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Article

Biomass of Bacterioplankton and Protists and Their Ecological Importance in the Bering Sea

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Abstract : The abundance, biomass and distribution of phytoplankton, bacterioplankton and heterotrophic protists in the Bering Sea were investigated from July to August 1999. Chlorophyll *a* concentrations in the surface waters ranged from 0.16 to 3.79 $\mu g\ l^{-1}$. Nano-phytoplankton were found to constitute from 63 to 98% of the total phytoplankton biomass, and were clearly the dominant primary producers. The biomass of bacterioplankton in the surface layers varied from 1.46 to 20.2 $\mu g\ C\ l^{-1}$ and accounted for 30% of the total phytoplankton biomass. The biomass of bacterioplankton integrated over a depth of 0 to 100 m averaged 65.4% of the total phytoplankton biomass. The surface biomass of heterotrophic protists ranged from 1.2 to 27.4 $\mu g\ C\ l^{-1}$, and was within the same order of magnitude as that of bacterioplankton. Of the total biomass of heterotrophic protists in the upper 100 m of the water column, 65% was attributed to protists in the nano-size class. The results of this study suggest that bacteria and nano-protists are important components of the planktonic community in the Bering Sea during the summer season. The abundance of bacterioplankton and planktonic protists decreased from the western to northeastern and eastern regions of the Bering Sea. The abundance of these organisms also decreased with depth. The available evidence suggests that variation in the abundance and distribution of these organisms may be affected by water currents and vertical temperature variation in the Bering Sea.

Key words : bacteria, protists, biomass, ecology, Bering Sea

1. Introduction

The Bering Sea is the 3rd largest sea and is known to be one of the most productive waters in the world. Food web models of this sea have shown that diatom-produced biomass, transferred through crustacean zooplankton, is highly important for the maintenance of the food web in this region (Kang *et al*. 1996; Hood 1999). In contrast, other studies have indicated that the nano-plankton dominate the phytoplankton community; these organisms, however, cannot be directly utilized by crustacean zooplankton, such as copepods (e.g., Welschmeyer *et al*. 1993; Boyd and Harrison 1999). A limited number of studies on the bacteria (and especially the heterotrophic protists) in this area have suggested that these organisms play an important role in the planktonic community. Steward *et al*. (1996) and Kopylov *et al*. (2001) have shown that bacterioplankton abundance in the eastern shelf area of the Bering Sea could reach concentrations of 10^8 cell l^{-1}, and constituted from 20 to 40% of the total primary production. A study conducted in the southeastern Bering Sea showed the grazing of micro-zooplankton, dominated by dinoflagellates and ciliates, accounted for similar proportions of the primary production (Olson and Strom 2002).

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Studies in other Arctic and subarctic areas have demonstrated the important role of the microbial loop for energy fluxes in the planktonic community (Hansen *et al*. 1996; Rysgaard *et al*. 1999; Vehzina and Savenkoff 1999). In northern areas of the Pacific Ocean, a food chain consisting of phytoplankton (2 to 5 μm)–protozoa–mesozooplantkon has been reported, based on model analysis (Vehzina and Savenkoff 1999). The aim of this paper is to analyze the structure of micro- and nano-plankton communities and thus contribute to our understanding of the ecological importance of these organisms in the Bering Sea.

2. Materials and methods

Sample collection

Samples were collected on board the R/V "Xuelong" between July 20 to August 1, 1999. The locations of sampling sites are shown in Fig. 1. Surface water samples were collected at 28 sites. Water column samples were also collected at 10 sites using a 10-l Niskin bottles at depths of 0, 10, 25, 50, 100 and 150 m.

Measurement of nutrients and chlorophyll *a* concentrations

Water temperature and salinity data were collected using a MARK III WOCE CTD installed on the research vessel. The concentrations of various nutrients were measured according to the methods of Strickland and Parsons (1968).

