

Productivity of picoplankton compared with that of larger phytoplankton in the subarctic region

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Abstract. We determined the productivity ($\mu\text{g C } \mu\text{g}^{-1} \text{ Chl } a \text{ h}^{-1}$) of size-fractionated phytoplankton in the northern North Pacific and the Bering Sea in summer and winter. Picoplankton ($<2 \mu\text{m}$) were more productive than larger sized phytoplankton (2–10 and 10–200 μm) in the subtropical region, where the *in situ* temperature was $>10^\circ\text{C}$; whereas picoplankton in the subarctic region were similar in productivity or less productive than larger sized plankton, where the *in situ* temperature was $<10^\circ\text{C}$. The result from the subtropical region in this study agrees with previous results from tropical and subtropical waters, which indicate that phytoplankton productivity tends to decrease with increasing cell size. The result from the subarctic region, however, differs from previous results. We observed a positive linear regression for *in situ* temperature and picoplankton productivity, but this trend was not seen in the larger sized phytoplankton. The results show that the productivity of picoplankton is markedly influenced by *in situ* temperature compared with that of larger sized plankton. Low temperature appears to account largely for the observation that the productivity of picoplankton is not significantly higher than that of larger sized phytoplankton in the subarctic region.

Introduction

Previous studies have shown that rates of metabolic processes in both multicellular and unicellular organisms decrease with increasing size (Fenchel, 1974; Banse, 1976, 1982; Peters, 1983). Results in culture experiments showed that the maximum growth rate of phytoplankton as well as phytoplankton productivity (production per unit of chlorophyll *a*) depend on cell size (Banse, 1976, 1982; Chan, 1978; Schlesinger *et al.*, 1981; Blasco *et al.*, 1982; Langdon, 1988; Sommer, 1989). Furthermore, field studies of size-fractionated phytoplankton productivity in tropical and subtropical regions demonstrated that phytoplankton productivity tends to be inversely proportional to phytoplankton cell size (Saijo and Takasue, 1965; Platt *et al.*, 1983; Takahashi and Bienfang, 1983; Joint, 1986; Taguchi and Laws, 1988).

Malone (1980) stated that netplankton ($>20 \mu\text{m}$) were noticeably less productive than nanoplankton ($<20 \mu\text{m}$) in warm (>9 – 20°C), nutrient-rich water, whereas netplankton were nearly as productive as nanoplankton in cold (<9 – 20°C), nutrient-rich water. Malone and Neale (1981) showed that in temperate estuarine and coastal environments, nanoplankton productivity was higher than netplankton productivity in warm (>9 – 16°C) water, while productivity was nearly equal in cold (<9 – 16°C) water. Furthermore, Maita and Odate (1988) showed that in subarctic coastal water, picoplankton ($<2 \mu\text{m}$) were more productive than larger sized phytoplankton (2–10 and $>10 \mu\text{m}$) in warm (10 – 20°C), nutrient-poor water in summer, while productivity was nearly equal in cold ($<10^\circ\text{C}$), nutrient-rich water in winter. In addition, the number of cyanobacterial cells, one of the main

picoplankton assemblages (Chisholm, 1992), is low in water colder than $\sim 10^{\circ}\text{C}$ (Murphy and Haugen, 1985; Joint, 1986; Odate, 1989). These previous results allow us to hypothesize that the productivity of picoplankton ($<2\ \mu\text{m}$) is not significantly higher than that of larger sized phytoplankton in water colder than $\sim 10^{\circ}\text{C}$.

The Subarctic Boundary is located around 42°N in the North Pacific Ocean; the boundary divides the ocean roughly into the subtropical and subarctic regions (Dodimead *et al.*, 1963). The surface temperature decreases as one goes north, falling below 10°C north of the boundary in summer and winter (Dodimead *et al.*, 1963; Dodimead, 1967). If our hypothesis is correct, therefore, the productivity of picoplankton ($<2\ \mu\text{m}$) will not be significantly higher than that of larger sized phytoplankton in the North Pacific north of the boundary and in the Bering Sea. The subarctic region should thus show a pattern which is different from that seen in the tropical and subtropical regions.

