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Comparison of Temperature Adaptation Patterns of Subtropical/tropical, Subantarctic and Antarctic Phytoplankton Communities.

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Abstract Carbon incorporation rate of natural phytoplankton communities in the Southern Hemisphere was measured using ^{14}C radioisotope under different temperature conditions including at *in situ* temperature. Photosynthetic activity of both the subtropical/tropical and the subantarctic regions decreased with raising and lowering of incubation temperature, *i.e.*, the communities north of the Polar Front attained the maximum photosynthetic activity at *in situ* temperatures. However, the decreasing trend in the calculated assimilation number at raised and lowered temperature was different between the subtropical/tropical and the subantarctic communities; the former showed a sharp decrease than the latter. These results may reflect the difference in seasonal temperature variation of each latitudinal sea region; usually stable temperature condition is expected in the subtropical/tropical region, while there exist relatively a large seasonal temperature variation in the subantarctic region. On the other hand, the photosynthetic activity of antarctic phytoplankton community south of the Polar Front increased *ca.* 1.5 times with raising of incubation temperature up to *ca.* 10°C compared to those at *in situ* temperature. This implies that photosynthesis of the antarctic phytoplankton is suppressed by the ambient sub-zero temperature. It can be concluded that phytoplankton communities in the respective regions in the Southern Hemisphere are considered to have been adapted to the respective environmental temperature conditions.

Key words: adaptation, chlorophyll, photosynthesis, phytoplankton, Southern Hemisphere, temperature

INTRODUCTION

It has been stated for the past two decades that phytoplankton biomass in the antarctic sea region is fairly low in spite of both sufficient nutrients and ample light (referring only for the summer season) for their growth (Holm-Hansen *et al.*, 1977; Franceschini, 1978). Yamaguchi *et al.* (1985) have reported that the irradiance of sun light is not a limiting factor of phytoplankton photosynthesis in the antarctic sea region in austral summer, on the basis of the experimental results which showed maximum photosynthetic rate under the condition of 50-64 % reduced light intensities to that of the surface layer. Neori and Holm-Hansen (1982) reported that phytoplankton community in the antarctic region increased their photosynthetic activity with raising water temperature up to 7°C. Yamaguchi *et al.* (1985) also obtained a similar experimental result showing the increase of assimilation number with increasing temperature, and the maximum rate at 7.5-10°C. Their results may indicate a common implication that the community in the antarctic region is consisted of many obligate

psychrophilic phytoplankton species.

During the cruise of the **"BIOMASS"** project, I carried out the photosynthetic experiments using ^{14}C radioisotope for natural phytoplankton assemblages with raising and lowering the experimental temperature other than the *in situ* temperature of respective sea regions from antarctic to tropic. Not only the natural phytoplankton community of antarctic region but also those in the tropical, subtropical and subantarctic regions revealed several interesting physiological features due to temperature change. The focus of this paper is to compare the adaptation patterns of natural phytoplankton communities to the environmental temperature in the respective regions from high to low latitudes of the Southern Hemisphere, particularly on their photosynthetic activity, and discuss the reason why they have acquired such different response patterns in the viewpoints of the seasonal change in temperature of the present age.

MATERIALS AND METHODS

Surface seawater was collected at 10 different stations in the Southern Hemisphere during the **"BIOMASS"** cruise of R.V. Hakuho Maru, from November 22, 1983 to February 24, 1984 (Fig. 1). Temperature of the seawater was measured using a mercury thermometer.

