Bull. Fac. Fish. Hokkaido Univ.
52(2), 95-101, 2001.

Biological Activity of Phytoplankton at the Polynya Area in the Bering Sea in Summer

Hitoshi TANAKA[1], Mitsuru YANADA[1] and Yoshiaki MAITA[1]

Abstract

The concentrations of chlorophyll *a* (Chl *a*), particulate organic carbon (POC), particulate deoxyribonucleic acid (P-DNA) and particulate adenosine triphosphate (P-ATP) were measured simultaneously to discuss the biological activity of phytoplankton at the polynya area near St. Lawrence Island in the Bering Sea in summer of both 1991 and 1994. The Chl *a* concentrations represented low values in the upper layer of the strong developed pycnocline and very high values in the lower layer. The concentrations of POC, P-DNA and P-ATP also represented low values in the upper layer and high values in the lower layer. The result of size-fractionated Chl *a* suggested that the small-sized phytoplankton dominated in the upper layer and the large-sized phytoplankton dominated in the lower layer. However, the weight ratios of each chemical component (POC/Chl *a*, POC/ATP, POC/DNA, ATP/Chl *a*, DNA/ATP, DNA/Chl *a*) implied that the biological activity of phytoplankton was relatively active in the upper layer although the phytoplankton biomass was very low, and relatively inactive in the lower layer in spite of the high phytoplankton biomass.

Key words: Biological activity, Chlorophyll *a*, Particulate organic carbon, Particulate deoxyribonucleic acid, Particulate adenosine triphosphate, Polynya area, Bering Sea

Introduction

The Bering Sea Shelf is a high productive habitat from primary producer to higher trophic organisms or benthos (e.g. Springer et al., 1996). In fact, the phytoplankton standing stock at the polynya area near St. Lawrence Island in summer (Imai et al., 1998; Shichinohe and Shiga, 1998) is nearly equal to that of the spring bloom level in some subarctic coastal regions (e.g. Funka Bay: Odate et al., 1993). This evidence seems to indicate a high primary production at the polynya area in summer. However, the vertical profile of Chl *a* concentration in this region in summer reveals a characteristic pattern; higher value in the lower layer than that in the upper layer (Imai et al., 1998; Shichinohe and Shiga, 1998). It is very important for the study of food chain and/or carbon cycle in the polynya area whether the phytoplankton at the lower layer is produced in situ or not, in other words, whether the phytoplankton has high biological activity or not.

The bio-mediated materials such as chlorophyll *a* (Chl *a*), adenosine triphosphate (ATP) and deoxyribonucleic acid (DNA) are significant indices of the biomass of organisms populations in seawater; Chl *a* for phytoplankton biomass (e.g. Kirchman et al., 1993), ATP for total organism biomass (e.g. Hewes et al., 1990) and DNA also for total organism biomass (e.g. Bailiff and Karl, 1991). Especially, since ATP is decomposed immediately after the cell dies, ATP concentration in seawater is index of living organisms biomass (Bailiff and Karl, 1991; Jones et al., 1996). However, since the content of ATP in living organisms may vary according to the biological activity of the living organisms (e.g. Jones et al., 1995), ATP concentration in seawater can be expressed as the biological activity of living organisms populations. On the other hand, P-DNA in seawater may exist as non-replicating DNA (dead, dormant or debilitated cell) in addition to living organisms (Winn and Karl, 1986). Therefore, the combination of these bio-mediated materials including particulate organic carbon (POC) may be an available way for defining the phytoplankton biomass and/or the biological activity of phytoplankton.

The purpose of this study is to discuss the biological activity, i.e. active or inactive, of phytoplankton existing at the polynya area in the Bering Sea in summer from simultaneous measurements of the bio-mediated materials.

Materials and Methods

Seawater sampling was conducted in the polynya area near St. Lawrence island in the Bering Sea (OS91139, OS94137, OS94151, OS94157) on cruises aboard the T/

[1] *Laboratory of Marine Environmental Science, Graduate School of Fisheries Sciences, Hokkaido University* (北海道大学大学院水産科学研究科資源環境科学講座)

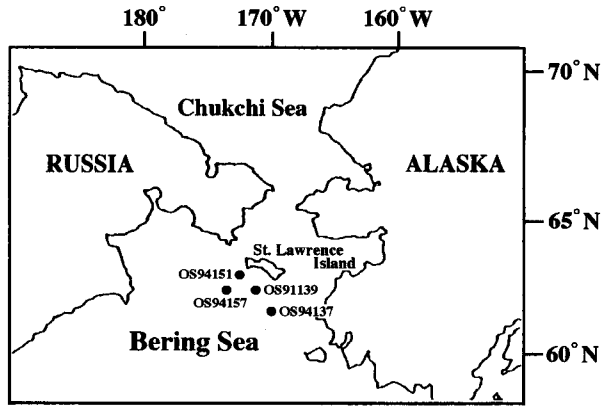

Fig. 1. Location of sampling stations at the polynya area in the Bering Sea.

