antarctic seas (Sakshaug et al., 1991). In these and other marine waters, silicate plays a central role in phytoplankton bloom development (Conley and Malone, 1992). The above analyses based on Eqs (1) and (2) indicated that silicate is a limiting factor for the growth of phytoplankton in Jiaozhou Bay.

4. Silicate and predominant species of phytoplankton

In terms of the ecological environment, the phytoplankton annual average density in the bay is 8×10^6 individual m^{-3}, indicating Jiaozhou Bay is one of the high phytoplankton density areas in China. Inside the bay, the phytoplankton are mainly diatoms with small cells (Guo and Yang, 1992). The predominant phytoplankton species in Jiaozhou Bay in winter is *Asterionella japonica* Cl., the mean number of which in February is 10^7 individual m^{-3}. The *Asterionella japonica* Cl., cold species is abundant in Jiaozhou Bay from December to March; and the most suitable temperature for its reproduction is 4 – 6℃ (Table 5).

Table 5 Chl-a, silicate and primary production measured at the same time and place

Station	4(Feb.1993)	5(Feb.1992)	6(Feb.1993)
Chlorophyll-a (mgC/m^3)	4.15	3.71	8.39
Temperature (℃)	3.535	4.58	3.43
Silicate-Si (μmol/L)	-	-	0.89
Primary Production (mgC/(m^2·d))	76.56	103.85	309.4
PO_4-P(μmol/L)	0.275	0.38	0.46
NO_3^- N(μmol/L)	1.7	0.9	2.95
NO_2^- N(μmol/L)	0.3	0.2	0.41
NH_4-N(μmol/L)	6.7	9.6	12.40

- : Silicate concentration below 0.05 μmol/L is termed as zero

Table 5 lists the chlorophyll-a, temperature, silicate and primary production measured at the same time and place. *Asterionella japonica* Cl. has more chlorophyll-a under the suitable temperature for its reproduction. In February in winter, daytime lasts for around 11.3 hours, the irradiance is enough, the chlorophyll-a is high, the temperature is suitable, and the nitrogen and phosphorous are ample for the predominant species *Asterionella japonica* Cl. in Jiaozhou Bay. However, the silicate concentration is very low, resulting in the low primary production of *Asterionella japonica* Cl. Therefore, silicon is a limiting factor for its growth.

5. Relation of transparency of marine water and primary production

The spatial distribution of the transparency of Jiaozhou Bay is relatively ordered; the distribution of the transparency line generally parallels that of the fathom line (Weng et al., 1992). The transparency inshore is low, while that offshore and in the area of the bay mouth is high (Weng et al., 1992). The spatial distribution of the transparency is opposite that of primary production, indicating that the variation of primary production is due to the variation of the coastal nutrients, not to the variation of the euphotic layer's thickness.

In winter (January - March), the transparency in the coastal area of Jiaozhou Bay is lower than 1.5 m, while in summer (July - September), that in almost all the regions of north and northeast of Jiaozhou Bay is low, lower than 1.0 m (Weng et al., 1992). Thus, in the regions north and northeast of Jiaozhou Bay, the transparency of the seawater in winter is higher than that in summer. However, the primary production in summer is much higher than that in winter. Analysis of the spatial distribution and seasonal variation of the transparency of seawater and primary production of Jiaozhou Bay showed that the effect of the seawater transparency on primary production in Jiaozhou Bay is not remarkable.

6. Structure of phytoplankton

That silicate is the limiting factor for primary production explains the ecological phenomena. It was noticeable that in the southwest part of the bay Station 8 (Station E1), the predominant components of phytoplankton were different from the others in ecological character. There the proportion of the predominant warm species *Ceratium macrocers* Cl. to total phytoplankton biomass increased obviously from July, a month earlier than that in the other stations in Jiaozhou Bay. Moreover, the growth of the predominant *Asterionella japonica* Cl. in winter in the bay's southwest (Station 8) was delayed for two months compared with that of the station near it inside Jiaozhou Bay, even three months compared with that at the north stations inside Jiaozhou Bay (Guo and Yang, 1992).

It is known that the silicate concentration of the southwest part of Jiaozhou Bay is lowest in the bay. First, In February, inside Jiaozhou Bay , the temperature was lower by 0.2 - 0.8℃ than that 3.5 - 4.5℃ in the southwest part (Station 8) of the bay. For the growth of *Asterionella japonica* Cl., the suitable temperature is 4 - 6℃. However, its growth in the southwest was delayed by two months that inside Jiaozhou Bay; its reproduction was slow; because the silicate concentration was low in the southwest (Station 8). Secondly, from July to September, water temperature inside Jiaozhou Bay was 2℃ higher than that in the southwest part of Jiaozhou Bay. The predominant species inside the bay were *Eucampia zoodiacus* Her., *Skeletonema costatum* Cl., etc. belonging to the diatoms. However, the warm species, *Ceratium macrocers* Cl, which does not belong to diatoms, grew in the southwest (Station 8), where diatoms were expected to grow. The much lower silicate concentration in the southwest part of the bay explains this phenomenon.