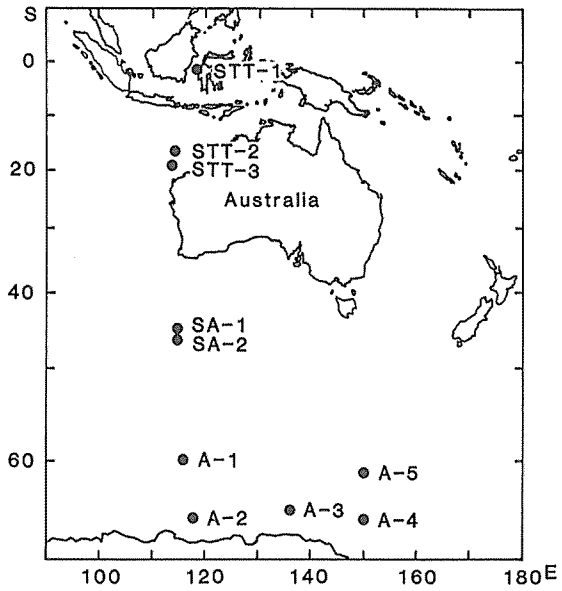

Fig. 1. Locations of the sampling stations. STT (subtropical/tropical stations): between the Equator and the Subtropical Convergence, SA (subantarctic stations): between the Subtropical Convergence and the Polar Front, and A (antarctic stations): south of the Polar Front. Samplings of surface water were carried out during the "BIOMASS" cruise of R.V. Hakuho Maru from November 22, 1983 to February 24, 1984.

Phytoplankton photosynthesis was measured basically according to the method of Steemann Nielsen (1952). After dispensing the seawater of 200 ml aliquot into 250 ml glass bottle, 5 μCi $NaH^{14}CO_3$ was inoculated. Usually, nine bottles in total were used for the incubation at one station. Three of them were treated as so-called dark bottle; DCMU (dichlorophenyl dimethylurea) was added at a final concentration of *ca.* 10^{-5} mole l^{-1} to cease the photosynthetic activity. These values were subtracted from the values of light bottles as the dark fixation. Three sets of 3 bottles, in which two were ^{14}C added bottles and the other one was ^{14}C plus DCMU added bottle, were incubated under three different temperature conditions usually including the *in situ* temperature. Incubation was carried out in the thermostatically water circulating container having transparent acrylic walls under the irradiance of 130 μmole photons m^{-2} s^{-1} by white fluorescent lamps. The incubation was started within 30 min after sampling, and continued for 4 hrs. The bottles were shaken at an interval of 15 min to keep particulate matter suspended. After the incubation, suspended matter was collected on a membrane filter (Millipore type HA, 0.45 μm pore size), and the radioactivity was measured with a scintillation counter (LKB Wallack, Rackbeta 1215).

Another aliquot of seawater was filtered through a Whatman GF/F glass fiber filter, and concentration of chlorophyll *a* (Chl *a*) was determined fluorometrically after the extraction in 90 % acetone solution using a Turner 111 fluorometer following the method of Yentsch and Menzel (1963). Assimilation number was calculated as ^{14}C uptake rate per hour per unit Chl *a* concentration.

Kendall's rank correlation test (Campbell, 1983) was done for all the measured parameters (temperature, Chl *a*, ^{14}C fixation rate and assimilation number). Multiple regression analysis (stepwise forward method) was applied according to Tanaka *et al.* (1987) to know the level of contribution of the respective measured parameter on the size of assimilation number.

Sampling stations were grouped into three regions by the locations of two major oceanic fronts, *i.e.,* the Subtropical Convergence and the Polar Front. Since these oceanic fronts have substantially marked boundary in the viewpoint of biogeography of oceanic plankters, the grouping makes it easier to discuss the differences in photosynthetic characteristics of natural phytoplankton communities in different latitudes. As a consequence, of 10 stations investigated, STT-1 through -3 (subtropical/tropical stations) were located between the equator and the Subtropical Convergence, SA-1 and -2 (subantarctic stations) were between the Subtropical Convergence and the Polar Front, and A-1 through -5 (antarctic stations) are south of the Polar Front (Fig. 1).

RESULTS

Latitudinal changes in physical and biological parameters

Temperature of surface seawater varied from -0.9 °C at Stn. A-3 to 29.2 °C at Stn. STT-2 (Fig. 2a, Table 1). The highest temperature during the cruise was recorded at Stn. STT-2 because of the austral summer.