S "Oshoro Maru" in July of both 1991 and 1994 (Fig. 1). Seawater samples were collected within the water column of 0–50 m using a 20-liter Van Dorn bottle. All seawater samples were immediately passed through a 350 μm mesh net to remove macrozooplankton. The seawater samples were filtered through a Whatman GF/F filter, which was previously heated at 450°C for 3 h, for the measurements of chlorophyll *a* (Chl *a*), particulate organic carbon (POC), particulate deoxyribonucleic acid (P-DNA) and particulate adenosine triphosphate (P-ATP). The seawater samples were also filtered through Nuclepore filters of 0.2 μm, 2 μm and 10 μm pore size for measuring size-fractionated Chl *a* concentration. The particulate sample on the filter for P-ATP measurement was immediately treated with the boiling trishydroxymethylaminomethane (pH 7.7) for extraction of P-ATP according to Parsons et al. (1984). The extract was kept frozen at −30°C until the analysis. The filters for the measurements of Chl *a*, POC and P-DNA and seawater samples for nutrient measurement were also kept frozen at −30°C until the analysis.

Chl *a* concentration was measured by the fluorometric method with 90% acetone using a Shimadzu RF-540 spectrophotometer according to Parsons et al. (1984). ATP concentration was measured by the luciferin-luciferase method using a Labo Science TD-4000 luminescence photometer according to Parsons et al. (1984). DNA concentration was measured by the fluorometric method using a Shimadzu RF-540 spectrophotometer according to Holm-Hansen et al. (1968) and Robertson and Tait (1971). POC concentration was measured using a CHN analyzer (Hitachi 026). Nutrient concentration was determined using Auto Analyzer II. The data on water temperature, salinity and sigma-t were cited from data reports (Fac. Fish. Hokkaido Univ., 1992, 1995).

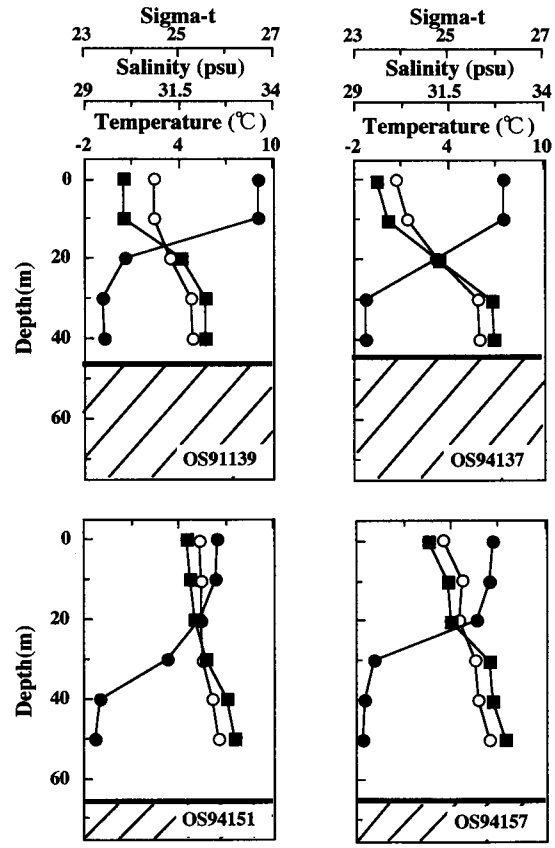

Fig. 2. Vertical profiles of temperature (●), salinity (○) and sigma-t (■) at the polynya area in the Bering Sea.

Results

Hydrographical and nutrient conditions

The intense thermoclines were observed between 10 m depth and 20 m depth in OS91139, between 10 m depth and 30 m depth in OS94137, between 20 m depth and 40 m depth in OS94151 and between 20 m depth and 30 m depth in OS94157 (Fig. 2). The water temperature ranged from 5°C to 9°C in the upper layer above the thermocline and was less than 0°C in the lower layer below the thermocline. The salinity varied between 30.1 psu and 32.6 psu and increased with depth. The relatively strong haloclines were observed between 10 m depth and 30 m depth in both OS94137 and OS91139. As a result of both the water temperature and the salinity, the intense pycnoclines were observed between 10 m depth and 30 m depth in both OS94137 and OS91139.

