Applied and Environmental Microbiology, May 1983, p. 1622–1632 Vol. 45, No. 5
0099-2240/83/051622-11$02.00/0
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Bacterioplankton in Antarctic Ocean Waters During Late Austral Winter: Abundance, Frequency of Dividing Cells, and Estimates of Production

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Received 6 December 1982/Accepted 4 February 1983

Bacterioplankton productivity in Antarctic waters of the eastern South Pacific Ocean and Drake Passage was estimated by direct counts and frequency of dividing cells (FDC). Total bacterioplankton assemblages were enumerated by epifluorescent microscopy. The experimentally determined relationship between in situ FDC and the potential instantaneous growth rate constant (μ) is best described by the regression equation $\ln \mu = 0.081\ \mathrm{FDC} - 3.73$. In the eastern South Pacific Ocean, bacterioplankton abundance (2×10^5 to 3.5×10^5 cells per ml) and FDC (11%) were highest at the Polar Front (Antarctic Convergence). North of the Subantarctic Front, abundance and FDC were between 1×10^5 to 2×10^5 cells per ml and 3 to 5%, respectively, and were vertically homogeneous to a depth of 600 m. In Drake Passage, abundance (10×10^5 cells per ml) and FDC (16%) were highest in waters south of the Polar Front and near the sea ice. Subantarctic waters in Drake Passage contained 4×10^5 cells per ml with 4 to 5% FDC. Instantaneous growth rate constants ranged between 0.029 and 0.088 h^{-1}. Using estimates of potential μ and measured standing stocks, we estimated productivity to range from 0.62 μg of C per liter · day in the eastern South Pacific Ocean to 17.1 μg of C per liter · day in the Drake Passage near the sea ice.

Bacterioplankton production in marine environments has been estimated by a variety of approaches (8, 16, 27, 45, 47; R. B. Hanson, H. K. Lowery, D. Shafer, R. Sorocco, D. H. Pope, in press). These approaches have uncertainties that limit the accuracy of production estimates. A method utilizing frequency of dividing cells (FDC) appears attractive (18, 30, 40) in that measurement of FDC is direct and does not involve the incubation of the samples. The rationale behind the FDC method is that FDC is directly related to growth rates of bacteria (10, 52), and this has been confirmed for mixed bacterial assemblages (7, 18, 40). Nevertheless, many questions remain before estimates using FDC or other approaches (or both) can be accepted (7, 30, 40, 41).

The Antarctic Ocean is the principal region where waters of the major oceans mix and interchange (26, 32, 38, 43, 51). Exchanges with the waters of the major ocean basins to the north are due to the northeast geotrophic flow of the Circumpolar Current. In the Antarctic Ocean there are four distinct zones, each with a characteristic temperature-salinity feature (51). Three fronts (barotropic currents) separate the four zones. The zones and fronts are: Continental Zone, Continental Water Boundary (Front), Antarctic Zone, Polar Frontal Zone, and Subantarctic Zone. The fronts influence biological, physical, and chemical processes between zones and oceans (21, 26, 36, 50, 51).

Many investigators have focused attention on Antarctic oceanic ecosystems, yet the significance of bacterioplankton in the food web remains unknown (5, 6, 12, 29, 33, 34, 39). The Antarctic oceanic food web has been considered a simple, linear food chain, with only a few keystone species. South of the Antarctic Convergence (Polar Front) diatoms dominate the phytoplankton, whereas north of the convergence dinoflagellates dominate (21). Most of the primary production flows through a herbivorous zooplankton chain dominated by *Euphausia superba* (39). Near sea ice, the food web is more complex because of the presence of eponitic and ice micro- and macroalgae. Nutrient-rich water is upwelled from beneath the sea ice (4, 5, 13, 42). The objective of this paper is to describe the spatial distribution of bacterioplankton assemblages in relation to the zones, fronts, and sea ice of the Antarctic Ocean in the late austral winter of 1980. Physical separation from the total population of large or "more active" (or

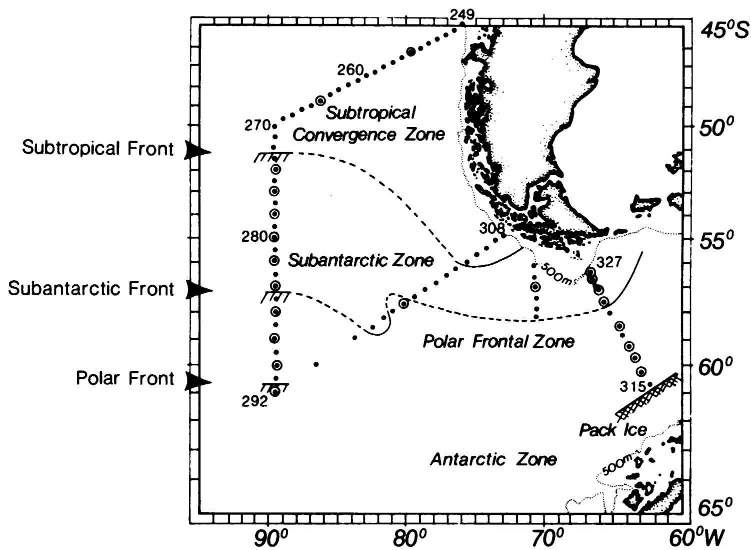

FIG. 1. Station locations in the eastern South Pacific Ocean and Drake Passage for R/V *Atlantis II* cruise 107 (XI), 13 September through 16 October 1980. Zones are based on CTD and XBT data (see Fig. 2). Symbols: ●, hydrological stations; ⊙, microbiological stations.

