Phytoplankton Communities in the Bering Sea and Adjacent Seas

I. Communities in Early Warming Season in Southern Areas*

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Abstract: Vertical distribution of phytoplankton in early warming season in the eastern Bering Sea and adjacent sea areas was investigated. In the surface layer which was under the influence of newly melted sea ice in the shelf water region of the Bering Sea in May, remarkably dense populations of *Thalassiosira hyalina* and *T. nordenskiöldii* and relatively large populations of *Fragilaria* and *Navicula* occupied large part of phytoplankton community. In June, although the *Thalassiosira* populations sunk into the bottom layer and withered, a certain part of the *Fragilaria-Navicula* populations was still suspended in subsurface layer. Thus, *Fragilaria-Navicula* were the leading components of the June community in the shelf region.

In the Bering Basin region, no dense phytoplankton populations were developed until a shallow thermocline was established. In June when the shallow thermocline developed near shelf edge, *Thalassiosira decipiens* burst out. As the shallow thermocline extended from near shelf to central part of the Basin region with surface warming, the areas of blooming also shifted from near shelf to the central part.

1. Introduction

Despite the well defined thermocline preventing nutrient supply to euphotic zone from underlying layers is established, phytoplankton production in the Bering Sea during warming season is distinctly higher than those in the tropical and subtropical sea areas. Such high productivity of the Bering Sea phytoplankton community, though large stock of nutrients is the most important factor, is probably induced by the depth of thermocline shallower than the compensation depth which keeps large part of the phytoplankton community within the euphotic zone (TANIGUCHI, 1972). Species composition

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and succession of the communities in the Bering Sea were extensively studied (cf. KAROHJI, 1972). However, the former studies had been done basing mainly on the samples gathered by vertical net hauls from below the thermocline or below the euphotic zone. Consequently, the seasonal succession of vertical structure of the communities which is largely controlled by the vertical stability of water is still obscure.

During the period from May 1972 to November 1973 the Research Institute of North Pacific Fisheries and the Plankton Laboratory of Hokkaido University carried out surveys of the seasonal changes in phytoplankton communities in the Bering Sea and adjacent sea areas. Based on the data obtained in May and June of 1972, the species succession of phytoplankton community during early warming season in the Bering Sea is discussed in the present paper.

2. Methods and materials

Nine stations located on a line from Latitude 50°N to 57°N at Longitude 172°W and 6 stations from 54°N to 58°30'N at 170°W were selected to investigate the phytoplankton popu-

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lations in the early warming season. The former 9 stations were occupied on May 5-11, 1972, on the cruise of the R.V. Habomai Maru chartered by the Hokkaido University, and the latter 6 stations on June 18-20, 1972, on the Cruise 45 of the T.S. Oshoro Maru of the University (Fig. 1). At each station two 250 ml aliquots of water samples collected from several depth layers down to 150 m were placed to the microscopic examinations of phytoplankters and to the determinations of phytoplankton pigments and inorganic nutrients. The sampling depths were 0, 10, 20, 30, 40, 50, 60, 70, 80, 100, 125 150 m in May and 0, 10, 20, 30, 50, 75, 100, 125 and 150 m in June, whereas in shallow shelf water region the deepest sampling depth was fitted to near the sea bottom.

By the methods described by STRICKLAND and PARSONS (1968), concentrations of phosphate-phosphorus, nitrite-, nitrate- and ammonium-nitrogen were measured in May, but in June only the phosphate-phosphorus concentration was measured. Since available data in May indicated that the vertical and horizontal distributions of nitrogen showed the same trend as those of phosphorus, the distribution of phosphorus might also follow the distribution of nitrogen in June. Concentrations of chlorophyll a and pheopigments were estimated by the fluorometric determination (YENTSCH and MENZEL, 1963 and SAIJO and NISHIZAWA, 1969). The pigment ratio (percentage of chlorophyll a in the sum of chlorophyll a and pheopigments)



Fig. 1. Stations in the eastern Bering Sea and Subarctic Pacific occupied by R. V. Habomai Maru(●) and Training Ship Oshoro Maru(⊕) in May and June, 1972.

was examined, as it is known that the ratio varies seasonally parallel with growth rate or productivity of the subarctic phytoplankton community (SPENCE and STEVEN, 1974).

The cell count was made under the Union Model 2-6 Inverted Microscope on a part of the samples which were concentrated to *ca*. 10 ml from 250 ml by the settling method.