The concentrations of nitrate+nitrite (NO_3+NO_2), phosphate (PO_4) and silicate (SiO_4) were in the ranges of 0.1–9.5 μM, 0.5–2.8 μM and 3–53 μM, respectively (Fig. 3). The nutrient concentrations were uniform above 20 m depth and slightly increased below 30 m depth in both OS91139 and OS94137. In OS94151, the nutrient concentrations were uniform above 40 m depth and

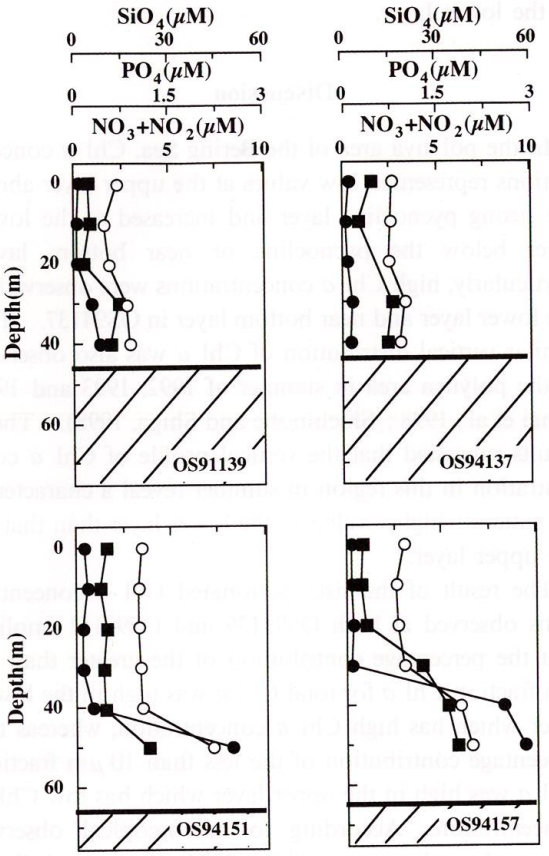

Fig. 3. Vertical profiles of nitrate plus nitrite (●), phosphate (○) and silicate (■) at the polynya area in the Bering Sea.

represented very high values at 50 m depth. In OS94157, the nutrient concentrations were uniform values above 20 m depth or 30 m depth and dramatically increased below 30 m depth or 40 m depth.

Bio-mediated materials

Chl *a* concentration ranged from 0.1 μg l^{-1} to 17.2 μg l^{-1} and tended to increase at the lower layer (Fig. 4). In the upper layer above the pycnocline, the Chl *a* concentrations were uniform values and ranged from 0.08 μg l^{-1} to 0.76 μg l^{-1} at all stations. In OS91139, OS94151 and OS94157, the Chl *a* concentrations in the lower layer below the pycnocline increased to about 2.0 μg l^{-1} which was approximately 10 times higher than that at the upper layer. Further, in OS94137, Chl *a* concentration in the lower layer dramatically increased to about 16 μg l^{-1} which was approximately 20 times higher than that (0.76 μg l^{-1}) at 20 m depth. In OS91139, the percentage contribution of Chl *a* content in 0.2-2 μm size-fraction was about 75% of the total Chl *a* at upper 20 m depth, whereas the Chl *a* contribution in the greater than 10 μm size-fraction was about 80% at below 30 m depth (Fig. 5). Vertical distribution of size-fractionated Chl *a* in OS94151 was similar to that in