The above findings clearly showed that silicate is a limiting factor for phytoplankton primary production.

7. Deficit process of nutrient silicon

It is supposed that the terrestrial source silicate's decreasing from the estuary nearshore to the Jiaozhou Bay mouth is due to the dilution of current and the uptake of phytoplankton. In addition, the average value of the silicate concentrations at the Stations 1, 4 and 8 along the transect from the nearshore of the estuaries to the mouth of Jiaozhou Bay may be considered as representative of the silicate concentration of the whole bay. And the average value of the silicate concentrations at Stations 9 and 10 can be considered to be representative of silicate concentration of the bay mouth, where the highly concentrated silicate from the estuaries is diluted by bay current and assimilated by phytoplankton. The calculated concentration of the silicate inside the bay and the diluted silicate concentration at the mouth of the Jiaozhou Bay due to dilution by the seawater exchange were compared in order to analyze and figure out the quantity of the silicate assimilated by phytoplankton, the intrinsic ratio of conversion of silicate into phytoplankton biomass and the proportion of silicate uptaken by phytoplankton to silicate uptaken by dilution current of silicate poor seawater in Jiaozhou Bay.

In summer, the dilution by current and the uptake by phytoplankton considerably reduce the silicate concentration. First, the variation in silicate concentration due to water exchange was calculated to determine the quantity of silicon assimilated by phytoplankton in Jiaozhou Bay. Salinity was chosen as the index for calculating seawater exchange. The average of the precipitation, evaporation and runoff in one tidal cycle, compared with the quantity of tidewater through the bay mouth in the corresponding time, were obviously very minimal; so, all three were neglected in calculating the water exchange (Wu et al., 1992).

The link between Tuan Island and Xuejia Island (through Station 9) was considered as the transect through the bay mouth. The total volume V_T of the seawater inside Jiaozhou Bay was

$$V_T = 3.021 \times 10^9\ m^3$$

The volume V_1 of the outside seawater flowing into the bay in the process of one flood tide is

$$V_1 = 9.45 \times 10^8\ m^3 \qquad \text{(Wu et al., 1992)}$$

So, $V_1 / V_T = 9.45 \times 10^8 / 3.021 \times 10^9 = 0.31$

So the volume of the outside seawater flowing into the bay was about one-third of the total volume of the seawater inside Jiaozhou Bay.

The average value ($Siso$) of the silicate concentrations ($Si1, Si4, Si8$) at Stations 1, 4 and 8 was regarded as the silicate concentration of the whole of Jiaozhou Bay, and the amount of silicate inside the Jiaozhou Bay was

$$Siso = (Si1 + Si4 + Si8)/3 \times (1 - 0.31)\, V_T$$

The silicate concentration ($Sidi$) (μmol/L) inside Jiaozhou Bay was diluted by the outside seawater flowing into the bay, so

$$Sidi = Siso / V_T = 0.23\ (Si1 + Si4 + Si8)$$

The average value (*Sime*) of the silicate concentrations at Stations 9 and 10 was regarded as the measured silicate concentration (μmol/L) at the bay mouth:

$$Sime = (Si9 + Si10)/2$$

The difference(*Sidi* − *Sime*) of the silicate concentration (μmol/L) explains that the silicate from the summer runoff was diluted by the water exchange and assimilated by phytoplankton, resulting in reducing the silicate concentration in seawater of the bay.

In summer, the silicate (*Sidi* − *Sime*) assimilated by phytoplankton was a certain proportion of the silicate (*Sidi*) diluted by the water exchange in the bay seawater,

$$Sipr = (Sidi - Sime)/Sidi \times 100\%$$

During summer, the proportion of silicate assimilated by phytoplankton to the silicate diluted by the water exchange in seawater of the bay was less than one − fifth (Table 6).