3. Hydrographic conditions

Vertical sections of temperature and salinity down to 300 m depth in May and June are given in Fig. 2. By these sections the areas investigated were demarcated into five regions; from south, oceanic Subarctic Pacific region (including Stn. Hb 18), neritic Alaskan Stream region (Hb 19), neritic mixed water region (Hb 20, 21 and 22), oceanic Bering Basin water region (Hb 23, 24, 25 and Os 23, 24, 25) and neritic shelf water region (Hb 26 and Os



Fig. 2. Hydrographic sections in May (top) and June (bottom). Solid and broken lines are isotherms (°C) and isohalines (‰), respectively.

20, 21, 22). In May, while indistinct halocline in the Alaskan Stream region and well defined thermo- and haloclines in the shelf water region were observed, no apparent vertical gradients of salinity and temperature existed in the top 150 m in the other regions. It must be noted that the low temperature - low salinity surface water covering the shelf region originated from newly melted sea ice. A few masses of the sea ice, though small, were drifting around the station on the day of sampling.

About a month later, in June, water in the Bering Basin region was slightly stabilized by surface warming. A seasonal thermocline was developing and tended to descend from the depth shallower than 50 m near the shelf edge to around 100 m depth at the center of the Basin region. It was the most characteristic feature in June that the high salinity-extremely low temperature bottom water lay below 40-50 m depth on the shelf. This cold bottom water had been formed around the central shelf region in situ in winter and hardly mixed with neighbouring bottom water as well as with the surface water throughout the year (OHTANI, 1973). Such a completely isolated steady condition of the bottom water will make possible the following assumption: Because thickness of the euphotic zone in the shelf region in summer is about 30 m (TANIGUCHI, 1969), light intensity may be too low for phytoplankton to grow within the bottom water below 40-50 m depth. Therefore, phytoplankton collected from the bottom



Fig. 3. Vertical sections of phosphate-phosphorus $(\mu g-at Pl^{-1})$ in May (top) and June (bottom).

water are not of the populations grown *in situ* but a part of the preceding surface populations which sunk into the bottom water before a sharp thermocline had been established.

Vertical sections of phosphate-phosphorus in the upper 150 m are illustrated in Fig. 3. The concentration of phosphate was generally high and ranged from 0.43 to 2.75 μ g-at Pl⁻¹ in the upper 150 m in both May and June. In the surface water on the shelf, however, the phosphate concentration lower than 1.0 μ g-at Pl⁻¹ was observed. At near shelf edge stations in the Bering Basin region the phosphate level in 0-50 m layer also decreased from about 1.5-2.0 μ g-at Pl⁻¹ in May to about 1.0-1.5 μ g-at Pl⁻¹ in June. These variations of phosphate would indicate local nutrient utilization by phytoplankton community.



Fig. 4. Vertical sections of chlorophyll $a (\mu g l^{-})$ in May (top) and June (above middle), and of the pigment ratio (%) in May (below middle) and June (bottom).

4. Phytoplankton community in May

High concentration of chlorophyll *a* occurred in the upper 60 m of the Alaskan Stream region $(0.26-1.06 \ \mu g \ l^{-1})$ and in the upper 50 m of the shelf water region $(2.49-3.13 \ \mu g \ l^{-1})$. In these regions, while available stock of phosphate in the surface water was relatively small, the high pigment ratio (more than 70% as shown in Fig. 4) would indicate that the productivity of these communities was high. Main components

Table 1. Summary of the size of phytoplankton community in cell number and chlorophyll concentration. Dominant species which occupied more than 20% of the total cell number at any depth layer are shown. When the size or dominant species changed markedly through water column, the column is separated into two depth ranges.