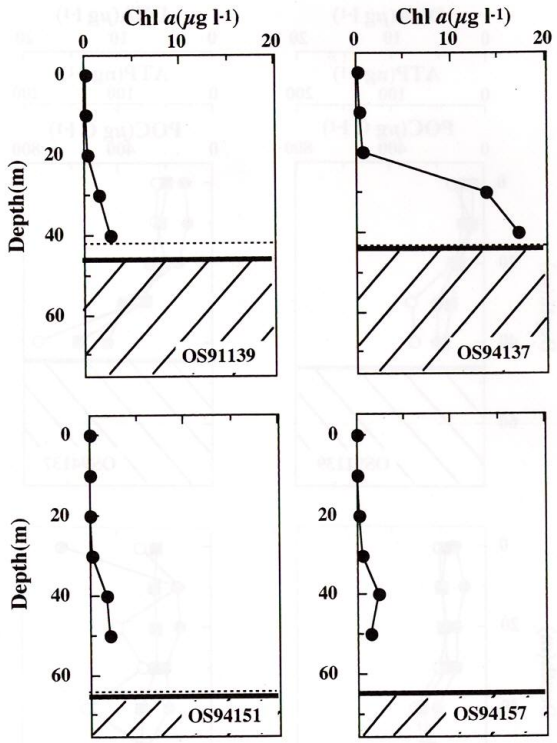

Fig. 4. Vertical profile of Chl *a* at the polynya area in the Bering Sea. The broken line expresses the depth of 1% surface PAR (OS94157 has no data).

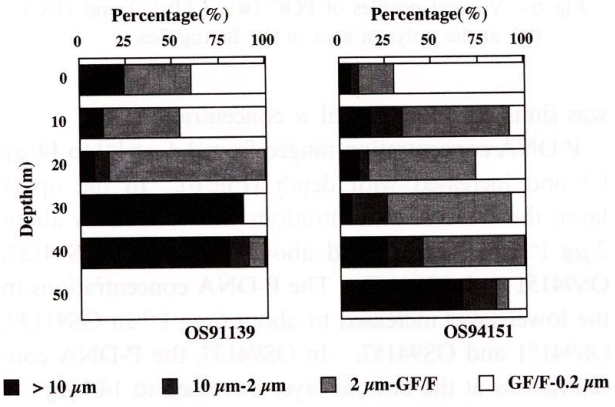

Fig. 5. Vertical profiles of size composition of Chl *a* at two stations (OS91139 and OS94151) at the polynya area in the Bering Sea.

OS91139.

POC concentration ranged from 92 μg C l^{-1} to 634 μg C l^{-1}. The POC concentration increased with depth, except at the surface of OS94157 which has extremely high POC concentration (Fig. 6). In the upper layer, the POC concentrations were uniformly about 100 μg C l^{-1}. The POC concentrations in the lower layer increased to about 200 μg l^{-1} in OS91139, OS94151 and OS94157. In OS94137, the POC concentrations in the lower layer increased remarkably to about 400 μg l^{-1}. The vertical profile of POC concentration at each station

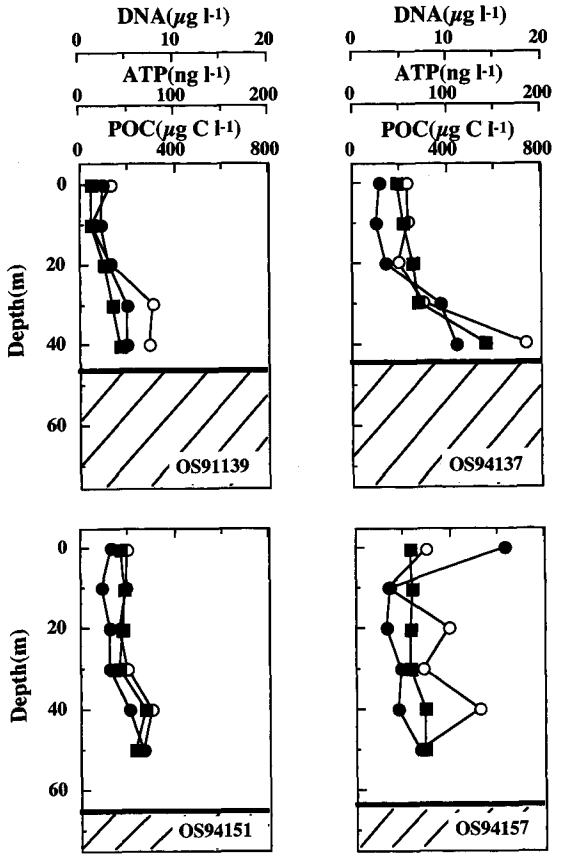

Fig. 6. Vertical profiles of POC (●), ATP (○) and DNA (■) at the polynya area in the Bering Sea.

was similar to that of Chl *a* concentration.