The increasing trend of Chl *a* concentration was found with increasing latitude (Fig. 2b), however the statistical analysis showed no significant relationship between the surface seawater temperature and Chl *a* concentration (Table 2). The Chl *a* concentrations were relatively low (0.018-0.297 μg l^{-1}), and were at any rate, in the range found normally in the open ocean.

Although ^{14}C fixation rate showed a similar pattern in latitudinal variation (Fig. 2c) to that of Chl *a*, the correlation coefficient of Kendall's rank test for them was low (τ = 0.200; Table 2). And the correlation coefficient between ^{14}C fixation rate and the seawater temperature was also insignificant (τ = 0.111; Table 2), suggesting that the ^{14}C fixation rate is a function not only of the enzymatic activity which is accelerated by temperature, but also of the amount of biomass represented as Chl *a*.

Assimilation number ranged from 1.8 to 17 μg C μg Chl a^{-1} h^{-1} (Table 1), and showed a signifi-

Table 1. ^{14}C fixation rates and calculated assimilation numbers of phytoplankton communities collected from different latitudinal regions. Incubation was done by raising and lowering temperatures other than the *in situ* temperature (underlined) under the irradiance of 130 μ mole photons m^{-2} s^{-1}.

Stn.	Temp.	Chl *a*	Temp.	Incubation ^{14}C fixation rate (Avg±SD) (μg C l^{-1} h^{-1})	Ass. No. (Avg±SD) (μg C μg Chl a^{-1} h^{-1})
			Subtropical/tropical region		
STT-1	27.7	0.078	27.8±0.4	1.3±0.1	17±1
			30.7±0.5	0.96±0.08	12±1
			33.5±0.2	0.69±0.02	8.8±0.2
STT-2	29.2	0.020	29.8±0.9	0.15±0.05	7.6±2.5
			31.8±1.3	0.11±0.00	5.2±0.1
			35.0±0.2	0.069±0.020	3.5±1.0
STT-3	28.7	0.018	27.0±1.0	0.11±0.04	5.8±2.1
			28.8±1.0	0.13±0.01	6.9±0.7
			31.9±0.2	0.099±0.007	5.5±0.4
			Subantarctic region		
SA-1	11.4	0.17	11.4±1.2	0.89±0.16	5.4±1.0
			14.9±1.7	0.81±0.31	4.9±1.9
			17.4±1.4	0.77±0.37	4.7±2.2
SA-2	9.3	0.11	5.2±0.2	0.55±0.09	5.0±0.8
			9.3±0.3	0.68±0.11	6.1±1.0
			20.0±0.1	0.46±0.14	4.2±1.2
			Antarctic region		
A-1	2.2	0.095	0.9±0.7	0.88±0.08	9.2±0.9
			8.0±1.2	1.1±0.1	11±1
			12.0±0.6	1.3±0.1	13±1
A-2	0.1	0.17	1.2±0.2	0.32±0.02	1.9±0.1
			15.2±0.2	0.26±0.03	1.6±0.2
A-3	-0.9	0.10	2.0±0.2	0.40±0.03	3.9±0.3
			10.4±0.4	0.46±0.07	4.5±0.6
			21.4±0.4	0.012±0.004	0.1±0.0
A-4	-0.4	0.10	0.4±0.1	0.25±0.01	2.4±0.1
			5.0±0.6	0.26±0.03	2.5±0.3
			9.6±0.1	0.29±0.02	2.8±0.2
A-5	0.0	0.30	0.5±0.1	0.52±0.04	1.8±0.1
			4.5±1.5	0.65±0.09	2.2±0.3
			9.5±1.0	0.71±0.09	2.4±0.3

cant positive correlation with temperature ($p < 0.05$) and a significant negative correlation with Chl *a* ($p < 0.01$; Table 2). Since the assimilation number is calculated as ^{14}C fixation rate per unit Chl *a* per hour, it is a function of both ^{14}C fixation rate and Chl *a*. The multiple regression analysis again showed that the variation of assimilation number was explained by the two parameters with the contribution