Station	Depth range (m)	Total cell number (×10 ³ l ⁻¹)	Chlorophyll a concentration $(\mu g l^{-1})$	Dominant species (in dominancy order)
May, 197	2	·		
Subarct	ic Pacific			
Hb 1	8 0-70	1.0-4.6	0.06-0.08	Pontosphaera sp., Thalassiosira nordenskiöldii, Denticula seminae, Fragilaria oceanica
	80-150	0.2-0.9	0.01-0.05	Pontosphaera sp., D. seminae, Coscinodiscus excentricus, Asteromphalus sp.
Alaskar	n Stream			
Hb 1	9 0-60	48.2-326.8	0.29-1.06	T. nordenskiöldii, T. gravida
	70-150	2.3-23.4	0.02-0.14	T. nordenskiöldii, T. hyalina
Mixed water				
Hb 2	0 0-150	9.5-23.1	0.08-0.19	T. nordenskiöldii, T. hyalina
Hb 2	1 0-150	4.7-13.9	0.08 - 0.14	T. nordenskiöldii
Hb 2	2 0-150	0.2-1.0	0.02-0.06	Pontosphaera sp., T. nordenskiöldii, Asteromphalus sp.
Bering Basin				
НЬ 2	3 0-150	0.4-1.6	0.01-0.06	T. nordenskiöldii, Pontosphaera sp., D. seminae, Dinophysis norvegica, Peridinium roseum, Cosc. excentricus, Asterom- phalus sp.
Hb 2	4 0-40	17.7-38.0	0.14-0.35	T. hyalina, T. nordenskiöldii, F. oceanica
	50-150	0.2-6.6	0.01-0.07	Pontosphaera sp., T. hyalina, Exuviaella haltica, Ceratium lineatum
Hb 2	5 0-60	14.1-131.2	0.09-0.76	T. hyalina, T. nordenskiöldii
	70-150	0.3-1.2	0.01-0.03	Pontosphaera sp., T. hyalina, Exuv. baltica, Navicula sp.
Shelf water				
Hb 2	6 0-50	827.5-2399.5	5 2.49-3.13	T. hyalina, T. nordenskiöldii, Fragilaria islandica
	60-70	58.9-64.5	0.06-0.32	F. islandica, Navicula granii, T. hyalina
June, 197	2			
Bering Basin				
Os 2	5 0-75	2.4-10.3	0.15-0.28	Thalassiosira spp. (damaged cells), Asteromphalus sp.
	100-150	0.5-0.8	-0.01	Thalassiosira spp. (damaged cells), T. gravida, T. hyalina, D. seminae, Per. roscum
Os 2	4 0-20	10.2-18.3	0.23-0.27	Thalassiosira decipiens
	30-150	0.7-8.8	0.01-0.14	T. decipiens, T. subtilis, Chaetoceros radicans, Ch. debilis
Os 2	23 0-30	12.7-68.9	0.75-0.98	T. decipiens
	50-125	1.4-7.6	0.01-0.27	T. decipiens, Thalassiosira spp. (damaged cells), Ch. furcel- latus
Shelf v	vater			
Os 2	2 0-30	(No data)	0.62-0.73	
	50-75	(No data)	0.79-1.33	
Os 2	1 0-30	2.6-6.5	0.01-0.08	F. islandica, Fragilaria spp., T. gravida
	50-70	11.4-16.9	0.08-0.24	F. islandica, Thalassiosira spp. (nordenskiöldii+hyalina+ gravida+damaged cells)
Os 2	0 0-20	9.6-15.4	0.02*	F. islandica
	30-70	12.6-20.6	0.14-0.17	F. islandica

* Only the surface datum was obtained.

of the communities were the neritic diatoms such as Thalassiosira nordenskiöldii and T. gravida in the Alaskan Stream region, and T. hyalina, T. nordenskiöldii and Fragilaria islandica in the shelf region. Total cell number in the upper 50 m was as high as 48.2-326.8 imes10³ cells l⁻¹ in the former region and 827.5- 2399.5×10^3 cells l⁻¹ in the latter region. In the underlying layers in both regions the standing crop of phytoplankton as well as the pigment ratio abruptly decreased (Fig. 4). While species composition of the community throughout the surface to underlying layers was uniform in the Alaskan Stream region, that in the shelf water region changed vertically. In the latter region Thalassiosira populations were the main components of the surface community followed by Fragilaria population, but Fragilaria and Navicula dominated in the underlying layers (Table 1).

In the Subarctic Pacific Region the size of the community was small $(0.01-0.08 \ \mu g \, chl. a \, l^{-1}; 0.2-4.6 \times 10^3 \, cells \, l^{-1})$ through vertical ranges from the surface to 150 m depth. The pigment ratio was also lower than 50 % (Fig. 4). The community was dominated principally by the oceanic forms such as a coccolithophore *Pontosphaera* sp. and a diatom *Denticula seminae*, while the neritic *T. nordenskiöldii* and *Fragilaria oceanica* occurred in certain numbers in the surface layer (Table 1).

In the Basin water region the community was dominated by neritic diatoms in the surface but by oceanic *Pontosphaera* and dinoflagellates (*Exuviaella baltica* and *Ceratium* spp.) in the underlying layers. The former diatom populations (T. hyalina and T. nordenskiöldii) indicate that the surface community in northern part of the Basin region in May was of settlers from the shelf region. However, in the central Basin region (Stn. Hb 23) the 6 dominant species excluding T. nordenskiöldii were oceanic forms. The neritic communities hardly extended their distribution to the central Basin region (Table 1).