Size fractionated chlorophyll *a* concentrations (<20 and ≥20 μm) were measured using a Turner Design 10-005R fluorometer, according to the method described in Holm-Hansen and Riemann (1978).

Microbial abundance and biovolume measurements

Water sample (250 m*l*) were preserved with particle-free 25% glutaraldehyde (final concentration of 1.0%) and stored at 4°C. Sub-samples (20 to 100 m*l*) were stained with DAPI for 8-10 min. and filtered onto 0.2-μm blackened Nuclepore filters using a low vacuum (<50 mm Hg) (Porter and Feig 1980). The blackened Nuclepore filters were supported by GF/F filters during the filtration process to facilitate a homogenous distribution of cells. Filtered samples were mounted on slides in immersion oil (OPTON 518C) and stored at −30°C in preparation for microscopic examination.

Microbial cells were enumerated using a Zeiss Axiovert-135 epifluorescence microscope with a blue BP 450-490 excitation filter, a FT510 beam splitter and a LP-520 barrier filter for blue light excitation. The microscope also contained a G 365 excitation filter, a FT395 beam splitter and a LP-420 barrier filter for UV light excitation. Approximately 400 to 1000 bacterial cells were counted per filter using the 1000× objective.

Heterotrophic nano-protists (<20 μm) were counted using the 1000× objective and micro-protists (≥20 μm) were enumerated using the 400× objective, as described in Sherr *et al*. (1993). Microbial cells in surface water samples from 16 sites were fractionated into size classes of 2-5 μm, 5-20 μm and ≥20 μm using a micrometer. The dimensions of at least 30 cells in the <5-μm size class were measured and the average value recorded. All cells >5 μm were counted directly, and the biovolume calculated according to shape and taxon (HELCOM 1989).

Biomass estimation

Phytoplankton biomass (including nano- and micro-fractions) was estimated based on the C:Chl *a* ratio of 50, which was reported for the northern Pacific Ocean by Booth *et al*. (1993). Bacterial biomass was estimated using a conversion factor of 20 fg C cell^{-1}, reported by Lee and Fuhrman (1987). The biomass of heterotrophic protists was estimated using the biovolumes of counted cells and applying a factor of 0.14 pg C μm^{-3}, which has been reported for Canadian Arctic waters by Lessard (1991).

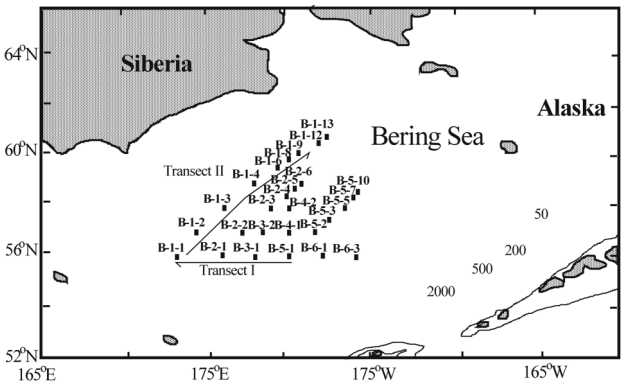

Fig. 1. Sampling sites in the Bering Sea.

3. Results

Nutrient and chlorophyll *a* concentrations

Table 1 shows spatial variation in surface water temperature, salinity and nutrients. Only small changes in the surface water temperature and salinity were recorded over the study period. Nutrient concentrations decreased from the southern to the northern parts of the study area (Fig. 2C). The trend was particularly evident for PO_4-P

Table 1. Variation of environmental factors in surface waters in the Bering Sea.