Table 6 The values of the diluted and measured silicate

	Aug.11,1991	Sept.2,1992	Aug.11,1993
Sidi (μmol/L)	1.500	2.425	4.041
Sime (μmol/L)	1.217	2.273	3.198
(*Sidi* − *Sime*)	0.283	0.152	0.842
Sipr	18%	6%	20%

In summer, the silicate assimilated in the bay in one day was about.

$$Sitotal = (Sidi - Sime) \times V_T$$

The intrinsic conversion rate of the nutrient silicate is defined as the quantity of the primary production obtained by assimilating per unit of silicate, namely the specific value of the phytoplankton primary production and the assimilated silicate quantity:

$$Q = PPtotal/Sitotal \qquad \text{(Table 7)}$$

Table 7 The intrinsic conversion rate of the nutrient silicate in Jiaozhou Bay into phytoplankton biomass

	Aug.11,1991	Sept.2,1992	Aug.11,1993
Sitotal (μmol/d)	0.856×10^{12}	0.461×10^{12}	2.54×10^{12}
PPtotal (mgC/d)	4.649×10^{11}	1.289×10^{11}	5.832×10^{11}
Q (mgC/μmol)	0.542	0.279	0.229
Sitotal (t/d)	24.748	13.33	73.58

In summer the variations of the diluted silicate concentration (*Sidi*) inside Jiaozhou Bay (μmol/L) and the measured silicate concentration(*Sime*) at the bay mouth (μmol/L) were almost the same, with the correlation of *Sidi* and *Sime* being high (0.98); which indicated that the terrestrial source silicate affected the variations of *Sidi* and *Sime* at the same time, and further proved that the runoff into Jiaozhou Bay provided abundant silicate.

The variations of silicate concentration (*Sitotal*) and variations of the corresponding primary production (*PPtotal*) were highly correlated (coefficient of 0.81); which indicated that the quantity of the silicate assimilated by phytoplankton and the primary production produced by phytoplankton were closely linked; that is, the quantity of the silicate assimilated by phytoplankton determined the quantity of primary production. Moreover, this was consistent with the output of the primary production, silicate, and water temperature of the dynamic model of Jiaozhou Bay.

The variations of the intrinsic conversion ratio *Q* of nutrient silicon of phytoplankton and the variations of PPtotal were unrelated. Perhaps this result also showed that the intrinsic conversion ratio of nutrient silicon into phytoplankton biomass is determined by phytoplankton itself.

In summer, the quantity of silicate assimilated by the bay's phytoplankton was about 13.33 - 73.58 t/d. The intrinsic conversion rate of silicon into phytoplankton biomass was 0.229 - 0.542 (mgC/μmol) and the proportion of the quantity of silicon uptaken by phytoplankton and diluted by the water exchange was 6:94 - 20:80.

CONCLUSION

After analysis of May 1991 to February 1994 Jiaozhou Bay data, and taking into consideration the spatiotemporal variations in temperature, light, nutrients (NO_3^--N, NO_2^--N, NH_4^+-N, SiO_3^{2-}-Si, PO_4^{3-}-P), phytoplankton and primary production in Jiaozhou Bay, the authors succeeded in determining the spatiotemporal variation patterns in SiO_3^{2-}-Si and primary production of Jiaozhou Bay. The results indicated that only silicate correlated well in time and space with primary production and had important effect on the characteristics, dynamic cycles and trends of primary production in Jiaozhou Bay; and subsequently developed a corresponding dynamic model of Primary Production-Silicate-Water Temperature in order to prove further the result. Eq.(1) of the model presents the dynamic process of the variation of the primary production controlled by that of the nutrient Si and affected by that of water temperature. Analysis of Eq. (1), and other findings obtained in this study showed that the main controlling factor of phytoplankton primary production is nutrient Si; that water temperature affects the composition of the phytoplankton assemblage structure; and that different populations of the phytoplankton assemblage occupy different ecological niches. Analyzed and probed in this study were the silicon source of Jiaozhou Bay and the biogeochemical process of the silicon in sediment; the predominant species, and the structure of phytoplankton. The conclusion is that silicon is a limiting factor of primary production in Jiaozhou Bay. The model derived in this work showed that silicate regulates primary production (PP); and that the model's predicted values of silicate, compared well with measured values. The variation of the PP was consistent with that of the silicate concentration. Eq. (2) of the model showed that the maximum growth (reduction) rate of the PP and of silicate concentration was in May (November). Abundant amount of silicate is brought into Jiaozhou Bay by the starting in May and ending in November runoffs in the rainy season. Waters farther from the coast with river mouth have relatively lower silicate concentration, which might be caused by the large-scale subsidence of silicate, its uptake by phytoplankton and dilution by current. In other words, biochemical processes continuously shifts silicon to the bottom.

The author holds that: First, the silicate concentration of waters far from the coast with estuaries, with low inflow and a narrow continental shelf, must be low and largely invariant with time. Second, the diatoms-silica-shelled primary production and biomass is low in the silicon-limited provinces. Third, the death and resulting decomposition of phytoplankton in and coming into silicon-limited waters produce relatively labile nitrogen and phosphorous. However, silicate concentration stays at low value due to its large-scale subsidence. So, with the nitrate and phosphate continuously increasing and silicate continuously decreasing, some waters present apparently high plant-nutrient concentrations but low phytoplankton biomass. The ecosystem can be turned to be silicon-limited in primary production.