In this study, we measured the productivity of picoplankton ($<2\ \mu\text{m}$ fraction) and larger sized plankton (2–10 and 10–200 μm fractions) in the northern North Pacific and the Bering Sea to determine the levels of productivity for the three fractions; thereby we tested our prediction.

Method

Water sampling and incubation experiments were conducted during the cruises of the R/V 'Wakatake Maru', belonging to the Education Bureau of Hokkaido, from 4 June to 23 July 1992 and from 10 June to 26 July 1993 (summer); and during the cruise of the R/V 'Kaiyo Maru', belonging to the Fisheries Agency of Japan, from 25 November 1992 to 24 March 1993 (winter) (Figure 1). Seawater samples were collected from the surface around noon using a plastic bucket. These samples were sieved through a 200 μm mesh screen to remove large-sized zooplankton and then incubated and analyzed chemically.

The samples (1 l) were dispensed into six 1 l polycarbonate bottles and enriched with ^{13}C NaHCO₃ (99 atom% ^{13}C) to $\sim 10\%$ of the total inorganic carbon in ambient water. The samples were then incubated in sunlight and cooled with surface seawater for 2–3 h. The samples were fractionated into size classes after incubation. Immediately following incubation, two samples were directly filtered through pre-combusted (450°C for 4 h) 47 mm Whatman GF/F filters (total). Two of the remaining four samples were filtered through Nuclepore filters with a pore size of 2 μm and another two with a pore size of 10 μm . The filtrate was refiltered onto a 47 mm Whatman GF/F filter (<2 or $<10\ \mu\text{m}$ fraction). The particulate matter on the Whatman GF/F filters was rinsed with pre-filtered seawater. The filters were immediately frozen and preserved for later isotope analysis on land. They were treated with HCl fumes for 4 h to remove inorganic carbon, and completely dried in a vacuum desiccator. The isotopic ratios of ^{13}C to ^{12}C were determined through IR absorption spectrometry using a JASCO EX-130S $^{13}\text{CO}_2$ analyzer (Japan Spectroscopic Inc., Japan), according to Satoh *et al.* (1985). Particulate organic carbon was determined simultaneously. Phytoplankton productivity was calculated according to the equation described by Hama *et al.* (1983).

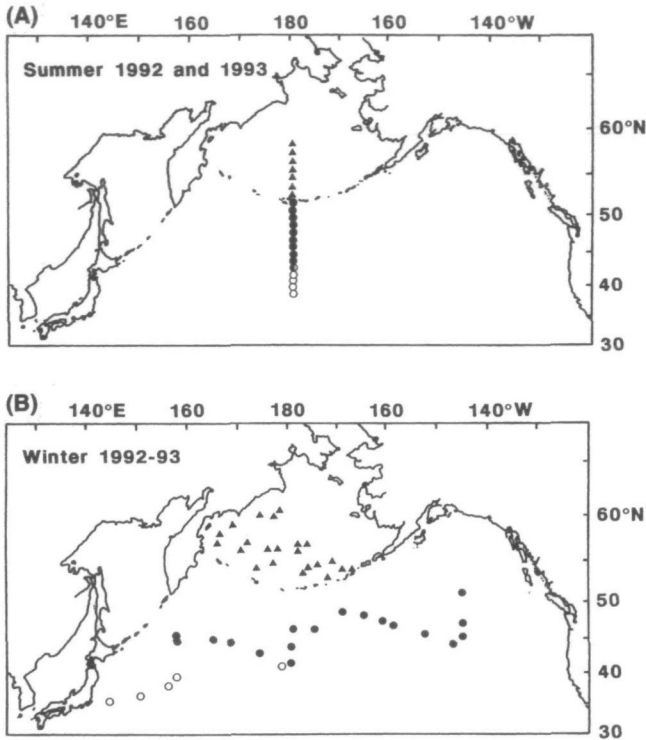


Fig. 1. Location of sampling stations in the northern North Pacific and the Bering Sea in (A) the summer of 1992 and 1993, and (B) the winter of 1992–93. Open circles, solid circles and solid triangles indicate stations in the subtropical North Pacific, the subarctic North Pacific and the Bering Sea, respectively.