P-DNA concentration ranged from 1.4 μg l^{-1} to 14 μg l^{-1} and increased with depth (Fig. 6). In the upper layer, the P-DNA concentrations were uniformly about 2 μg l^{-1} in OS91139 and about 5 μg l^{-1} in OS94137, OS94151 and OS94157. The P-DNA concentrations in the lower layer increased to about 6 μg l^{-1} in OS91139, OS94151 and OS94157. In OS94137, the P-DNA concentrations at the bottom layer increased to 14.1 μg l^{-1}. The P-DNA concentration was high at the lower layer, similar to these of POC and Chl *a*.

P-ATP concentration ranged from 13 ng l^{-1} to 184 ng l^{-1} (Fig. 6). The P-ATP concentration also increased with depth and the vertical profile in each station was similar to that of the other bio-mediated materials, except in OS94157 where the concentrations varied widely. In OS91139, the P-ATP concentrations were uniformly about 25 ng l^{-1} in the upper layer and increased to about 75 ng l^{-1} in the lower layer. In OS94137, the P-ATP concentrations were uniformly about 50 ng l^{-1} in the upper layer and increased remarkably to 184 ng l^{-1} at the bottom layer. In OS94151, the P-ATP concentrations were uniform about 50 ng l^{-1} in the upper layer and slightly increased to about 70 ng l^{-1} in the lower layer.

Discussion

In the polynya area of the Bering Sea, Chl *a* concentrations represented low values at the upper layer above the strong pycnocline layer and increased at the lower layer below the pycnocline or near bottom layer. Particularly, high Chl *a* concentrations were observed at the lower layer and near bottom layer in OS94137. The similar vertical distribution of Chl *a* was also observed at the polynya area in summer of 1992, 1993 and 1996 (Imai et al., 1998 ; Shichinohe and Shiga, 1998). These results suggested that the vertical profile of Chl *a* concentration in this region in summer reveal a characteristic pattern ; higher value in the lower layer than that in the upper layer.

The result of the size-fractionated Chl *a* concentrations observed at both OS91139 and OS94151 implied that the percentage contribution of the greater than 10 μm fraction Chl *a* for total Chl *a* was high in the lower layer which has high Chl *a* concentration, whereas the percentage contribution of the less than 10 μm fraction Chl *a* was high in the upper layer which has low Chl *a* concentration. According to microscopical observation in the polynya area (Imai, 1994), the vertical distributions of total cell count and total biovolume of phytoplankton were similar to that of Chl *a* ; the phytoplankton assemblage was dominated by diatoms at the high Chl *a* layer and by dinoflagellates at the low Chl *a* layer. Shichinohe and Shiga (1998) also reported that the phytoplankton assemblage at the polynya area in summer of 1996 was mainly dominated by *Prorocentrum* sp. and small flagellates at the upper layer which had low phytoplankton cell abundance and by *Chaetoceros compressus, Ch. socialis* and *Nitzschia* spp. at the lower layer which had high phytoplankton cell abundance. Basically, the high Chl *a* concentrations at the lower layer encountered in the polynya area in both 1991 and 1994 were caused by the dominant large-sized diatoms, whereas the low Chl *a* concentrations at the upper layer were caused by the dominant small-sized dinoflagellates.

The vertical distributions of POC, P-ATP and P-DNA were coupled with that of Chl *a* with significant positive relationships (Table 1). This result implied that the vertical distributions of these bio-mediated materials apparently depended on that of phytoplankton biomass. Here, since the concentrations of each bio-mediated material varied remarkably at the boundary of pycnocline, the mean values of the each bio-mediated material in the upper layer and the lower layer are shown in Table 2. The mean concentrations of the

Table 1. Correlation coefficients between each bio-mediated material at the polynya area in the Bering Sea. All relationships are significant ($p<0.01$, $n=21$).

	POC	DNA	ATP
Chl *a*	0.89	0.74	0.68
POC		0.78	0.70
DNA			0.85

each bio-mediated material in the lower layer were obviously higher than those in the upper layer. Similar high concentrations of POC, Chl *a* and P-DNA have been observed at the euphotic zone in the spring bloom of Funka Bay, subarctic coastal region (Yanada et al., 2000).

The POC/Chl *a* ratio, expressed as the contribution of phytoplankton to all particulate organic matter including zooplankton and/or detritus, revealed the low value (93) in the lower layer and the very high value (546) in the upper layer (Table 3). The C/Chl *a* ratio in "living" phytoplankton is reported to be approximately 40-50 (e.g. Holm-Hansen and Mitchell, 1991). The POC/Chl *a* ratio found in the polynya area during summer is extremely high in the upper layer and slightly high in the lower layer, as compared to the C/Chl *a* ratio of the "living" phytoplankton. The extremely high POC/Chl *a* ratio in the upper layer might imply that most POC was accounted for zooplankton and/or detritus. In the upper layer, the POC/ATP ratios, expressed as the contribution of "living" organisms including phytoplankton and zooplankton, were

Table 2. The concentration of the bio-mediated materials at the upper layer and the lower layer in the polynya area in the Bering Sea.