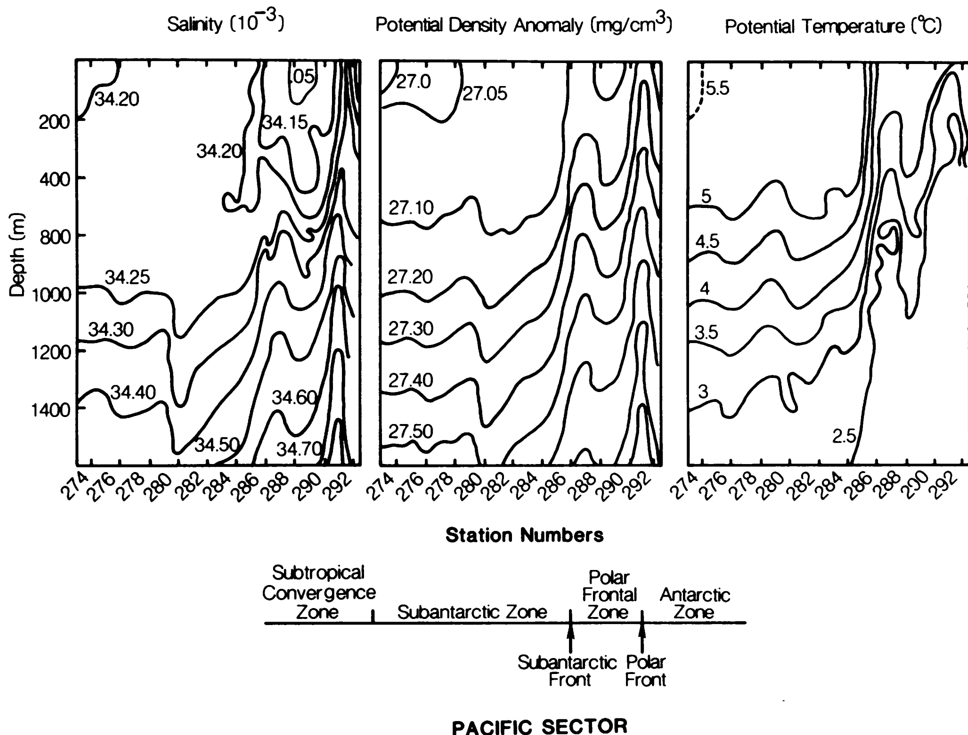

FIG. 2. Physical characteristics of water column along 90°W longitude. The shallow pycnoline north of station 174 marks the Subtropical Convergence, and south of station 286 lies the Subantarctic Front. The Subantarctic Zone lies between stations 274 and 284, and south of station 290 lies the Polar Front. The Polar Frontal Zone lies between stations 284 and 290, and south of station 292 marks the Antarctic Zone. Position of zones and fronts along transect is shown below the depiction of potential density anomaly. Physical data were provided by M. McCartney of Woods Hole Oceanographic Institution.

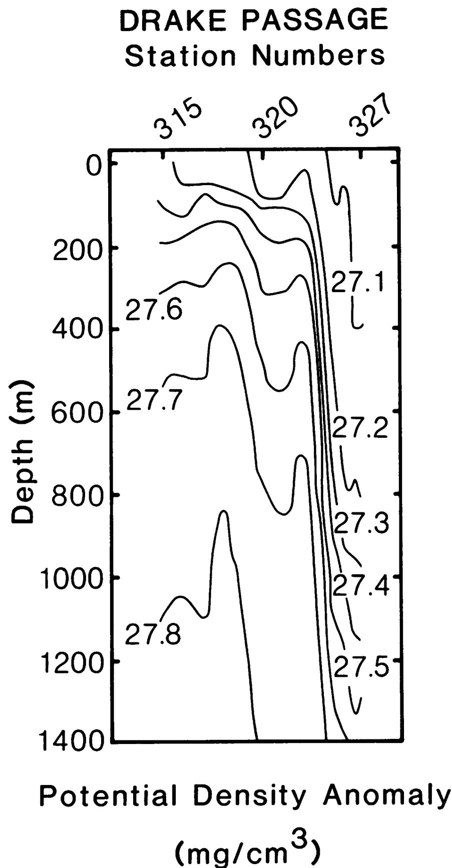

FIG. 3. Potential density anomaly (mg/cm^3) for the Drake Passage in October 1980 near 66°W longitude. Station 323 shows Subantarctic Zone water: σ, 27.115 mg/cm^3; salinity, 34.182 × 10^{-3}; potential temperature, 4.41°C. Data were provided by M. McCartney of Woods Hole Oceanographic Institution.

both) bacterioplankton on particles and free in the water was examined to determine whether bacterial growth is related to their size.

MATERIALS AND METHODS

Study area. Water samples were collected along two transects of the Antarctic Ocean: (i) along 90°W longitude from 50°S to 61°S in the eastern South Pacific Ocean, and (ii) across the Drake Passage from the sea ice (61°S) to continental slope waters off Cape Horn, Chile (Fig. 1). The hydrology was determined with Neil Brown CTD supplemented with water samples from a General Oceanic (24 bottle) rosette sampler (Fig. 2 and 3). Water for bacterioplankton studies was collected in 5- and 10-liter Niskin samplers which had been washed, rinsed with 70% isopropyl alcohol, and air dried before use.