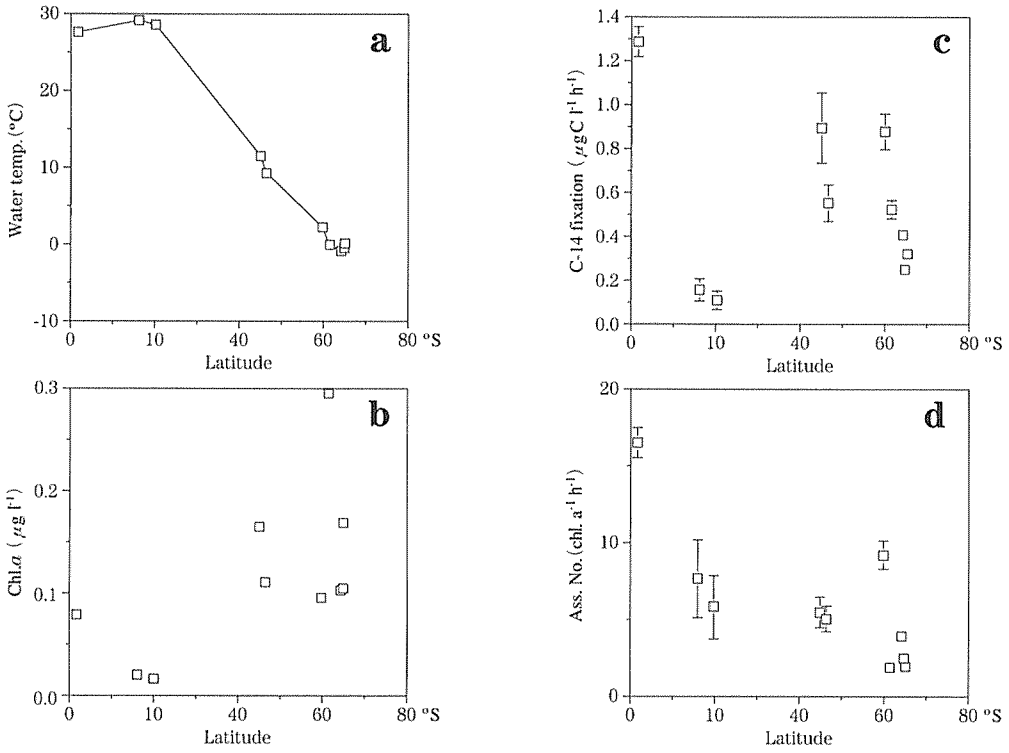

Fig. 2. Latitudinal changes in (a) surface seawater temperature, (b) Chl *a*, (c) ^{14}C fixation rate, and (d) assimilation number.

Table 2. Kendall's rank correlation coefficient (τ) between four parameters obtained from surface seawater at various latitudes in the Southern Hemisphere. n = 10.

	Temp	Chl *a*	^{14}C fix	Ass. No.
Temp	-	-	-	-
Chl *a*	-0.422	-	-	-
^{14}C fix	0.111	0.200	-	-
Ass. No.	0.511*	-0.689**	0.244	-

* and ** denote significant correlations at 5 and 1 % levels, respectively.

of 86.5 % ($r = 0.930$, significant at $p < 0.001$; Table 3). And ^{14}C fixation was a primary parameter contributing (48.5 %) to the variation of the assimilation number ($r = 0.696$, significant at $p < 0.05$; Table 3), whereas the rank correlation coefficient between them was fairly low ($\tau = 0.244$; Table 2).

Temperature, on the other hand, was rejected in the process of the multiple regression analysis because of no significance in F-test, whereas the rank correlation coefficient between temperature and the assimilation number had a significant correlation (Table 2).

Comparison of the photosynthetic activity was made for the three different regions. At first, to compare the variance of assimilation number obtained from those regions, F-test was applied to the

Table 3. Regression between the assimilation number (AN) and other parameters. Stepwise forward method. Chlorophyll *a* (CHL) and ^{14}C fixation rate (CF). SPRC: Standard Partial Regression Coefficient.