Upper layer

Station	Depth interval	POC (μg Cl^{-1})	Chl *a* (μg l^{-1})	ATP (ng l^{-1})	DNA (μg l^{-1})
OS91139	0-20 m	102	0.2	24	1.7
OS94137	0-20 m	118	0.4	57	5.5
OS94151	0-30 m	114	0.1	48	4.3
OS94157	10-30 m	152	0.3	76	5.9
	mean	122	0.3	51	4.3
	SD	22	0.1	22	1.9

Lower layer

Station	Depth interval	POC (μg Cl^{-1})	Chl *a* (μg l^{-1})	ATP (ng l^{-1})	DNA (μg l^{-1})
OS91139	30-40 m	200	2.0	77	4.0
OS94137	30-40 m	411	15.5	130	10.5
OS94151	40-50 m	236	1.9	73	6.3
OS94157	40-50 m	228	1.9	101	7.3
	mean	269	5.3	95	7.0
	SD	96	6.8	26	2.7

Table 3. The weight ratios of each parameter at the upper layer and the lower layer in the polynya area in the Bering Sea.

Upper layer

Station	Depth interval	POC/Chl *a*	POC/ATP	POC/DNA	ATP/Ch *a*	DNA/ATP	DNA/Chl *a*
OS91139	0-20 m	593	4,292	60	0.138	71	10
OS94137	0-20 m	267	2,070	21	0.129	97	12
OS94151	0-30 m	821	2,396	26	0.343	91	31
OS94157	10-30 m	505	2,003	26	0.252	77	19
	mean	546	2,690	34	0.215	84	18
	SD	229	1,081	18	0.102	12	10

Lower layer

Station	Depth interval	POC/Chl *a*	POC/ATP	POC/DNA	ATP/Chl *a*	DNA/ATP	DNA/Chl *a*
OS91139	30-40 m	98	2,610	50	0.038	52	2
OS94137	30-40 m	26	3,171	39	0.008	81	1
OS94151	40-50 m	123	3,222	38	0.038	86	3
OS94157	40-50 m	123	2,263	31	0.054	73	4
	mean	93	2,817	39	0.035	73	2
	SD	46	462	8	0.019	15	1

extremely higher than the reported traditional ratio of "living" phytoplankton (C : ATP=250 : Holm-Hansen, 1969; Sakshaug and Holm-Hansen, 1977; Karl, 1980; Hewes et al., 1990) by an order of magnitude. It is reasonable to suppose that the most POC was accounted for detritus in the upper layer. The biological activity of phytoplankton, i.e. whether the phytoplankton was "active living" or "inactive living", can be predicted by ATP/Chl *a* ratio. If C/Chl *a* ratio and C/ATP ratio of "living" phytoplankton in the multiplication phase were defined as a carbon conversion factor of C/Chl *a*=40–50 and C/ATP=250, the ATP/Chl *a* ratio of the phytoplankton was about 0.2. The ATP/Chl *a* ratio (mean; 0.22) in the upper layer almost agreed with the calculated value. This result indicated that the phytoplankton in the upper layer represented the high biological activity, e.g. "active living", although the phytoplankton biomass was very low.

The slightly high POC/Chl *a* ratio in the lower layer might imply that the most POC apparently derived from phytoplankton. However, the POC/ATP ratios were also extremely higher than the reported traditional ratio of "living" phytoplankton by an order of magnitude. Also, the ATP/Chl *a* ratio (mean; 0.035) at the lower layer was an order of magnitude lower than that at the upper layer and the calculated value. These results might suggest that the phytoplankton at the lower layer showed lower biological activity, e.g. "inactive living" or "non-living", although the phytoplankton biomass was very high.