Bacterioplankton abundance and FDC. Upon retrieval of samples, the water was prescreened through a 100-μm Nitex mesh to remove large plankton and debris. Water was dispensed into 15-ml sterile plastic vials and immediately preserved with 0.2-μm-filtered formaldehyde (final concentration, 2 to 3%). Within 1 month of collection, the acridine orange direct count (AODC) method was used to enumerate the bacterioplankton (19). Acridine orange dye (Sigma Chemical Co.) was made fresh daily with 0.2-μm-filtered seawater and formaldehyde solutions. One milliliter of water was mixed with 1 ml of 0.02% acridine orange dye and allowed to stand for 2 min in a Millipore filtration unit. The sample was then drawn through a 0.2-μm, 25-mm-diameter Nuclepore filter. The filters were prestained with irgalan black (19) or with Sudan black (54). A 0.45-μm Millipore filter was positioned between the Nuclepore filter and the filtration base to promote uniform vacuum and dispersion of bacterioplankton on the filters. Filters were thoroughly washed with 0.2-μm-filtered formaldehyde (2%) to remove the dye and salts (19) and then filtered under a vacuum of 50 mmHg (ca. 66.65 kPa). Filters were than placed on a slide with Cargille type A immersion oil above and below and covered with a cover slip. Filters were examined at ×1,000 under epifluorescent illumination (Zeiss standard 18 research microscope with an HBO 100-W lamp).

Bacterioplankton fluorescing green, yellow, and red with a definite cell shape were counted in 10 microscope fields or until 300 cells were counted. Fluorescing cells with a clear invagination were counted in 30 microscope fields or until 30 dividing cells were counted. Two investigators (D.S. and T.R.) counted samples during the cruise. There was a coefficient of variation of 20% between the counts of these investigators. To reduce this variation, the investigators were assigned specific samples and experiments. Bacterioplankton abundance was calculated from the average number of cells per microscope grid, the number of grids per effective filtration area, and the volume of sample filtered. The FDC was calculated from the average number of dividing cells per grid divided by the average number of total cells per grid. This value was multiplied by 100 to transform to percentage. The coefficient of variation ranged from 20 to 40% for the bacterioplankton counts and 50 to 110% for dividing cells. Large variation was due to the limited number of replicates (three) counted at some stations or depths, the volume filtered, and the patchy distribution of bacterioplankton (28, 40).

Experimental incubations. The FDC method of estimating bacterioplankton production is based on theoretical considerations and experimental evidence that FDC is directly related to the growth rate of bacteria in culture (18, 40, 52). To determine the relationship between FDC and growth rates of Antarctic bacterioplankton, bottle incubation experiments were performed in which nutrients and temperature were varied. The purpose of these experiments was to induce a variety of growth rates and FDC's under different growth conditions.

For nutrient enrichments, sterile yeast extract solutions were added to <100-μm-screened and <3-μm-filtered seawater. Four concentrations of yeast extract were used to simulate levels of natural dissolved organic carbon (0, 1, 5, and 10 mg/liter). Bottles (250 ml) were acid washed and sterilized by dry heat (160°C for 4 to 6 h). Zero-time samples (2 ml) were taken from each bottle after agitation and preserved with 2% (final concentration) bacteria-free formaldehyde. Enriched

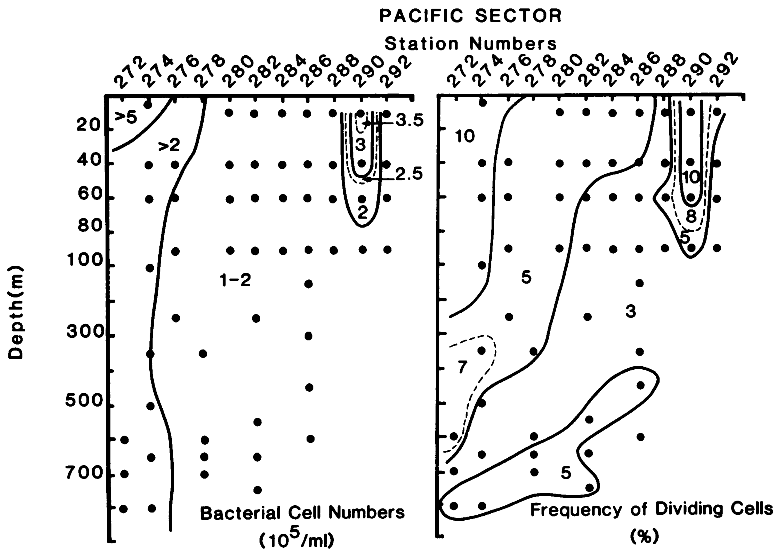

FIG. 4. Bacterial cell numbers (×10^{5} per ml) by AODC and FDC (%) in the water column along 90°W longitude (eastern South Pacific Ocean).

samples were incubated in the dark at in situ temperature in Blue M refrigerated water baths and periodically sampled. For temperature-shift experiments, 3-μm-filtered seawater was incubated at 0, 5, 10, and 15°C.

Instantaneous growth rate constants (μ) were generated from the cell densities over time in each experiment (18, 40). The formula:

$$\mu = \frac{\ln N_{t2} - N_{t1}}{(t_2 - t_1)}$$

where N_{t2} and N_{t1} are cell densities at times 1 and 2 and $(t_2 - t_1)$ is the time interval in hours, was used (48). Linear regression analysis was performed on values for FDC at t_2 and μ (ln μ) for $t_2 - t_1$. Only values that were within the period of increasing numbers of cells were used to determine the relation between FDC and μ (ln μ) (40). Zero-time values were not used.