Temperature (°C)	Salinity (psu)	PO_4-P (μM)	SiO_3-Si (μM)	NO_3-N (μM)	NO_2-N (μM)
7.0-8.5	32.8-33.5	0.32-1.41	1.5-34.3	1.5-15.9	0.00-0.23

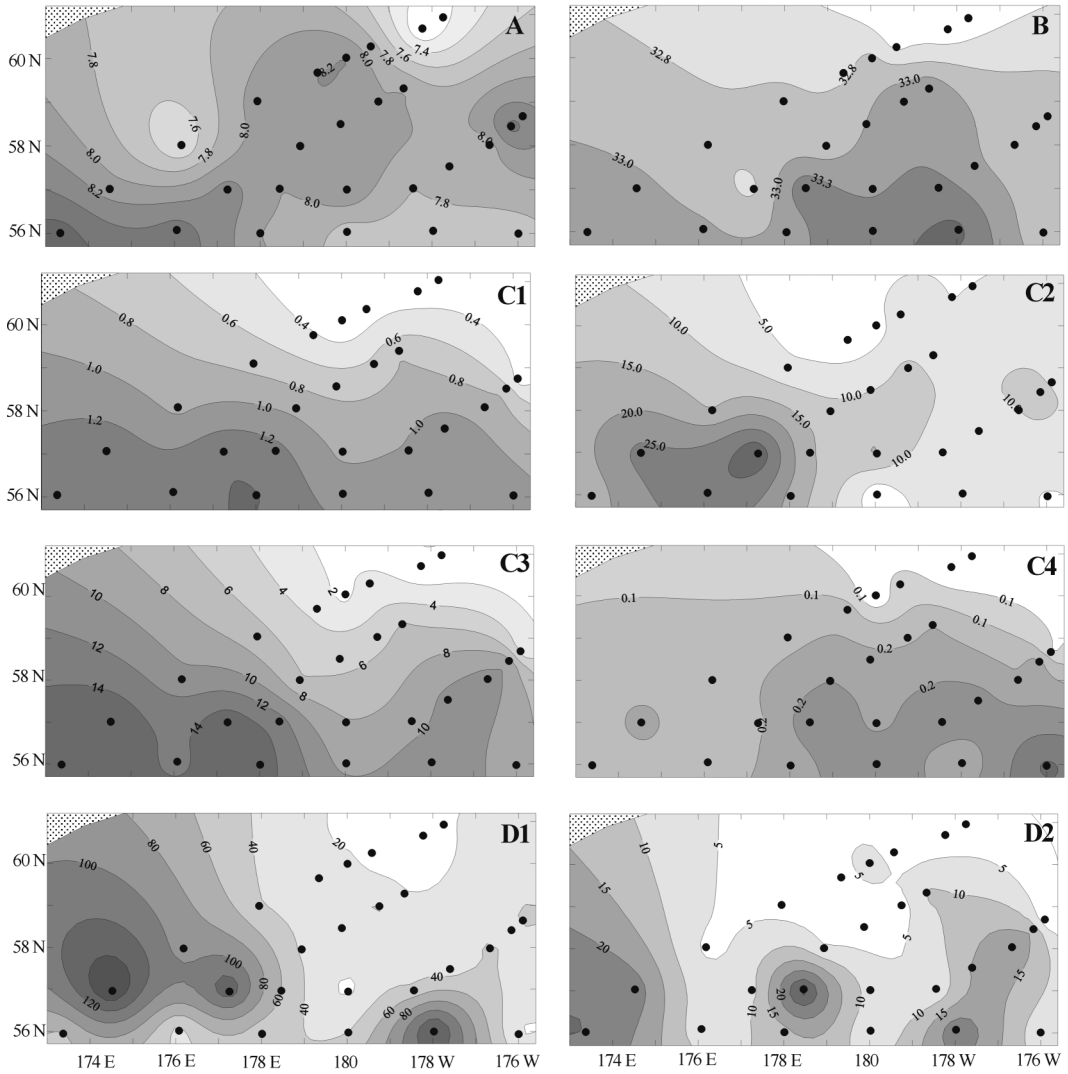

Fig. 2. Spatial variation in environmental factors and phytoplankton biomass in the surface water at the sampling sites. (A) Water temperature (°C); (B) salinity (psu); (C1-4) PO_4-P, SiO_3-Si, NO_3-N, NO_2-N (μM); (D1) nano-phytoplankton biomass (μg C l^{-1}); (D2) micro-phytoplankton biomass (μg C l^{-1}).

and NO_3-N.