Repeatability of the tracer experiment was 7.3% as the coefficient of variation for nine replications. The same methods were used for the size fractionation of chlorophyll *a* (Chl *a*) concentration. The concentration was measured with a Hitachi F-2000 fluorophotometer, according to Parsons *et al.* (1984), for samples extracted with 90% acetone. Phytoplankton production and Chl *a* concentration were thus estimated for the <2, 2–10 and 10–200 μm fractions.

We expressed phytoplankton productivity in terms of production per unit of Chl *a* ($\mu\text{g C } \mu\text{g}^{-1} \text{ Chl } a \text{ h}^{-1}$). We performed non-parametric one-way analysis of variance (ANOVA) to decide the rank order of productivity for the three fractions (Barnard *et al.*, 1993). We also performed the Kruskal–Wallis test to determine whether there were any differences in the productivity of the three fractions when the rank order was not significant at the 5% level.

Surface temperature and salinity were measured with a thermometer and an Auto Lab salinometer, respectively. Subsurface temperature and salinity were monitored by a memory STD sensor (Alec Electronics Inc., Japan) in the ‘Wakatake Maru’ cruises, and a Neil Brown CTD Mark II in the ‘Kaiyo Maru’ cruise. Surface water samples for nutrient determinations from the ‘Wakatake

Table I. Mean \pm SD (σ_{n-1}) of temperature, NO₂ + NO₃ concentration, chlorophyll *a* (Chl *a*) concentration and percentage composition of Chl *a* at the surface

Region	Year	Season	Temperature (°C)	NO ₂ + NO ₃ ($\mu\text{mol l}^{-1}$)	Chl <i>a</i> ($\mu\text{g l}^{-1}$)	Chl <i>a</i> (%)			
						<2 μm	2–10 μm	10–200 μm	
Subtropical North Pacific	1992	Summer	12.8 \pm 0.8	3.4 \pm 1.6	0.49 \pm 0.23	(4)	45 \pm 14	26 \pm 10	30 \pm 12
	1993	Summer	12.9 \pm 1.0	4.2 \pm 1.7	0.84 \pm 0.28	(5)	39 \pm 7	28 \pm 3	33 \pm 7
	1992–93	Winter	17.5 \pm 3.2	2.4 \pm 2.0	0.58 \pm 0.17	(5)	55 \pm 22	17 \pm 9	29 \pm 27
Subarctic North Pacific	1992	Summer	7.4 \pm 1.3	10.9 \pm 2.9	0.23 \pm 0.11	(10)	60 \pm 11	24 \pm 16	16 \pm 19
	1993	Summer	7.4 \pm 1.2	14.3 \pm 3.9	0.75 \pm 0.47	(9)	52 \pm 12	19 \pm 5	29 \pm 13
	1992–93	Winter	7.4 \pm 2.0	13.2 \pm 4.9	0.75 \pm 0.55	(19)	42 \pm 20	21 \pm 14	37 \pm 22
Bering Sea	1992	Summer	5.9 \pm 0.3	12.8 \pm 4.7	0.46 \pm 0.19	(6)	47 \pm 12	23 \pm 5	30 \pm 11
	1993	Summer	6.7 \pm 0.6	15.9 \pm 3.9	0.83 \pm 0.32	(7)	48 \pm 17	31 \pm 14	21 \pm 11
	1992–93	Winter	2.2 \pm 1.1	27.0 \pm 2.6	0.33 \pm 0.14	(23)	55 \pm 13	13 \pm 8	32 \pm 16

Figures in parentheses indicate numbers of data in the calculation of mean \pm SD.