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References

Brzezinski, M. A., 1992. Cell-cycle effects on the kinetics of silicic acid uptake and resource competition among diatoms. *Journal of Plankton Research* 14: 1511 - 1536.

Brzezinski, M. A., Olson, R. J., Chisholm S.W., 1990. Silicon availability and cell-cycle progression in marine diatoms. *Marine Ecology Progress Series* 67: 83 - 96.

Chen, C., Wiesenbury, D. A., Xie, L., 1997. Influence of river discharge on biological production in the inner shelf: A coupled biological and physical model of the Louisiana-Texas Shelf. *J. Mar. Res.* 55: 293 - 320.

Conley, D. J., Malone, T. C., 1992. Annual cycle of dissolved silicate in Chesapeake Bay: implications for the production and fate of phytoplankton biomass. *Marine Ecology Progress Series* 81: 121 - 128.

Dong, Jinhai, Jiao, Nianzhi, 1995. Ecology Resources preface of Jiaozhou Bay *In*: Dong Jinhai, Jiao Nianzhi, ed. Ecology Resources of Jiaozhou Bay, Science Press Beijing, p. 2 - 6. (in Chinese)

Dugdale, R. C., 1972. Chemical oceanography and primary productivity in upwelling regions. *Geoforum* 11: 47 - 61.

Dugdale, R. C., 1985. The effects of varying nutrient concentration on biological production in upwelling regions. *CalCOFI Report* 26: 93 - 96.

Dugdale, R. C., Goering, J. J., 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography* 12: 196 - 206.

Dugdale, R. C., Jones, B. H., Macclsaac, J. J. et al., 1981. Adaptation of nutrient assimilation. *In*: Platt, T., ed., physiological bases of phytoplankton ecology. *Canadian Bulletin of Fisheries and Agriculture Sciences* 210: 234 - 250.

Dugdale, R. C., Wilkerson, F. P., Minas, H. J., 1995. The role of a silicate pump in driving new production. *Deep-Sea Res(I)* 42(5): 697 - 719.

Dugale, R. C., Wilkerson, F. P., 1998. Silicate regulation of new production in the equatorial Pacific upwelling. *Nature* 391(6664): 270 - 273.

Guo, Yujie, Yang, Zeyu, 1992. Biological environment in Jiaozhou Bay: primary productivity. *In*: Ruiyu Liu, ed., Ecology and Living Resources of Jiaozhou Bay ,Science Press, Beijing, p. 110 - 125. (in Chinese)

Jeffery, S. W., Humphery, G. P., 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 on higher plant, algae and natural phytoplankton,Biochem,Physiol. *Pflanzen* 167: 191 - 194.

Lewin, J. C., 1962. Silicification. *In*: Lewin, R. E., ed., Physiology and biochemistry of the algae, Academic Press, Oxford. p. 445 - 455.

Sakshaug, E., Slagstad, D., Holm-Hansen, O., 1991. Factors controlling the development of phytoplankton blooms in the Antarctic Ocean- a mathematical model. *Marine Chemistry* 35: 259 - 271.

Shen, Zhiliang, 1995. The study of nutrient change of Jiaozhou Bay. *In*: Dong Jinhai and Jiao Nianzhi ed., Ecology Resources of Jiaozhou Bay, Science Press, Beijing, p. 47 - 51. (in Chinese)

Wang, Rong, Jiao, Nianzhi, Li, Chaolong et al., 1995. Primary productivity of Jiaozhou Bay and new productivity, *In*: Dong Jinhai and Jiao Nianzhi ed. Ecology Resources of Jiaozhou Bay, Science Press, Beijing, p. 125 - 135. (in Chinese)

Weng, Xuechuan, Zhu Lanbu, Wang Yifei, 1992. Physical Oceanography: The structure and change of water temperature factor. *In*: Ruiyu Liu, ed., Ecology and Living Resources of Jiaozhou Bay, Science Press, Beijing, p. 33 - 37. (in Chinese)

Wu, Jiacheng, Wang, Congmin, Zhang, Yien et al., 1992. Physical Environment of Jiaozhou Bay: Seawater exchange and blending pervasion. *In*: Ruiyu Liu, ed. Ecology and Living Resources of Jiaozhou Bay. Science Press Beijing, p.57 - 72 (in Chinese)

Wu Yulin, Zhang, Yongshan, 1995. Chlorophyll-a of Jiaozhou Bay and characteristic distribution of primary productivity. *In*: Dong Jinhai and Jiao Nianzhi ed., Ecology Resources of Jiaozhou Bay, Science Press, Beijing, p. 137 - 149. (in Chinese)

Zhang, Junshun, Shen, Zhiliang, 1997. The study of nutrient structure change of Jiaozhou Bay. *Oceanol. et Limnol. Sin.* **285**:529 - 535. (in Chinese)