The spatial variation in surface chlorophyll *a* concentration showed a similar trend, decreasing from the western to the northeastern regions of the study area (Fig. 2D). No clear relationships were detected between nutrients and chlorophyll *a* concentrations. The integrated biomass of phytoplankton in the upper 100 m of the water column varied from 1219 to 5867 mg C m^{-2} (Fig. 3). Nano-phytoplankton chlorophyll *a* concentration in the surface waters accounted for 63 to 98% (average 82%) of the total surface chlorophyll *a* concentrations. Nano-phytoplankton dominated the phytoplankton assemblages in the surface layers. These organisms were found to be the dominant primary producers in the Bering Sea over the entire study period.

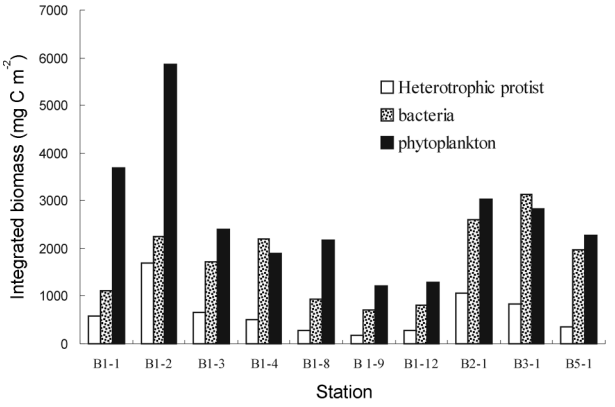

Fig. 3. Integrated biomass of phytoplankton, bacteria and heterotrophic protists in the upper 100 m of the water column (mg C m^{-2}) at several sampling sites in the Bering Sea.

Distribution, abundance and biomass of bacteria

The abundance of bacteria in the surface waters of the Bering Sea ranged from 0.7 to 10.1×10^5 cells ml^{-1}, with an average of 5.1×10^5 cells ml^{-1}. Bacterial biomass varied from 1.46 to 20.2 μg C l^{-1} at the surface, with an average value of 10.1 μg C l^{-1}. Bacterial abundance and biomass at the surface layers in the Bering Sea decreased from the western to the eastern regions of the study area, in terms of longitudinal distribution, and also decreased from the southern to the northern regions, in terms of latitudinal distribution (Fig. 4A1/B1). Both the abundance and biomass of bacteria decreased with depth (Fig. 5A).

The integrated bacterial biomass in the upper 100 m of the water column varied from 971 to 2514 mg C m^{-2} at 10 sites along the two transects (Fig. 1). The mean bacterial