Table II. Rank order of productivity for the <2-, 2–10 and 10–200 μm fractions. Non-parametric one-way ANOVA (Barnard *et al.*, 1993) was used to test significance. The Kruskal–Wallis test was also used to determine whether there are any differences in the productivity of the three fractions when the rank order was not significant at the 5% level ($Z \leq 1.64$). NS indicates no significance in the Kruskal–Wallis test at the 5% level (d.f. = 2, $H \leq 5.99$)

Region	Season	Year	Rank			Z	H
			1 (High)	2 (Middle)	3 (Low)		
Subtropical North Pacific	Summer	1992	<2 μm	2–10 μm	10–200 μm	1.86*	
	Summer	1993	<2 μm	2–10 μm	10–200 μm	1.70*	
	Winter	1992–93	2–10 μm	<2 μm	10–200 μm	2.00*	
Subarctic North Pacific	Summer	1992		NS		1.25	
	Summer	1993		NS		1.08	
	Winter	1992–93	2–10 μm	10–200 μm	<2 μm	2.41**	2.11 (d.f. = 2)
Bering Sea	Summer	1992	2–10 μm	10–200 μm	<2 μm	2.62**	
	Summer	1993	<2 μm	10–200 μm	2–10 μm	1.69*	
	Winter	1992–93	2–10 μm	10–200 μm	<2 μm	4.08***	1.16 (d.f. = 2)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$.

Maru' cruises were stored frozen and determinations were carried out using a Brab and Luebbe Traacs 800, while those from the 'Kaiyo Maru' cruise were determined immediately after collection with a Bran and Luebbe Auto Analyzer II. Total inorganic carbon in the water was measured with an IR analyzer (Shimadzu TOC 5000).

Results and discussion

The Subarctic Boundary is defined as a vertical 34.0 isohaline from the surface to ~200 or 400 m in summer and winter seasons (Dodimead *et al.*, 1963; Dodimead, 1967). Based on the vertical profiles of salinity, the locations of the boundary were determined, and the stations in the North Pacific were divided into subtropical (surface salinity > 34.0) and subarctic (surface salinity < 34.0) regions. Our stations were thus divided into three regions in the summer and winter: the subtropical North Pacific, the subarctic North Pacific and the Bering Sea (Figure 1).

Mean surface temperatures in summer in both years were nearly equal in all regions (Table I). Mean surface temperature in winter was somewhat higher than those in summer in the subtropical North Pacific; the mean value in winter was almost equal to those in summer in the subarctic North Pacific; the mean value in winter was one-third as high as those in summer in the Bering Sea. The mean temperatures were <10°C in the subarctic regions in both summer and winter.

Mean surface nitrite + nitrate concentrations in summer, for both years, were nearly equal in all regions (Table I). The mean concentrations in winter were nearly equal to those in summer in the subtropical and subarctic North Pacific; the mean winter concentration was about twice as high as the mean summer values in the Bering Sea. The mean concentrations were >10 µmol l⁻¹ in the subarctic regions in the summer and winter.

Mean surface total Chl *a* concentrations showed yearly, seasonal and regional variations (Table I). The <2 µm fraction (picoplankton), however, predominated in the Chl *a* concentration in all cases (Table I).

The ranges and means of the size-fractionated phytoplankton productivities are shown in Figure 2. The mean productivity tended to decrease with increasing cell size in the subtropical North Pacific, but no such trend was found in the subarctic North Pacific or the Bering Sea. Moreover, the mean productivity of the <2 µm fraction was higher in the subtropical North Pacific than in the subarctic North Pacific and the Bering Sea.

The rank order of productivity for the three phytoplankton fractions is summarized in Table II. In the subtropical North Pacific, the productivity of the <2 µm fraction was highest, that of the 2–10 µm fraction was next and that of the 10–200 µm fraction was lowest in the summers of 1992 and 1993. Productivity of the 2–10 µm fraction was highest, that of the <2 µm fraction was next and that of the 10–200 µm fraction was lowest in the winter of 1992–93. In the subarctic North Pacific, no significant difference was observed in productivity for the three fractions in the summers of 1992 and 1993. Productivity of the 2–10 µm fraction was highest, that of the 10–200 µm fraction was next and that of the <2 µm fraction was lowest in the winter of 1992–93. In the Bering Sea, productivity of the 2–10