On the other hand, both POC/DNA and DNA/ATP ratios in relation to DNA were almost the same in both the upper layer and the lower layer, but DNA/Chl *a* ratio was low in the lower layer than in the upper layer by an order of magnitude. Calculated from the traditional conversion factor of C/DNA=50 (Holm-Hansen, 1969; DeFlaun et al., 1987; Karl and Bailiff, 1989) and the ratios of C/ATP=250 and C/Chl *a*=40 as described above, the ratios of C/DNA, DNA/ATP and DNA/Chl *a* in "living" phytoplankton were estimated to be about 50, 5 and 1, respectively. In the upper layer, DNA/ATP and DNA/Chl *a* ratios were higher than these calculated values although POC/DNA ratio was slightly low. These high values of DNA/ATP and DNA/Chl *a* ratios in the upper layer depended on DNA which is associated with "non-living" particles, because P-DNA in seawater is associated with not only "living" organisms but also "non-living" particles (Holm-Hansen et al., 1968; Winn and Karl, 1986; Boucher et al., 1991). In contrast, the DNA/Chl *a* ratio in the lower layer was extremely close to that in "living" phytoplankton, suggesting that most DNA in the lower layer seemed to associate with "living" phytoplankton. However, the DNA/ATP ratios in the lower layer were very much higher than the calculated value in "living" phytoplankton. Jones et al. (1995) reported that the DNA/ATP ratio of marine phytoplankton in laboratory cultures averaged about 17, and the value was likely much higher in senescent cells. The DNA/ATP ratio in the lower layer was higher than the calculated ratio from the traditional conversion factor or the ratio reported by Jones et al. (1995). This result also suggested that the phytoplankton in the lower layer existed as "inactive living" phytoplankton, as predicted from POC/ATP and ATP/Chl *a* ratio.

At the polynya area in summer, the water column was separated upper and lower layer by strong pycnocline. The water mass at the upper layer was occupied with the Alaska Coastal Water which had low nutrient concentrations (Imai et al., 1998). Therefore, the primary production at the upper layer was predicted to be low in summer. As the result, the standing stock of Chl *a* may be maintained at a low value. In fact, in this study, the nutrient concentration at the upper layer was low and the phytoplankton biomass dominated by small-sized phytoplankton was low although the biological activity of phytoplankton was relatively active. In contrast, the water mass at the lower layer was occupied with the Anadyr Water which had rich nutrient concentrations (Imai et al., 1998). In this study, the nutrient concentrations in the lower layer also represented very high values. The euphotic zone calculated from Secchi depth reached to near bottom layer (see Fig. 4). Hence, the light and nutrient environments at the lower layer in the polynya area in summer seemed to be sufficient to maintain the production of the phytoplankton. However, the concentrations and ratios in related to P-DNA and P-ATP did not indicate the evidence for *in situ* production of the phytoplankton. In the Bering Sea, the diatoms which was observed at the lower layer in the polynya area in summer by Shichinohe and Shiga (1998) are dominated in the spring bloom (e.g. Springer et al., 1996). Also, Shichinohe and Shiga (1998) simultaneously reported that the resting spore of *Chaetoceros* was abundance at the lower layer. Consequently, the high Chl *a* concentration observed at the lower layer of the polynya area in summer depended on inactive (probably dormant, debilitated and senescent) large-sized phytoplankton which was previously produced at the upper layer during the spring bloom period.

Acknowledgements

We are grateful to the captain, crews, scientists and cadets of the T/S "Oshoro Maru" for their kind help with sampling. We are also grateful to Dr. I. Kudo,

Laboratory of Marine Environmental Science, Graduate School of Fisheries Scinece, Hokkaido University, for encouragement and useful discussion. We wish to thank Dr. A. Shiomoto, National Research Institute of Far Seas Fisheries, for valuable comment. We would like to thank Dr. N. Shiga and Miss Y. Shichinohe, Laboratory of Marine Biodiversity, Graduate School of Fisheries Science, Hokkaido University, for valuable advice.

References

Bailiff, M.D. and Karl, D.M. (1991). Dissolved and particulate DNA dynamics during a spring bloom in the Antarctic Peninsula region, 1986-87. *Deep-Sea Res.*, **38**, 1077-1095.

Boucher, B., Vaulot, D. and Partensky, F. (1991). Flow cytometric determination of phytoplankton DNA in cultures and oceanic populations. *Mar. Ecol. Prog. Ser.*, **71**, 75-84.

DeFlaun, M.F., Paul, J.H. and Jeffrey, W.H. (1987). Distribution and molecular weight of dissolved DNA in subtropical estuarine and oceanic environments. *Mar. Ecol. Prog. Ser.*, **38**, 65-73.

Faculty of Fisheries, Hokkaido University (1992). *Data Record of Oceanographic Observations and Exploratory Fishing.* **35**, Hakodate, 374 p.