Size fractionation and predation experiments. Differential filtration was used to determine the relative size distribution of bacterioplankton. Nuclepore filters with porosities of 0.2 and 3 μm were used to examine AODC and FDC.

Possible microprotozoa effects on AODC and FDC over time were examined by concentrating (2×) samples. Particles were gently concentrated in water above 3-μm Nuclepore filters by gravity filtration; these filters retain the larger microprotozoa and particles. Unconcentrated and concentrated seawater from the incubations were periodically sampled and preserved.

RESULTS

Distribution patterns of bacterioplankton. In surface waters of the eastern South Pacific Ocean (Fig. 4), bacterioplankton concentrations decreased from 7.2×10^5 cells per ml in the Subtropical Convergence Zone (station 272) to 1.3×10^5 at the Subantarctic Front (station 284). There was no significant change in the standing stock across the Subantarctic Front. At the Polar Front (station 290), the standing stock increased to 3.5×10^5 cells per ml. Below approximately 100 m, abundance remained low, near 1×10^5 to 2×10^5 cells per ml, between the Subantarctic Zone and the Antarctic Zone.

In the Drake Passage, the standing stocks of bacterioplankton were 2 to 3 times higher than those in the eastern South Pacific Ocean. A cross-section of their distribution from the sea ice to the continental slope waters off Cape Horn is shown in Fig. 5. Two areas of high concentration were found in euphotic waters of the Antarctic Zone (station 316) near the sea ice and in the Subantarctic Front (station 323). Mesopelagic waters (400 to 600 m) near the South American continental shelf also had some high abundances.

Distribution patterns of dividing bacterioplankton. The FDC for bacterioplankton in the eastern South Pacific Ocean is shown in Fig. 4. Northern waters of the Subantarctic Zone and the Polar Front possessed the highest FDC (10%) whereas most samples along the 90°W longitudinal section contained bacterioplankton with FDC's of 3 to 5%.

In the Drake Passage, FDC's were generally higher than in the eastern South Pacific Ocean (Fig. 5). Populations in the waters of the southernmost section of the Passage and near the sea ice had the highest FDC (10 to 16%). FDC

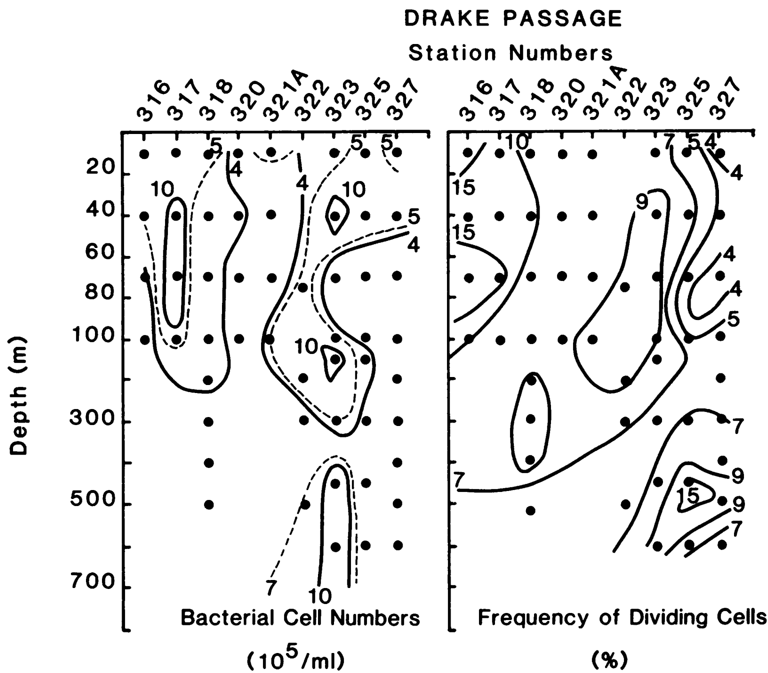

FIG. 5. Bacterial cell numbers ($\times 10^5$ per ml) and FDC (%) in the water column of Drake Passage.

decreased across the Passage into warmer Subantarctic Zone waters. In deep slope water (400 to 600 m) off Cape Horn, populations had a relatively high FDC of 10 to 15%.

Experimental incubations. The growth response of mixed bacterioplankton assemblages to changes in water temperature, filtration treatment, and nutrient concentration were examined. Figure 6 shows the change in AODC and FDC in 3-μm-filtered seawater from station 265 enriched with yeast extract. At the concentrations employed, yeast extract did not increase AODC or alter FDC values relative to unenriched seawater. Similar growth curves were observed for yeast extract enrichments of 100-μm-screened water from stations 255 (10°C ambient water temperature) and 298 (5°C ambient water temperature), although the maximum AODC were 35 to 96% lower than in 3-μm-filtered seawater. Our temperature-shift experiment in which the ambient water temperature of 4.9°C at station 311 was altered to 0, 5, 10, and 15°C indicated that growth in 3-μm-filtered seawater was not influenced by a 10°C increase or 5°C decrease in ambient temperature (data not shown).