In the mixed water region the vertical variations in standing crop and species composition of the community were negligible. The principal components of the community at the stations in this region were the neritic T. *nordenskiöldii* and T. *hyalina* populations. In addition to these, at Station Hb 22 which was located near the central Basin region the oceanic *Pontosphaera* sp. and *Asterompharus* sp. populations also dominated.

It was noteworthy that centric diatoms such as Chaetoceros convolutus, Rhizosolenia alata, Biddulphia aurita, Corethron hystrix, etc., the cells of which were heavily damaged, occurred in certain numbers at the northern-most station (Hb 26) on the shelf. These species are confirmed in the shelf water region as the oceanic summer species which are seasonally brought by the surface current during summer to fall from the southern Basin region. However, in the present investigation period, they could not be found in the Basin region. Therefore, the damaged cells mentioned above might be a part of residue from the previous summer-fall community in the shelf region rather than the cells brought from the south in this period. It may be possible in shallow shelf region that the cells accumulated in the bottom layer could be temporarily resuspended by the vertical mixing of water in winter.

5. Phytoplankton community in June

Area of blooming of the surface phytoplankton shifted from the shelf region in May to near shelf part of the Basin region in June. Above the shallow thermocline which developed around 40 m depth in the latter part (Fig. 2), total cell number was $12.7-68.9 \times 10^3$ cells l⁻¹ and concentration of chlorophyll *a* was $0.75-0.98 \,\mu g l^{-1}$ (Table 1). These values and the pigment ratio (50-60%) are very close to those observed in May at the same location (Fig. 4). This seems to suggest that the June community was the survivor of the May community. However, the species composition was different; the latter community was dominated by Thalassiosira hyalina, T. nordenskiöldii and Fragilaria islandica, but in June T. decipiens was the dominant species (Table 1). CUPP (1937) also recognized that, at the Scotch Cap Light of Unimak Island, T. decipiens occurs following the early spring populations of T. gravida, T. nordenskiöldii and F. islandica.

As in May, the oceanic summer species such as Coscinodiscus asterompharus, Rhizosolenia habetata, R. alata, Corethron hystrix, Chaetoceros atlanticus, C. decipiens, etc. were also found in the near shelf part of the Basin region, but the cells were damaged. They were hardly found in the oceanic central part of the Basin region, although the other oceanic species occurred.

Apart from the surface community, remarkably high concentration of chlorophyll a and high pigment ratio were observed in the bottom layers at Stn. Os 22 in the shelf water region in June. Unfortunately, no data are available on the phytoplankton species composition at this station. At the neighbouring two stations (Os 20 and 21) where the isolated cold bottom water existed, the concentration of chlorophyll a, pigment ratio and cell number tended to increase in the bottom layer (Fig. 4). The *Fragilaria* populations occupied main parts of the community throughout the vertical ranges. The *Fragilaria* cells in the bottom layers were observed as healthy.

On the other hand, the *Thalassiosira* populations, which had been the important components of the surface community in May, became small in number in the surface layer in June. Although *Thalassiosira* occurred in certain numbers in the bottom layer (Table 1), no healthy cells were found in June.

6. Species succession during early warming season

To describe the species succession of the phytoplankton community during early warming season, the summarized data in Table 1 could

be referred. In addition, the mean size of community expressed in chlorophyll a concentration and cell number in the surface layer is illustrated in Fig. 5. The surface layer is defined here as the layer under which marked gradient. of parameters or of phytoplankton distribution existed. When the parameters were homogeneous through the water column as in the mixed water region, the size of community was calculated by averaging the values in the top 50 m. As shown in Fig. 5, the mean size of community increased in the Basin region but decreased in the shelf region during the period from May to June. By referring to the pigment. ratios (Fig. 4), it will be reasonably concluded that the surface phytoplankton community in June in the shelf region was of senescent phase. while that in the Basin region was of active phase. These two June communities were alsoquite dissimilar in both size and species composition, *i.e.* several species of *Fragilaria* and Thalassiosira gravida dominated in small and senescent community in the shelf region but T. decipiens mass occurred in the Basin region.