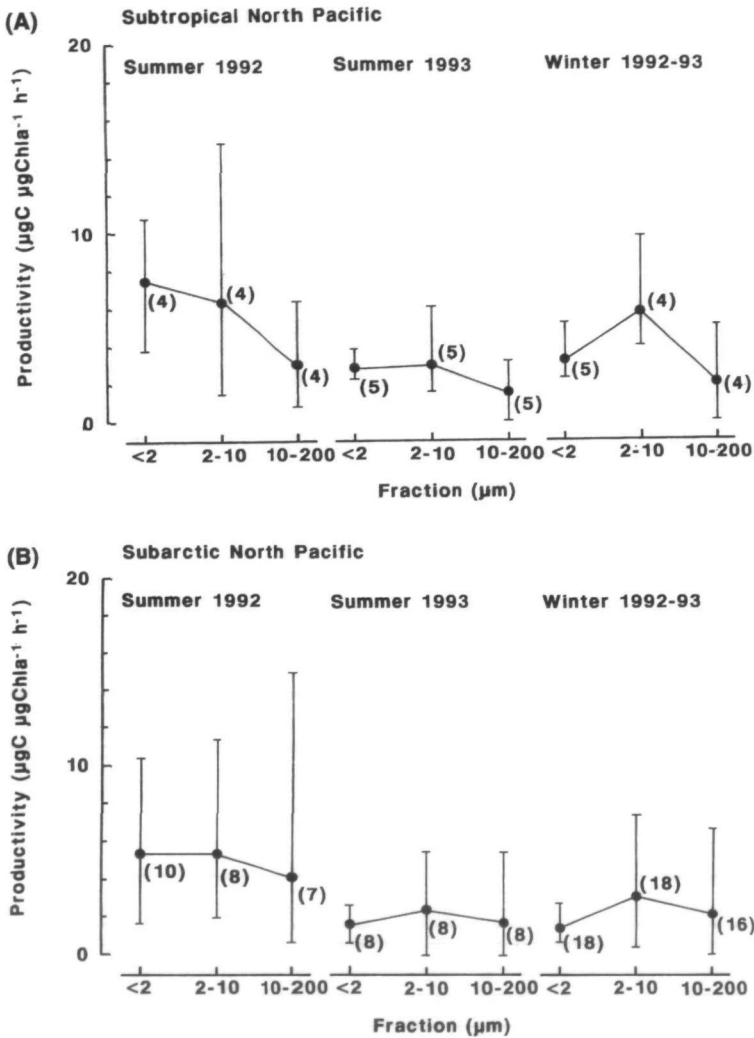


Fig. 2.

μm fraction was highest, that of the 10–200 μm fraction was next and that of the <2 μm fraction was lowest in the summer of 1992 and the winter of 1992–93. Productivity of the <2 μm fraction was highest, that of the 10–200 μm fraction was next and that of the 2–10 μm fraction was lowest in the summer of 1993. Although picoplankton (<2 μm fraction) were not always the most productive type in the subtropical region, productivity tended to decrease with increasing cell size. By contrast, such trends were not generally observed in the subarctic region. Picoplankton productivity was generally nearly equal to or lower than that of larger sized phytoplankton. The result from the subtropical region agrees with previous results from tropical and subtropical waters, which indicate that phytoplankton productivity tends to decrease with increasing cell size (Saijo and