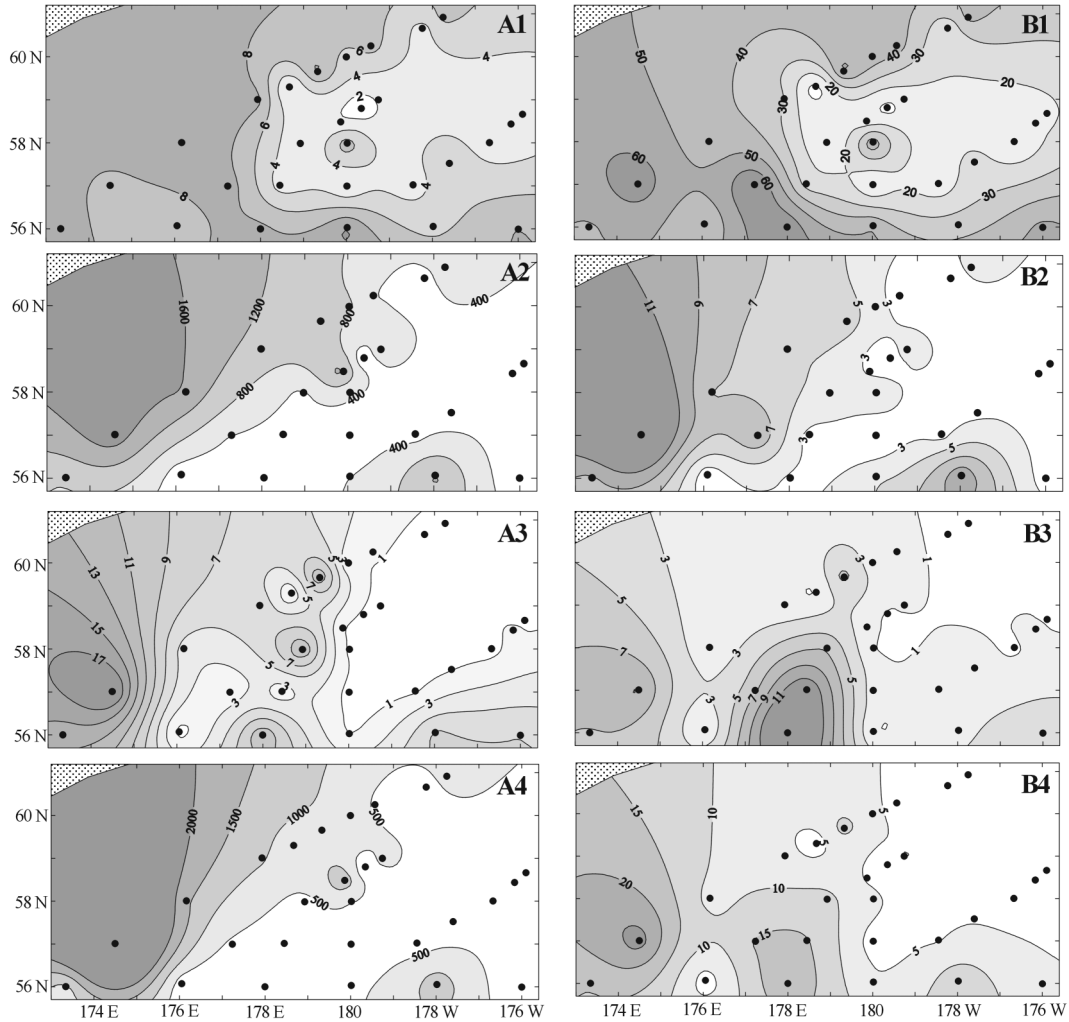

Fig. 4. Spatial variation in the abundance (A) and biomass (B) of bacteria and heterotrophic protists in surface water of the Bering Sea. A1: bacterial abundance ($\times10^5$ cells ml^{-1}); B1: bacterial biomass (μg C l^{-1}); A2-4: abundance of nano-, micro- and total heterotrophic protists (cells ml^{-1}); B2-4: biomass of nano-, micro- and total heterotrophic protists (μg C l^{-1}).

biomass was estimated to be 30% of the total phytoplankton biomass in the surface waters. The integrated bacterial biomass for the upper 100 m of the water column ranged from 31.8 to 117.2% (average 65.4%), indicating that bacteria were distributed throughout the upper 100 m of the water column during the study period.

Distribution, abundance and biomass of heterotrophic protists

Fig. 4 shows the spatial variation in abundance and biomass of nano-, micro- and total heterotrophic protists at several sampling sites in the Bering Sea. The total abundance of heterotrophic protists decreased from southwestern to northeastern regions of the study area. The vertical distribution profiles showed a similar trend to that of the surface, decreasing from the western to the eastern and northeastern regions of the study area (Fig. 5B).