Instantaneous growth rates (μ) from various experiments were calculated for specific time intervals when cell numbers were increasing. Linear regression statistics (Table 1) indicate that growth rates correlated significantly with FDC and that the slopes were significantly different from zero ($P < 0.1$ to $P < 0.001$). Because regressions 1 through 3 show negative y-intercepts and to determine whether the data sets could be pooled, the slopes were tested for equality (H_0: $\beta_1 = \beta_2 = \beta_3 = \beta_4$) by analysis of covariance. The analysis indicated that the slopes were not significantly different [F ratio < F(0.05) degrees of freedom 3, 30]. Therefore the data were pooled and the regression of μ on FDC was determined (regression 5, Table 1). This regression was highly significant ($P < 0.001$), with the y-intercept near zero (0.0003 ± 0.0023). Linear regressions of the untransformed data, however, indicated high coefficients of variation (0.39 to 0.67). To reduce variation and for theoretical considerations of bacterial growth, growth rates were transformed to natural logarithms (ln μ) and plotted against FDC (Fig. 7). Linear regression statistics for regressions of ln μ on FDC are presented in Table 1. Coefficients of variation of the transformed data (0.15 to 0.27) averaged 63% lower than those for the untransformed data.

Instantaneous growth rates (μ) and generation times ($1/\mu$) were calculated from the linear regression of the pooled, transformed data ($\ln \mu = 0.081$ FDC $- 3.73$; Fig. 7). This equation was used because of the lower coefficient of variation (0.26 as opposed to 0.73 for the untransformed data), and the regression slopes of the

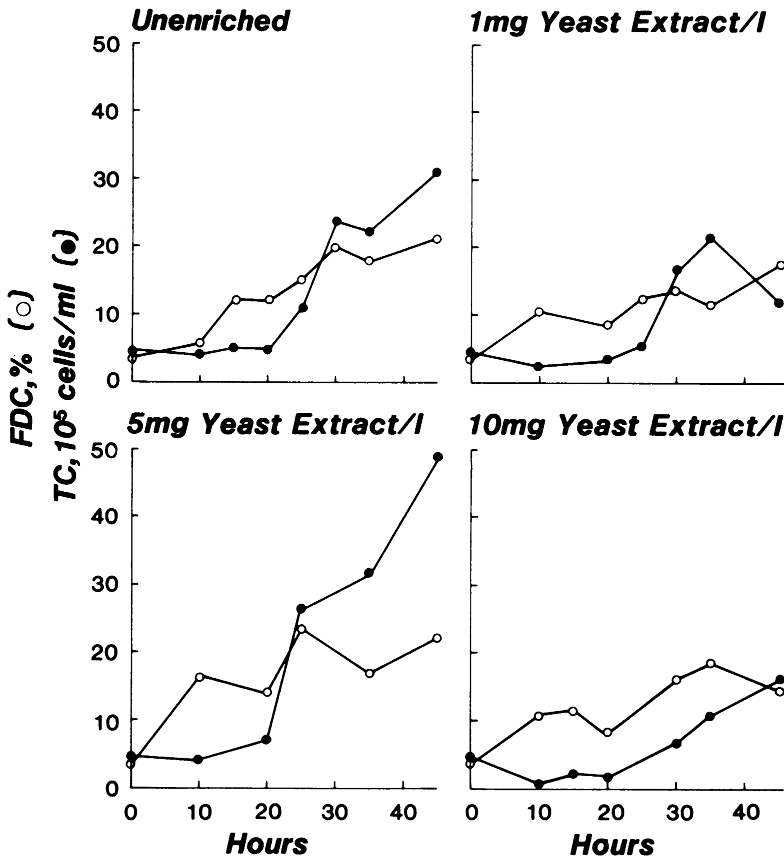

FIG. 6. Changes in AODC per ml (TC) (●) and FDC (○) with time for unenriched and enriched (1, 5, and 10 mg of yeast extract per liter) <3-μm-filtered 6°C water from 40 m at station 265. Bottles were incubated at 6°C.

untransformed data were not significantly different. Predicted growth rates and generation times for zones and fronts in the eastern South Pacific and Drake Passage are presented in Table 2. Growth rates and generation times estimated from FDC, using the regression equation, ranged from 0.088 to 0.032 h^{-1} and 11 to 31 h, respectively. Bacterioplankton assemblages in the eastern South Pacific Ocean had the highest growth rate and shortest generation times at the

TABLE 1. Linear regression statistics for regressions of μ and ln μ on FDC from bottle incubation experiments[a]

No.	Station	N	Regression	Slope ± SD[b]	y-Intercept ± SD	r	F[c]	CV
1	255	5	μ on FDC	0.004 ± 0.001[A]	−0.016 ± 0.017	0.89	11.30**	0.46
			ln μ on FDC	0.105 ± 0.034	−4.80 ± 0.497	0.87	9.39**	0.15
2	265	14	μ on FDC	0.012 ± 0.003[A]	−0.086 ± 0.060	0.70	11.30***	0.65
			ln μ on FDC	0.112 ± 0.038	−4.09 ± 0.598	0.64	8.51**	0.27
3	298	4	μ on FDC	0.013 ± 0.005[A]	−0.037 ± 0.043	0.88	7.07*	0.39
			ln μ on FDC	0.191 ± 0.078	−4.82 ± 0.642	0.88	6.88*	0.17
4	311	7	μ on FDC	0.003 ± 0.001[A]	0.012 ± 0.010	0.76	6.93**	0.67
			ln μ on FDC	0.068 ± 0.034	−3.86 ± 0.040	0.67	4.03*	0.22
5	Pooled 1–4	30	μ on FDC	0.006 ± 0.001	0.000 ± 0.023	0.59	14.00****	0.73
			ln μ on FDC	0.081 ± 0.020	−3.73 ± 0.278	0.58	14.30****	0.26

[a] Abbreviations: N, number of paired data; r, correlation coefficient; F, calculated F value; CV, coefficient of variation (σ_y/Y).