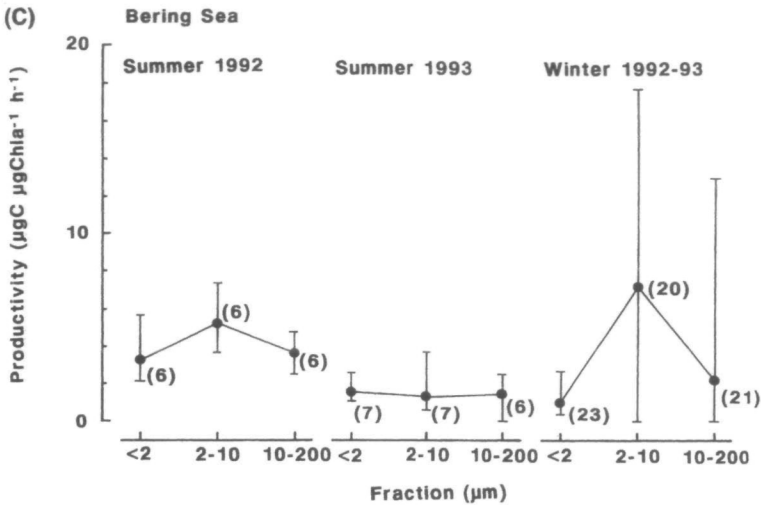


Fig. 2. Phytoplankton productivity of the <2, 2–10 and 10–200 µm fractions in the summer of 1992, the summer of 1993 and the winter of 1992–93 in (A) the subtropical North Pacific, (B) the subarctic North Pacific and (C) the Bering Sea. Solid circles indicate mean values. Upper horizontal bars and lower ones indicate maximum and minimum phytoplankton productivity, respectively. Figures in parentheses indicate numbers of data in the calculation of mean values.

Takasue, 1965; Platt *et al.*, 1983; Takahashi and Bienfang, 1983; Joint, 1986; Taguchi and Laws, 1988), whereas the result from the subarctic region differs from the previous results.

We measured productivity in conditions similar to those found *in situ*. Our results thus reflect *in situ* ranking for phytoplankton productivities of the <2, 2–10 and 10–200 µm fractions. We conducted the observations in summer and winter, and thereby the results are probably found throughout the year in the subarctic region. The results presented here substantiate our prediction that picoplankton productivity is not higher than productivities of larger sized phytoplankton in the subarctic region.

Previous studies (Malone, 1977; Malone and Neale, 1981; Platt *et al.*, 1993) indicate an exponential or linear relationship for *in situ* temperature and maximum productivity in small-sized phytoplankton (nano- and picoplankton productivity). These results suggest that *in situ* temperature plays an important role in controlling picoplankton productivity. Hence, we examined the relationship between *in situ* temperature and the productivity of each size fraction (Figure 3). A significant positive linear relationship was found for *in situ* temperature and picoplankton productivity (<2 µm fraction), and the slopes were significantly different from zero ($P < 0.01$), in all cases. However, the same results were not found in larger sized phytoplankton (2–10 and 10–200 µm fractions); furthermore, no significant Spearman rank correlation was found for *in situ* temperature and the productivity of the larger-sized phytoplankton ($P > 0.05$). Picoplankton productivity is likely to be more sensitive to *in situ* temperature than that of larger sized phytoplankton. Moreover, the ratio of the contribution (r^2) was 0.41 in the summer of 1992, 0.46 in the summer of 1993 and 0.59 in the winter of 1992–93. *In situ*