AN = 1.60 + 8.14CF		
r = 0.696*	[SPRC]	CF : 0.696
AN = 4.83 - 34.3CHL + 9.52CF		
r = 0.930**	[SPRC]	CHL : -0.628
		CF : 0.815

* and ** denote significant correlations at 5 and 0.1 % levels, respectively.

data sets. The variances of assimilation number between those two regions were not significantly different each other except those between STT group and SA group ($p < 0.05$). As a next step, t-test was applied to test the difference between the mean values of the assimilation number of them. The results of the t-test showed that assimilation number of STT group was significantly different from that of A group whereas those between STT group and SA group and between SA group and A group were not different ($p < 0.05$). In other words, the statistical results say that the phytoplankton community in the tropical/subtropical region has higher photosynthetic activity than that in the antarctic region. Apart from the statistical analysis, it should be mentioned that Stn. STT-1, whose value seemed to have contribute to raise the average, was located in coastal area in the Makassar Strait between Borneo Is. and Celebes Is. The statistical difference was not recognized among three groups if the data of Stn. STT-1 were removed. In Fig. 2d and Table 1, the assimilation number in the antarctic region are generally around 3 except a rather high value of 9.2 ± 0.9 μg C μg Chl a^{-1} h^{-1} at Stn. A-1 (around 60°S). And it should be noted that the highest value of the antarctic region was higher than those of the subtropical/tropical and subantarctic regions, excepted that of the coastal station STT-1.

Results of raising and lowering temperature experiments

Assimilation numbers obtained in the experiments of different temperature conditions were shown as relative values to those obtained at the *in situ* temperature, considering the latter to be unity. Experimental results were fitted by cubic curves; the cubic curve showed the higher correlation coefficients than the curve of second degree in all cases, because the data points were skewed somewhat either to higher or lower temperature side. The coefficient of determinations (r^2) were 0.799, 0.971 and 0.903 for the populations of the subtropical/tropical, subantarctic and antarctic regions, respectively.

Photosynthetic activity both in the subtropical/tropical and the subantarctic regions decreased either with raising or lowering of incubation temperature (Figs. 3a and 3b). In other words, the community in the north of the Polar Front attained the maximum photosynthetic activity at the *in situ* temperature. However, the decreasing trends of the calculated assimilation numbers at higher and

lower temperature were different between the subtropical/tropical community and the subantarctic community; the former showed a sharper decrease both in raising and lowering of temperature than the latter.

On the other hand, the photosynthetic activity of the antarctic phytoplankton community increased with raising the incubation temperature up to *ca.* 10°C, decreased to the equivalent level obtained at the *in situ* temperature at *ca.* 15°C, and was then lost at *ca.* 22°C (Fig. 3c). The temperature range in which they could survive is considered to be *ca.* 20°C. The maximum value was actually obtained at experimental temperature of 12°C when the phytoplankton assemblage of Stn. A-1 was offered (Table 1), and the value 13±1 was about 1.5 times higher than the value 9.2±0.9 obtained at the sub-zero temperature *in situ*. The elevated activity was higher than those obtained in the subantarctic region, and nearly comparable to the maximum value obtained at the *in situ* temperature of Stn. STT-1 in the subtropical/tropical region (17±1)(Table 1).

DISCUSSION

It is interesting to note that the phytoplankton communities both in the subtropical/tropical and subantarctic regions showed the maximum assimilation number at the *in situ* temperature (Fig. 3). However, the pattern of decrease in the relative activity to raising and lowering of the incubation temperature was obviously different, showing a sharp decline in the subtropical/tropical region and a gentle decline in the subantarctic region. These results seem to reflect the temperature variations in each different geographical sea region. There found little seasonal variation of seawater temperature in the subtropical/tropical region. Therefore, acquiring the ability to respond to an unexpected temperature change would not be necessary for the phytoplankton inhabiting in the subtropical /tropical region. On the other hand, during the long geohistorical process of evolution, the phytoplankton in the subantarctic region may have acquired the ability to maintain the photosynthetic activity even in a wide-range of seasonal variation