Faculty of Fisheries, Hokkaido University (1995). *Data Record of Oceanographic Observations and Exploratory Fishing.* **38**, Hakodate, 363 p.

Hewes, C.D., Sakshaug, E., Reid, F.M.H. and Holm-Hansen, O. (1990). Microbial autotrophic and heterotrophic eucaryotes in Antarctic waters: relationships between biomass and chlorophyll, adenosine triphosphate and particulate organic carbon. *Mar. Ecol. Prog. Ser.*, **63**, 27-35.

Holm-Hansen, O. (1969). Determination of microbial biomass in ocean profiles. *Limnol. Oceanogr.*, **14**, 740-747.

Holm-Hansen, O. and Mitchell, B.G. (1991). Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. *Deep-Sea Res.*, **38**, 961-980.

Holm-Hansen, O., Sutcliffe, Jr., W.H. and Sharp, J. (1968). Measurement of deoxyribonucleic acid in the ocean and its ecological significance. *Limnol. Oceanogr.*, **13**, 507-514.

Imai, K. (1994). *Study on the characteristic and biomass of biological particles of coastal in the Arctic Ocean in summer.* (in Japanese). Master's Thesis, Hokkaido University, 33 p.

Imai, K., Yanada, M. and Maita, Y. (1998). Relationship between water masses and chlorophyll a concentration in bottom water on the northern Bering shelf in summer. *Bull. Fac. Fish. Hokkaido Univ.*, **49**, 41-49.

Jones, D.R., Karl, D.M. and Laws, E.A. (1995). DNA: ATP ratios in marine microalgae and bacteria: implications for growth rate estimates based on rates of DNA synthesis. *J. Phycol.*, **31**, 215-223.

Jones, D.R., Karl, D.M. and Laws, E.A. (1996). Growth rates and production of heterotrophic bacteria and phytoplankton in the North Pacific subtropical gyre. *Deep-Sea Res.*, **43**, 1567-1580.

Karl, D.M. (1980). Cellular nucleotide measurements and applications in microbial ecology. *Microbiol. Rev.*, **44**, 739-796.

Karl, D.M. and Bailiff, M.D. (1989). The measurement and distribution of dissolved nucleic acids in aquatic environments. *Limnol. Oceanogr.*, **34**, 543-558.

Kirchman, D.L., Keil, R.G., Simon, M. and Welschmeyer, N.A. (1993). Biomass and production of heterotrophic bacterioplankton in the oceanic subarctic Pacific. *Deep-Sea Res.*, **40**, 967-988.

Odate, T., Yanada, M., Mizuta, H. and Maita, Y. (1993). Phytoplankton carbon biomass estimated from the size-fractionated chlorophyll a concentration and cell density in the northern coastal waters from spring bloom to summer. *Bull. Plankton Soc. Japan*, **39**, 127-144.

Parsons, T.R., Maita, Y. and Lalli, C.M. (1984). *A manual of chemical and biological methods for seawater analysis*. Pergamon Press, Oxford, 173 p.

Robertson, F.W. and Tait, K. (1971). Optimal condition for the fluorometric determination of DNA. *Anal. Biochem.*, **41**, 477-481.

Sakshaug, E. and Holm-Hansen, O. (1977). Chemical composition of Skeletonema costatum (Grev.) Cleve and Pavlova (Monochrysis) lutheri (Droop) Green as function of nitrate-, phosphate-, and iron-limited growth. *J. Exp. l Mar. Biol. Ecol.*, **29**, 1-34.

Shichinohe, Y. and Shiga, N. (1998). Structure and distribution of phytoplankton community south of St. Lawrence Island, northern Bering Sea Shelf in summer 1996. *Bull. Jap. Soc. Fish. Oceanogr.*, **62**, 343-355. (In Japanese with English abstract).

Springer, A.M.x, McRoy, C.P. and Flint, M.V. (1996). The Bering Sea Green Belt: shelf-edge processes and ecosystem production. *Fish. Oceanogr.*, **5**, 205-223.

Winn, C.D. and Karl, D.M. (1986). Diel nucleic acid synthesis and particulate DNA concentrations: Conflicts with division rate estimates by DNA accumulation. *Limnol. Oceanogr.*, **31**, 637-645.

Yanada, M., Tanaka, H. and Maita, Y. (2000). Temporal variation of particulate deoxyribonucleic acid in subarctic coastal seawater. *Bull. Soc. Sea Water Sci. Jpn.*, **54**, 380-389.