KAWARADA and OHWADA (1975) described seasonal succession of dominant species of phytoplankton community in the Bering Basin region. Dense spring populations of neritic *Thalassiosira* in April were followed by the mixed populations of oceanic *Chaetoceros* and *Denticula* with *Thalassiosira* in May-June. Then, in July, these mixed populations were replaced by the

Fig. 5. Mean size of phytoplankton communities through the surface layer (see text) expressed by cell number (open circle: cells l^{-1}) and by chlorophyll *a* concentration (solid circle: $\mu g l^{-1}$). Horizontal bar indicates the range of changes in cell number. The range in chlorophyll concentration was very small.

completely oceanic community.

In the shelf region, the extensive growth of pennate diatoms which occurs in the sea ice before the onset of blooming of centric diatoms in water column (MCROY and GOERING, 1974) must be taken into account. The dominant species of the ice algae are probably of genera *Fragilaria*, *Nitzschia* and *Navicula*, etc. (cf. HORNER and ALEXANDER, 1972).

6.1. In the shelf water region

The surface phytoplankton community under the influence of newly melted sea ice was as large in number as $827.5-2397.5 \times 10^3$ cells l⁻¹ and represented by both the *Thalassiosira* (35.9-55.8% in number) and *Fragilaria* (33.5-39.4%)—*Navicula* (13.2-20.3\%) populations. In the underlying layers, although the community was also dominated by these populations, the dominancy order was reversed, *i.e. Fragilaria* (34.7-58.3%)—*Navicula* (17.5-30.3\%) exceeded *Thalassiosira* (25.9-44.7\%).

About a month later, in June, the surface community became small in number $(2.6-15.4 \times$ 10³ cells l⁻¹). Except for Thalassiosira gravida which occupied 20.6% of the surface community at Stn. Os 21, the previousely occurred Thalassiosira populations almost completely disappeared from the surface layer. The Thalassiosira cells found in the bottom layer, since the cells were heavily damaged, indicated that the Thalassiosira populations sunk from the surface laver withered in the bottom layer. On the contrary, Fragilaria-Navicula maintained their healthy populations of considerable size throughout water column, and the size increased with They occupied 69.2-76.2% of the depth. bottom community in June.

The above-mentioned successions of species composition and of vertical structure of phytoplankton community in the shelf region were doubtlessly complicated by the sea ice. Effect of the ice will be discussed in the next part of our study.

6.2. In the Bering Basin water region

Because the Basin region is opened throughout the year, the seasonal succession of phytoplankton community during the early warming season is to be rather simple. The surface phytoplankton community starts to grow as a shallow thermocline is established. The thermocline becomes shallower as the surface warming advances, and this ascending process of thermocline seems to progress from near shelf edge to the central part of the Basin region (Fig. 2). Therefore, areas of the phytoplankton blooming may also progress from near shelf to the central part (Fig. 5).

Although the Fragilaria-Navicula populations dominantly occurred in the shelf region, the occurrences of Fragilaria-Navicula in the Basin region were sporadic. The main component of the spring community in the Basin region was the Thalassiosira population as was in the shelf region, but the species (T. decipiens) was different from those (T. hyalina, T. nordenskiöldii and T. gravida) in the shelf region. Furthermore, it should be noted that the latter three species, though they were distributed further north as compared with T. decipiens, burst into blooming earlier than the blooming of T. decipiens in the Basin region. The all matters mentioned above indicate that in the early warming season the Basin community is quite different from the shelf community in both the origin and the developmental processes.

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ベーリング海およびその周辺海域の植物プランクトン群集 I. 南部水域における春季の群集

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要旨: ベーリング海東南部および北部北太平洋におけ る春季(1972年5~6月)の 植物 プランクトン群集の調 査を行なった. ベーリング海陸 棚水 域では、5月には Thalassiosira hyalina および T. nordenskiöldii を主 要群とし、次いで Fragilaria および Navicula 属の数 種群の優占度が高い、極めて濃密な植物プランクトン群

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集が表層に出現する. 6月になると、このうち Thalassiosira 群は海底に沈降するが, Fragilaria-Navicula 群 の一部はなお中層に浮游しつづけるので,後者が6月の 群集の最重要種群になる.

ペーリング海盆水域では, 浅層に季節的の水温躍層が 形成されはじめる6月になってから, 植物プランクトン 群集は増大しはじめる. この時の主要 種 群 は Thalas siosira decipiens であった. ベーリング海盆水域で浅層 に発達する水温躍層は, 陸棚縁辺部から海盆中央部にか けて順次形成されるので, 植物プランクトンの増殖水域 もまた, 時をおって, 陸棚縁辺部から中央部へと移行す る.