The abundance of heterotrophic protists in the surface waters varied from 24 to 1907 cells ml^{-1}, with an average of 589 cells ml^{-1}. The biomass ranged from 1.2 to 27.4 μg C l^{-1} and accounted for approximately 16% of the surface phytoplankton biomass. Nano-sized heterotrophic protists were the dominant size class at most of the sampling sites. The biomass of nano-sized heterotrophic protists in the surface layers constituted over 50% of the total biomass of heterotrophic protists at 75% of the sites and contributed 60%, on average, to the integrated biomass in the upper 100 m of the water column. The average integrated biomass of heterotrophic protists was 32%; it was 21% for phytoplankton in the upper 100 m of the water column. This indicates that the abundance of heterotrophic protists in the Bering Sea was inferior to that of bacteria populations measured during the study period.

4. Discussion

Previous studies investigating the plankton community in the Bering Sea have shown that nano-phytoplankton species are the dominant organisms in terms of abundance and biomass. Anderson (1988) reported that nano-plankton account for 64% of the total primary production at some sites in the Chukchi Sea and northern Bering Sea. It was also reported by Boyd and Harrison (1999) that phytoplankton <5 μm constituted more than half the total phytoplankton biomass and primary production. Welschmeyer *et al*. (1993) reported that phytoplankton <3 μm accounted for 70% of the total primary production in spring and autumn. However, there have been few studies investigating the contribution of micro-phytoplankton to the phytoplankton communities in the marine environment (Odate 1996).

Based on the results of this study, nano-phytoplankton biomass accounted for 82% of the total phytoplankton biomass at the surface, indicating the importance of nano-phytoplankton in the processes of primary production in the Bering Sea during the summer season.

This investigation indicates that bacteria and heterotrophic protists play a significant role in the Bering Sea. The bacterial concentrations found in this study were similar to those reported for sub-arctic water of the northwest Pacific Ocean, the eastern Bering Sea and some areas of the Arctic Ocean (Steward *et al*. 1996; Sherr *et al*. 1997; Lee *et al*. 2001). Bacterial production was found to be 6.4 μg C l^{-1} day^{-1} (Chen Min personal communication). Based on the phytoplankton growth rate of 0.41 day^{-1} in the

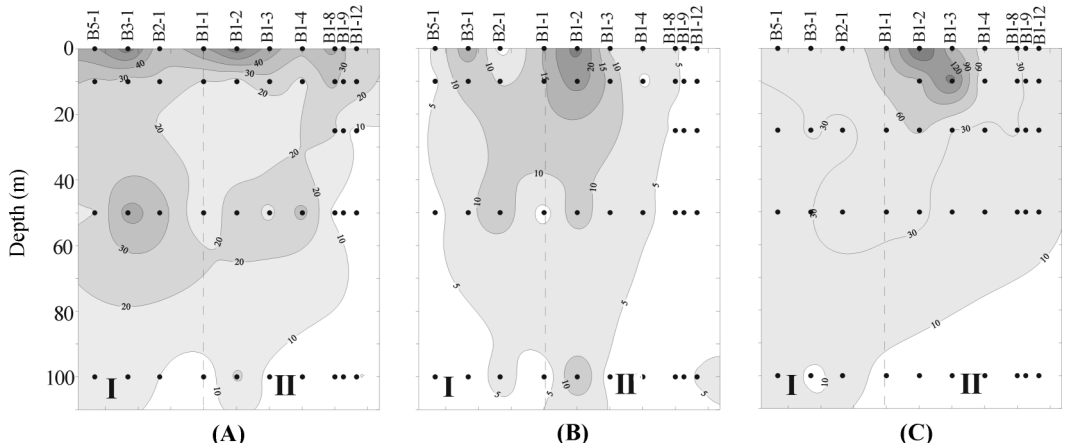

Fig. 5. Variation in the vertical distribution of (A) bacteria, (B) heterotrophic protists and (C) phytoplankton biomass (μg C l^{-1}). I: Transect I along 56°N, II: Transect II from the site B1-1 to B1-13.