[b] Slopes with same letters indicate no significant difference at the 95% confidence level.

[c] Asterisks indicate the level of significance: *, 0.1; **, 0.05; ***, 0.01; ****, 0.001.

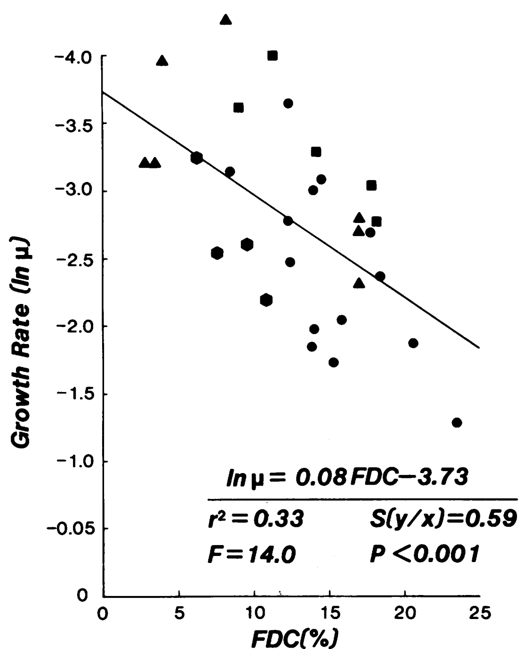

FIG. 7. Linear regression for ln μ on FDC from bottle incubation experiments. Experiments include nutrient enrichments with 0, 1, 5, and 10 mg of yeast extract per liter; 10°C water from 40 m at station 255 (■); <3-μm-filtered, 6°C water from 40 m at station 265 (⬣) at 0, 5, 10, and 15°C; 5°C water from 40 m at station 298 (●); and incubation of <3-μm-filtered, 5°C water from 40 m at station 311 (▲). Instantaneous growth rates (μ) were calculated from differences in AODC per ml within the period of (exponential or linear) growth for each enrichment or incubation temperature.

Polar Front and in northern Subantarctic Zone waters. In Drake Passage, growth rates decreased and generation times increased from the sea ice in the Antarctic Zone to warmer waters in the Subantarctic Zone.

In general, 57 to 135% (average, 92%) of the bacterioplankton in Antarctic waters were in 3-μm-filtered seawater (Table 3). Active bacterioplankton were not excluded from the incubations. In most cases, FDC's were as high in the 3-μm-filtered seawater as in unfiltered samples. Thus, size fractionation (<3 μm) did not bias the experimental incubations toward small and inactive bacterioplankton but may have eliminated many predators and extraneous particles.

The influence of predation and particles on AODC and FDC in incubations is illustrated in Fig. 8. AODC's were lowest and FDC's highest in the treatment in which the concentrations of bacterivores and particles were approximately doubled by concentration of the samples.

DISCUSSION

The influence of oceanic fronts on biological productivity has received increasing attention. It has been suggested, from increased biological activity noted at fronts, that a suitable chemical and nutrient environment exists for high productivity (3, 14, 22, 44). In the Antarctic Ocean, most past biological investigations have indicated that the Polar Front (Antarctic Convergence) is an important biological-physical feature (21, 37, 50). Our results indicate that bacterioplankton populations are also greatest and appear most active at the Polar Front relative to other fronts and zones in the Antarctic Ocean. At the Polar Front in the eastern South Pacific Ocean (see Fig. 2), strong isopycnals produce a dynamic physical-chemical environment which enhances bacterioplankton productivity. At the Subantarctic Front, there was a strong vertical isopycnal (σ = 27.1), and waters north of the front were isothermal (5°C) and chemically homogeneous to a depth of about 600 m. Consequently, bacterioplankton productivity apparently was favored in the Polar Front as no variation in FDC or standing stocks was ob-

TABLE 2. Predicted growth rates and generation times of bacterioplankton assemblages in 10-m waters in the eastern South Pacific Ocean and Drake Passage[a]

Area	Station	Zone/Front[b]	Total cell count (×10^5 per ml)	FDC (%)	μ (h⁻¹)	1/μ (h)
Pacific sector	274	SAZ	7.2	9.5	0.052	19
	276	SAZ	ND[c]	ND	ND	ND
	280	SAZ	1.5	5.4	0.037	27
	282	SAZ	1.3	5.7	0.038	26
	284	SAF	1.4	5.4	0.037	27
	288	PFZ	0.9	3.8	0.033	31
	290	PF	3.6	11.2	0.059	17
	292	AZ	1.3	5.0	0.036	28
Drake Passage	316	AZ (Sea ice)	5.2	16.0	0.088	11
	317	PF	6.9	12.0	0.063	16
	318	PF	5.8	9.1	0.050	20
	320	PFZ	2.9	8.4	0.047	21
	321	PFZ	4.0	7.8	0.045	22
	323	SAF	4.9	7.2	0.042	23
	325	SAZ	5.8	6.2	0.040	25
	327	SAZ	4.4	3.7	0.032	31

[a] Calculations based on the regression of ln μ on FDC (Fig. 7).
[b] Abbreviations: SAZ, Subantarctic Zone; SAF, Subantarctic Front; PFZ, Polar Frontal Zone; PF, Polar Front; AZ, Antarctic Zone.
[c] ND, Not determined.