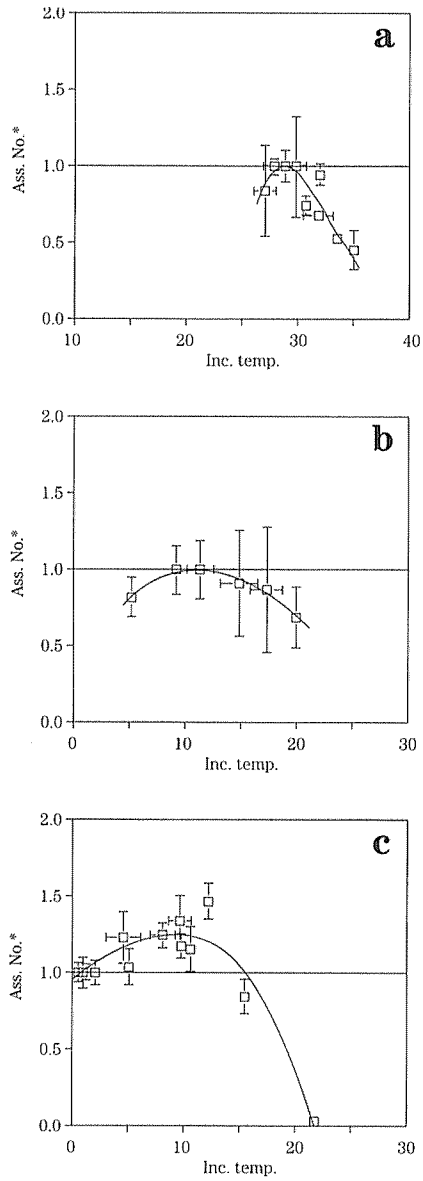

Fig. 3. Relative assimilation number (Ass. No.*), the ratio of the assimilation number in raising and lowering the incubation temperature to those in the *in situ* temperature against incubation temperature (Inc. temp.). Equations of fitted curves are (a) $Y = -113 + 10.9X - 0.343X^2 + 3.56 \times 10^{-3}X^3$ ($r^2 = 0.799$), (b) $Y = 0.292 + 0.142X - 8.15 \times 10^{-3}X^2 + 1.05 \times 10^{-4}X^3$ ($r^2 = 0.971$) and (c) $Y = 0.959 + 4.05 \times 10^{-2}X + 1.21 \times 10^{-3}X^2 - 2.42 \times 10^{-4}X^3$ ($r^2 = 0.903$).

of seawater temperature.

Being different from the two communities in the regions north of the Polar Front described above, the phytoplankton in the antarctic region showed the increase in the assimilation number with raising incubation temperature up to *ca.* 10°C. Increasing trend in photosynthetic activity with raising temperature, has already been reported by Neori and Holm-Hansen (1982) and Yamaguchi *et al.* (1985). They found that the maximum photosynthetic activity was attained at 7°-10°C. It must be true that increasing temperature helps to accelerate the photosynthetic activity of phytoplankton inhabited in the low temperature condition of the Antarctic Sea. In other words, this definitely indicates that the photosynthetic activity of the antarctic phytoplankton is suppressed by the extremely low temperature.

It is not sure, but it can be easily expected that the respiration rate of the phytoplankton would also elevate with raising temperature. The elevation in the respiration rate might cancel the increase of photosynthetic rate around 10°C. Supposing Q_{10}= 2, respiration rate generally increase 2 times with 10°C raising in temperature, which is higher than 1.5 times increase of the assimilation number observed at Stn. A-1 (Table 1). The elevation in photosynthesis of the antarctic phytoplankton at the Polar Front was supposed as a consequence of conveying process by the north west wind prevailing in the antarctic circumpolar area (Neori and Holm-Hansen, 1982). The elevated photosynthesis was actually observed at the Polar Front in the continuous survey across the front (Yamamoto, 1986). However, it seems not to be necessarily advantageous for the antarctic phytoplankton if we take the increase of respiration rate into consideration.