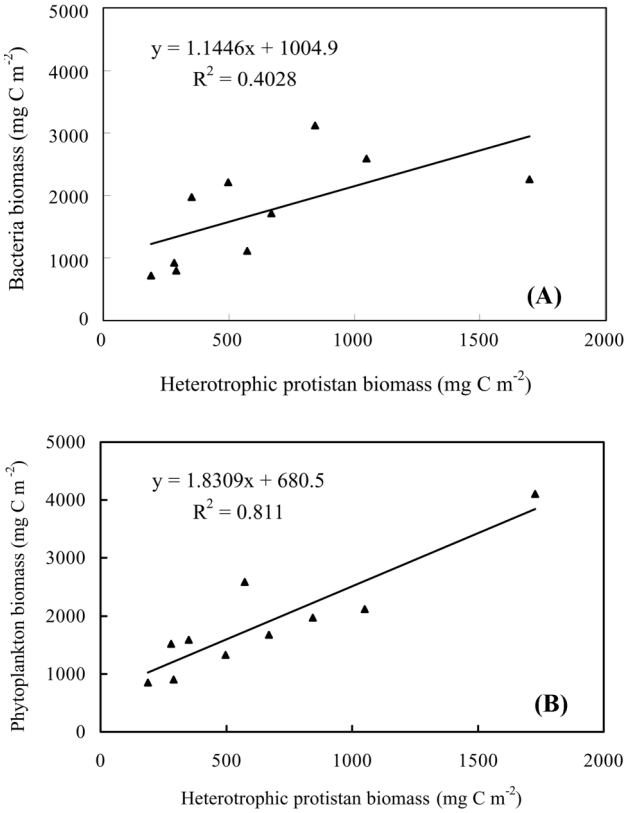

Fig. 6. Correlations between heterotrophic protists and bacteria (A), and heterotrophic protists and phytoplankton (B) in the upper 100 m of the water column.

southern Bering Sea (Liu *et al*. 2002), surface bacterial production accounted for approximately 17% of primary production at study sites in the central Bering Sea. This value was slightly lower than the range of 20 to 40% reported for eastern shallow waters of the Bering Sea (Kopylov *et al*. 2001), but very close to the value of 18% reported for sub-arctic waters of the northern Pacific Ocean (Anderson and Ducklow 2001). The ratio of bacteria to phytoplankton in the upper 100 m of the water column was found to be 67%, which was close to the value reported for the shallow eastern waters of the Bering Sea (Kopylov *et al*. 2001) but lower than the value reported for the northern Pacific Ocean (Cho and Azam 1990; Kirchman *et al*. 1993). This result indicates that bacteria are dominant in terms of abundance and biomass and are an important part of the plankton community in the Bering Sea.

Interestingly, a positive correlation was found between the biomass of heterotrophic protists and phytoplankton (Fig. 6). Research in the central Arctic Ocean has shown that phytoplankton is an important food source for protozoa (Sherr *et al*. 1997). Studies conducted in the northern Pacific Ocean, northern Bering Sea and Chukchi Sea have shown that protozoa play an important role in the nutrient flow dynamics in these ecosystems, especially in areas where nano-phytoplankton dominate the phytoplankton community (Anderson 1988; Boyd and Harrison 1993; Vehzina and Savenkoff 1999; Bury *et al*. 2001). However,