TABLE 3. Bacterioplankton abundance and FDC in water samples from <100-µm (total) and <3-µm fractionations[a]

Location	Station	Depth (m)	No. of cells (×10^5 per ml)		Cells <3 µm	FDC	
			Total	<3 µm		Total	<3 µm
Pacific transect	274	5	7.2	5.4	75	10	2
		40	3.0	1.7	57	4	8
		60	3.1	3.0	97	11	6
		100	3.4	2.5	74	11	16
	280	10	1.7	1.5	82	4	3
		40	1.8	1.3	72	5	5
		60	1.3	1.1	85	6	6
		90	1.2	1.1	92	5	6
	296	10	1.7	1.7	100	7	6
		40	1.4	1.9	135	5	3
		60	1.7	1.7	100	3	4
		90	1.9	1.8	94		
	292	10	1.3	1.5	115	5	4
		40	1.5	1.7	113	4	4
		60	1.3	1.2	92	4	5
		90	1.2			3	
Drake Passage Transect	316	10	5.2	4.7	90	16	27
		40	5.0	4.5	90	12	14
		70	3.8	3.4	90	15	14
		100	3.8	3.4	90	13	20

[a] Stations in the eastern South Pacific Ocean were along 90°W longitude, and stations in Drake Passage were near 66°W longitude.

served across the Subantarctic Zone or with depth.

In the Drake Passage where Antarctic fronts and zones are constricted, the Antarctic Polar Front meanders seasonally up to 100 km north and south of its mean path (51). At times, meanders pinch off and form cyclonic rings containing cold-core water (25, 43). Presumably, different barotropic and baroclinic processes occur seasonally and geographically across the Polar Frontal Zone as the Antarctic Circumpolar Current flows east (36). Whether the sea ice influences the spatial scales of fronts and zones in the Passage has not been determined. Our results indicate that bacterioplankton populations in the Drake Passage were not concentrated at the Polar Front as in the eastern South Pacific. In the Drake Passage, the Subantarctic Front ($\sigma = 27.1$) delineates waters containing highly productive bacterioplankton (FDC > 7%) of the Antarctic and Polar Frontal Zones from waters with moderately productive populations (FDC < 5%) in the Subantarctic Zone.

South of the Polar Front, in the vicinity of the sea ice, bacterioplankton productivity was influenced by processes at the ice edge. Sea ice covers 16×10^6 to 20×10^6 km^2 and extends hundreds of kilometers out to sea (5, 6). The productivity of the ecosystem is greatly affected in the vicinity of sea ice throughout the year (2, 20, 31). Enhanced biological productivity at the ice edge has been attributed to: (i) the release of microalgae and nutrients from the sea ice during ice deterioration (1, 5, 13); (ii) upwelling of nutrient-rich waters from beneath the sea ice that is attributed to wind-driven Ekman transport (2, 4, 42); and (iii) lateral movement of water away from the pack ice.

Compared with available information on photosynthetic production in and adjacent to sea ice, far less is known about heterotrophic microbial production. Microheterotrophs in a pack-ice area (Ross Sea Ice Shelf) have high metabolic activity (17, 37). In our study of populations across the Drake Passage, bacterial standing stocks were high from the sea ice to approximately 110 km north of the ice edge. The area of highest productivity (FDC, 10 to 16%) was within 50 km of the sea ice. Bacterioplankton populations were not measured at the ice edge (station 315, Fig. 1). The ice edge in early October was starting to disintegrate and break up from sea waves.

Bacteria are the most abundant, yet the least understood, organisms in planktonic oceanic communities. One reason for this is our inability to accurately measure their productivity. Although several methods are available for estimating productivity, only the FDC (18) and thymidine (16) procedures have been used to examine bacterioplankton dynamics.

FDC measured in natural waters requires calibration with natural or axenic experimental cultures to determine the relation between FDC and growth rates (18, 40). Accurate interpretation of FDC data depends on the growth kinetics of the natural assemblages and whether their growth resembles that in bacterial cultures (23, 24, 30, 40). We observed that bacterioplankton abundance did not increase until 10 to 20 h after incubation, although FDC increased after 10 h. These results suggest that growth was slow or that only a part of the assemblage was growing exponentially (7). Fuhrman and Azam (15) assumed linear growth for marine bacteria in culture, whereas Newell and Christian (40) assumed exponential growth in experimental cultures of mixed assemblages. These conflicting assumptions indicate that problems remain in applying the FDC approach to estimate production (7, 18, 30, 40, 41). These problems are illustrated by some specific questions. (i) Do different physiological and functional bacterioplankton types possess different FDC-growth rate relations? (ii) Do mixed (natural) bacterioplankton assemblages exhibit exponential or lin-