Morita (1975) described different terminologies for bacteria that are habitable in different environmental temperature. Organisms that show the optimum growth at temperature lower than 15°C and maximum growth around 20°C and grow even at temperature lower than 1°C are named 'psychrophile'. Another term 'psychrotroph' is applied for the organisms which show the maximum growth at temperature higher than 20°C and are also able to grow at 0°C. Adhering to the definition, the phytoplankton community in the antarctic region can be called as psychrophilic community. On the other hand, concerning to the subantarctic community, decreasing trend of the photosynthetic activity at *ca.* 15°C was not clear to those at the temperature of *ca.* 10°C *in situ*, and moreover they seems to grow at 0°C. Therefore, the subantarctic community may deserve to be called as psychrotroph. Since natural community is a mixture of many kinds of species, the subantarctic community must contain both psychrophilic species and psychrotrophic species. And the subantarctic community are considered to have acquired the ability to tolerate the wide seasonal temperature variation in the long geological history.

It must be a wrong diagnosis to assert that, from the experimental results, the phytoplankton in the antarctic region were not adapted to the surrounding environment of sub-zero temperature. Because there are many kinds of characteristics other than physiological state to describe whether an organism is adapted to the inhabiting environment or not. On the contrary, it must be natural to consider that the antarctic phytoplankton community are adapted well to the ambient low temperature condition, because their assimilation number of *ca.* 3 is considered to be similarly high compared to those in the other two regions. Since natural selection has generally acted to maximize the growth rate of organisms, the organism possessing higher growth rate in the inhabiting environmental temperature might be considered to be adapted to the inhabiting temperature. Although ^{14}C uptake rate is not equivalent to the growth rate in the strict sense, it would be accepted as an estimate of growth rate using the assimilation number in the case of phytoplankton; both the assimilation number and the growth rate are considered to be reciprocal if the population asynchronously grow in the steady state condition in nature.

Diatoms generally predominate in the Antarctic Sea south of the Polar Front (Kozlova, 1964; Yamamoto, 1986). According to Lipps (1970), emergence of diatom group (Bacillariophyceae) was in the late Cretaceous period of about 100 million years ago. In the Cenozoic era, however, the establishment of the Polar Front made the phytoplankton laid in some geographical isolation (Thunell, 1981). The antarctic phytoplankton species of the present age, therefore, are expected to have characteristics being adapted to the surrounding sub-zero temperature.

As a conclusion, the marine phytoplankton communities of the respective regions in the Southern Hemisphere are considered to have been adapted to the respective characteristic environmental temperature by different patterns.

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亜熱帯・熱帯海域，亜寒帯海域および南極海域植物プランクトン群集の水温適応パターンの比較

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南半球の植物プランクトン自然群集の炭素同化速度を，放射性同位体元素^{14}Cを用いて，現場水温を含む異なる温度で測定した。亜熱帯・熱帯海域および亜寒帯海域の植物プランクトンの光合成活性は，温度を上げた場合でも下げた場合でも低下した。すなわち，極前線の北の群集は現場水温において最大光合成活性を示した。しかしながら，温度の上下にともなう光合成指数の低下傾向は，亜熱帯・熱帯海域と亜寒帯海域の群集では異なり，後者に比べて前者で急激であった。これらの結果は，各海域における水温の季節変動の違いを反映しているのかもしれない。すなわち，水温は亜熱帯・熱帯海域では年間を通して比較的一定しているのに対して，亜寒帯海域では季節変動が大きい。一方，極前線南の南極海域植物プランクトン群集の光合成活性は，現場水温よりも温度を10°C上げることによって1.5倍になった。このことは，南極海域の植物プランクトンの光合成は0°C以下にもなる低い環境水温によって抑制されていることを示している。南半球におけるそれぞれの海域の植物プランクトン群集は，それぞれの水温環境に適応してきたと考えられる。

キーワード：温度，クロロフィル，光合成，植物プランクトン，適応，南半球