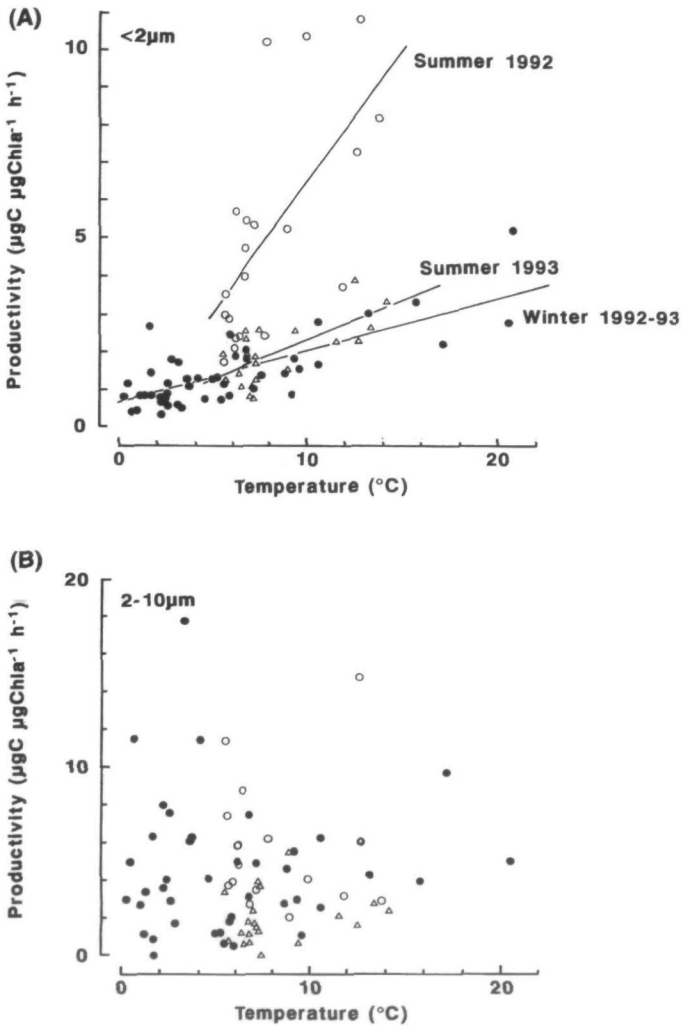


Fig. 3.

temperature accounts for nearly half the variation in picoplankton productivity. *In situ* temperature is, therefore, likely to play an important role in determining picoplankton productivity.

We examined the relationship between *in situ* temperature and productivity by using data from both the south and north of the Subarctic Boundary. Ishizaka *et al.* (1994) demonstrated that the species composition of the picoplankton community at the north of the boundary is different from that at the south of it. Thus, the linear regressions shown in Figure 3 may result from the difference in productivity among species. However, significant linear relationships were also found in the summer of 1992 ($y = 1.51x - 5.76$; $r = 0.706$, $n = 16$, $P < 0.01$) and in the winter of 1992–93 ($y = 0.10x + 0.78$; $r = 0.489$, $n = 41$, $P < 0.002$), using data from the

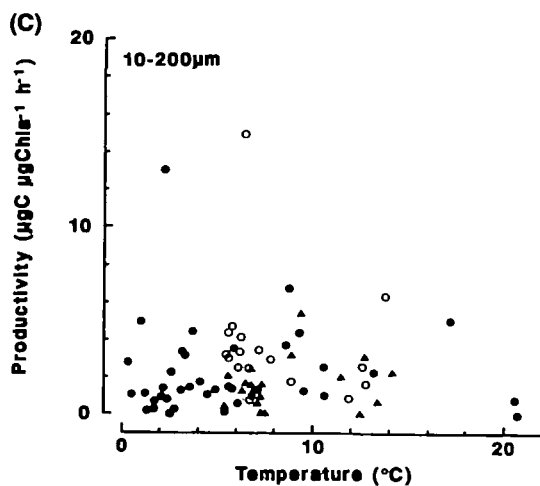


Fig. 3. Relationships between *in situ* temperature and productivity of (A) the <2, (B) 2–10 and (C) 10–200 μm fractions in the summer of 1992 (○), the summer of 1993 (Δ) and the winter of 1992–93 (●). Lines for the <2 μm fraction were obtained by least squares methods: $y = 0.69x - 0.38$ ($r = 0.642$, $n = 20$, $P < 0.01$) in the summer of 1992; $y = 0.21x + 0.25$ ($r = 0.677$, $n = 21$, $P < 0.001$) in the summer of 1993; $y = 0.14x + 0.63$ ($r = 0.765$, $n = 46$, $P < 0.001$) in the winter of 1992–93.

subarctic North Pacific and the Bering Sea ($<10^{\circ}\text{C}$). These relationships are unlikely to be due to the difference in productivities among species. This supports the importance of *in situ* temperature in determining picoplankton productivity.

Picoplankton productivity was lower in the subarctic North Pacific and the Bering Sea than in the subtropical North Pacific, whereas the productivity of larger sized plankton was roughly constant throughout the study area (Figures 2 and 3). The low picoplankton productivity results in the observation that picoplankton are not significantly more productive than larger sized plankton in these subarctic regions. The low productivity of picoplankton in the subarctic regions is likely to be due to low *in situ* temperature. It is, therefore, likely that low *in situ* temperature accounts largely for the fact that picoplankton are not significantly more productive than larger sized phytoplankton in the subarctic region.

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