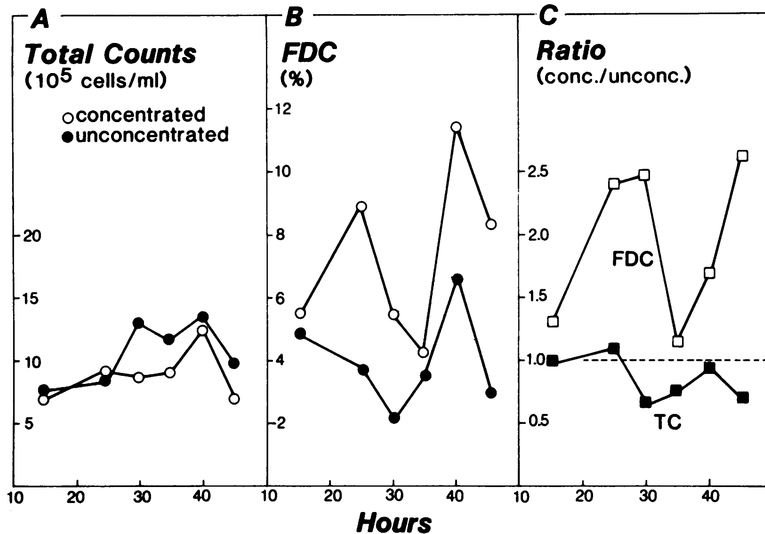

FIG. 8. Particle concentration effects on (A) bacterial cell numbers (AODC) and (B) FDC (%) in bottle incubations. Water samples from station 311 were concentrated (○) 2× (>3 μm) and compared with unconcentrated (●) samples. Incubation temperature was 4°C. (C) The concentrated/unconcentrated ratio is plotted for FDC (□) and total counts (TC, ■).

ear growth? (iii) Are bacterioplankton in steady-state growth? (iv) Do experimental cultures alter the growth state or size structure (or both) of natural assemblages? (v) Do bacterivores modify or stimulate growth of bacterioplankton? Until these questions are answered, the FDC approach for estimating bacterioplankton production must be used cautiously.

A mathematical relationship between FDC values and growth rates of Antarctic bacterioplankton was determined under a variety of simulated environmental conditions. Our data confirm that there is a statistically significant linear relationship between calculated growth rate constants (μ) and FDC values and that simple linear regression of μ on FDC (coefficient of variation, 0.73) was not as good a fit as the transformed data of ln μ on FDC (coefficient of variations, 0.26). Therefore, we applied the regression formula from the transformed data to estimate instantaneous growth rate constants. These constants (μ) were estimated from field FDC values (range 3 to 16%) by using the derived regression equation $\ln \mu = 0.081\ \mathrm{FDC} - 3.73$. The computed μ values (range, 0.029 to 0.088 h^{-1}) were very similar to those calculated by Hagström et al. (0.01 to 0.1 h^{-1}) (18) and Newell and Christian (0.017 to 0.063 h^{-1}) (40). Sorokin et al. (47) estimated the growth rates of marine bacteria to be between 0.013 and 0.042 h^{-1}.

The extrapolation of instantaneous growth rate to production also depends on the steady-state growth condition of the population. Not all cells are active (49, 53), and short-term (hours) variations in microbial activity occur (35). However, oceanic bacterioplankton populations appear to be in quasi-steady-state growth (23, 24; R. B. Hanson and H. K. Lowery, in press). Therefore, there are relatively large differences in FDC values, the derived regression equation should provide predictive estimates of productivity.

Production rates were estimated from the computed instantaneous growth rate constants (μ). In the eastern South Pacific, μ and bacterioplankton abundance varied from 0.033 to 0.059 h^{-1} and 1×10^5 to 3.6×10^5 cells per ml, respectively. Assuming a conversion factor for cells to carbon of 8.3×10^{-15} g of C per cell (15), our estimates of production range from 0.62 to 4.1 μg of C per liter · day. In Drake Passage, where μ and bacterioplankton abundance were between 0.032 to 0.088 h^{-1} and 4×10^5 to 10×10^5 cells per ml, production was approximately 4 times higher, ranging from 2.6 to 17.1 μg of C per liter · day. Production rates calculated from FDC for other systems are (in μg of C per liter · day): Baltic Sea, 2.2 (8); Atlantic coastal waters, 2 to 96 (41); eutrophic area of Baltic Sea, 10 to 60 (30); and salt marsh estuary, 14 to 422 (40). Thus, our values fall at the lower end of other estimates.

In coastal regions of McMurdo Sound, Antarctica, Fuhrman and Azam (15), using the thymidine incorporation method, found rates of bacterioplankton production from 0.004 to 2.9 μg of C per liter · day. Using the thymidine and

adenine incorporation method, we found rates of production from 0.0002 to 0.054 μg of C per liter · day in Drake Passage during austral summer 1980 (Hanson et al., in press). Considering the levels of primary production in coastal and oceanic regions, different rates of bacterioplankton production in the two regions appear reasonable. However, our estimates with FDC were almost three orders of magnitude greater than those previously measured (Hanson et al., in press). Part of the disparity may be due to differences in bacterioplankton abundance and to the methods employed. In summer 1980, bacterial cell numbers were less than 10^4 cells per ml, nearly an order of magnitude lower than in winter 1980. One report (41) shows that FDC productivity estimates can be 2 to 7 times greater than thymidine estimates in planktonic bacterial assemblages. A possibility is that nucleic acid synthesis and cell division are not synchronized in slowly growing bacteria (9, 10).

In conclusion, our results indicate that bacterioplankton populations actively grow in regions of Antarctic fronts and sea ice. In these regions, where most primary production estimates are approximately 13 to 45 μg of C per liter · day (11, 13, 21, 46), bacterioplankton secondary productivity may be 15 to 45% of the primary productivity.

ACKNOWLEDGMENTS

This research was supported by grant DPP-78-21507 from the National Science Foundation Division of Polar Programs.

We thank Michael McCartney of Woods Hole Oceanographic Institution for permitting us to participate on cruise leg XI of the R/V *Atlantis II* and providing physical data to describe Antarctic waters. We also thank S. Newell, R. Fallon, and R. Christian for critical comments on an earlier version of this communication.

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