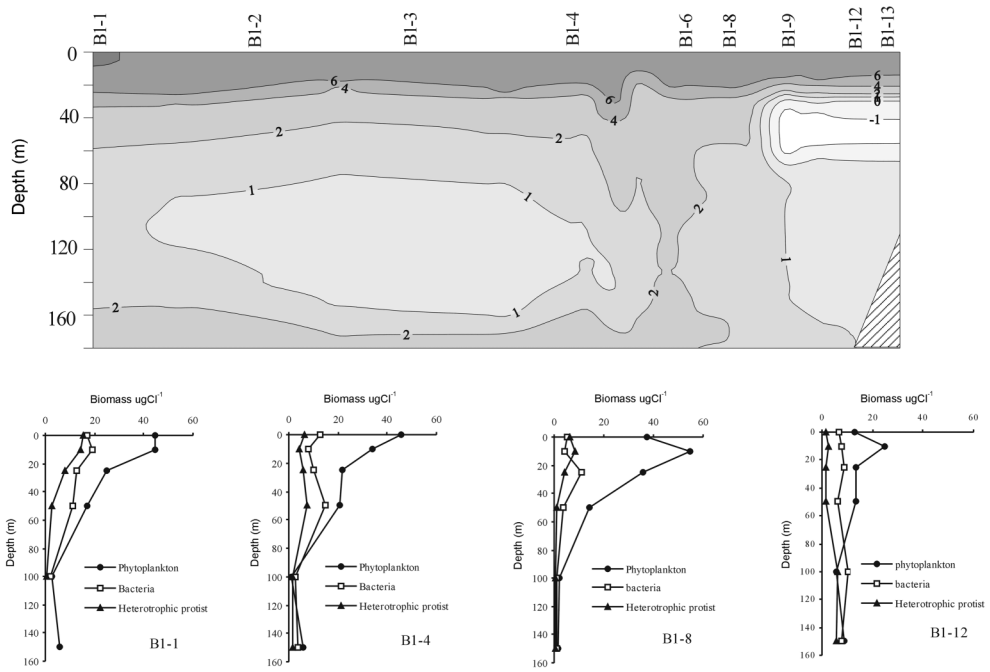

Fig. 7. Vertical distribution of temperature (ºC, the top figure) and bacterioplankton, heterotrophic protists and phytoplankton biomass for Transect II in the Bering Sea.

the abundance of heterotrophic protists in this study was lower than that of the northern Bering Sea, and similar to that reported for the central Arctic Ocean (Anderson 1988; Sherr *et al*. 1997). The great abundance of macro-zooplankton in the Bering Sea (50 g C m^{-2} in the upper 100 m of the water column, Lin *et al*. 2002) suggests that grazing pressure might be an important factor leading to a lower biomass of micro-protists.

Temperature is regarded as an important factor influencing the activity of bacteria and heterotrophic protists (Cota *et al*. 1996; Rivkin *et al*. 1999). However, in several studies, no clear relationships between temperature and bacterial activities have been reported (Rivkin *et al*. 1996; Pomeroy and Wiebe 2001). Fig. 7 shows the vertical distribution of temperature in the upper 150 m of the water column along transect II. A clear thermocline, separating the summer surface water and underlying winter water was observed at a depth of 20 to 25 m. The temperature of the water above the thermocline was consistently higher than 6°C (also see Gao *et al*. 2002). Water temperature might be an important factor affecting the vertical distribution of bacteria and heterotrophic protists, which were found to decrease in abundance with depth. The vertical distribution of planktonic organisms might also be influenced by the topography of the seabed. At site B-12, near the shelf, the abundance of bacteria and heterotrophic protists increased slightly with depth. The abundance of these organisms in the surface waters decreased markedly along the transect line (Fig. 7, also see Fig. 5). This feature might be related to the influx of surface water from the northern Pacific Ocean (Stabeno and Reed 1994).

5. Conclusion

1. The biomass of nano-phytoplankton accounted for 82% of the total phytoplankton biomass. Nano-phytoplankton was found to be the dominant primary producers in the Bering Sea during the summer season.

2. Bacterio-plankton accounted for 67% of the total phytoplankton biomass, which was similar to the biomass of phytoplankton in the upper 100 m of the water column.

3. The biomass of heterotrophic protists in integrated samples was 21% that of phytoplankton in the upper 100 m of the water column. The grazing pressure from macro-zooplankton might lead to a lower relative biomass of heterotrophic protists, which indicates a limited role for heterotrophic protists in the microbial loop.

4. The influx of surface water and variation in environmental factors with depths might also play an important role in the distribution of bacteria and protists in the Bering Sea.

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