Palmer LTER: Relative activities of several bacterial exoenzymes in the western Antarctic Peninsula during austral summer: Evidence of sea-ice influence on pelagic bacterial communities

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In mid-to-late austral summer (6 January to 12 February) 1994, aboard the R/V *Polar Duke* (*PD*94-01), we surveyed the region south and west of Palmer Station, along the 300, 400, 500, and 600 lines of the Palmer Long-Term Ecological Research (LTER) sampling grid (Waters and Smith 1992). Activities of the bacterial exoenzymes leucine aminopeptidase (LAPase), α-glucosidase (AGase), and β-glucosidase (BGase) were determined at most stations, following the methods of Hoppe (1983) and Somville and Billen (1983). Activities are determined at saturating substrate concentration and so must be considered potential activities rather than estimates of activity *in situ*. Activities were also determined in specialized microenvironments such as pack ice rich in microalgae ("brown ice") and fecal pellets of the antarctic krill *Euphausia superba* Dana.

Trends in exoprotease (LAPase) activity across the LTER sampling grid were very different from those observed in mid-to-late autumn of the previous year, at which time stations at the southern end of the grid were beginning to show signs of winter oligotrophy (Christian and Karl 1993). In the January to February 1994 period, the activities on the 300 line were the greatest observed except for three stations on the 500 line and were greatest at the station (300.040) nearest the peninsula (figure 1). On the 400 line, depth-integrated LAPase was also elevated at the inshore stations, declining across the shelf (figure 1). We hypothesize that the north-south and onshore-offshore trends result from the recent presence of the annual pack ice, which extended to the inshore end of the 300 and 400 lines on this cruise but had long since disappeared further north.

Along a southward transect from Palmer Station to Crystal Sound through the Lemaire and Grandidier Channels (days 13–17, *see* table), fragments of brown ice were encountered with increasing frequency. Depth-integrated LAPase gradually increased along this track. The southernmost stations (382.010 and 375.020) were completely ice-covered (but note that the ice by this time is fragmented and, therefore, moves as the wind shifts). These had intermediate depth-integrated activities, lower than most of the (ice-free) stations of the 300 line, but activities at or just below the surface were among the highest observed (figure 1). Near-surface BGase activities were also greatest at the ice stations. AGase was also slightly elevated at station 375.020. BGase activity never approached the levels observed near the receding pack ice in Marguerite Bay in 1991–1992 (up to 17 nanomoles per liter per day; see Karl et al. 1992 and Dore et al. 1992 for a description of the field experiment).

Potential activities of AGase and BGase in antarctic waters are low relative to LAPase (Christian and Karl 1992). The ratios of LAPase to AGase and BGase are also relatively high in brown ice and in krill fecal pellets. AGase/BGase, however, is very different in these two microenvironments. AGase exceeds BGase by a factor of about two in krill pellets; in brown ice AGase is almost completely absent.

The AGase/BGase ratios in the water column show a relative decline from the northern to the southern end of the sampling area, and the AGase/BGase ratio declines as BGase increases (figure 2). This suggests influence of ice melt on the

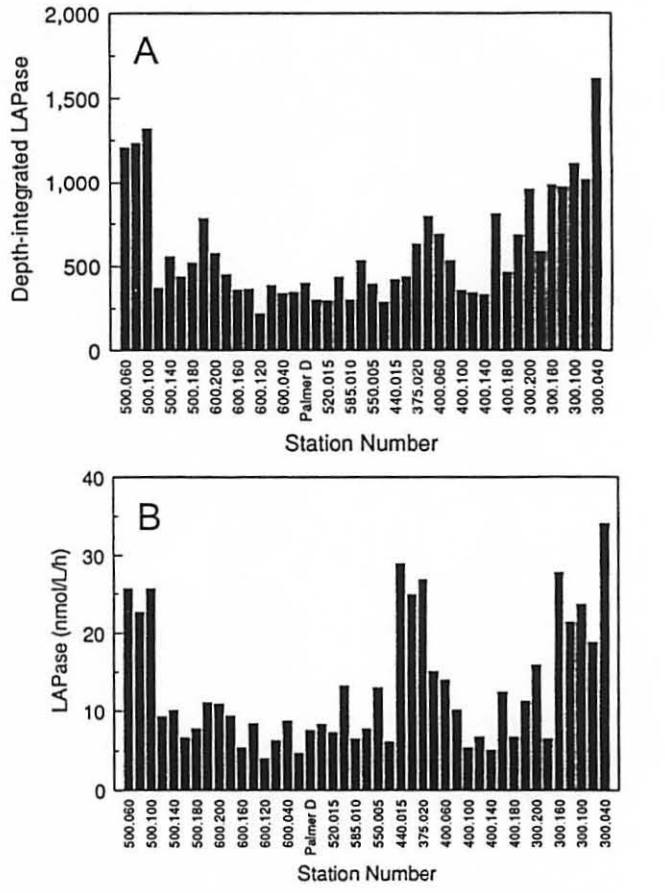

Figure 1. *A.* Leucine aminopeptidase (LAPase) activity integrated to 80 meters (trapezoid rule), in micromoles per square meter per hour. *B.* Leucine aminopeptidase (LAPase) activity at the shallowest depth sampled at each station (10 meters at station 500.100, just below surface at all other stations), in nanomoles per liter per hour. Stations are shown in order occupied; only alternate stations are named (*see* table for names of other stations).

Stations occupied on PD94-01 with dates and positions

Station	Date (m/d/y)	Day[a]	Latitude (S)	Longitude (W)
500.060	1/12/94	0	65.48°	66.15°
500.080	1/12/94	0	65.36°	66.46°
500.100	1/13/94	1	65.23°	66.78°
500.120	1/13/94	1	65.11°	67.09°
500.140	1/14/94	2	64.99°	67.39°
500.160	1/14/94	2	64.86°	67.69°
500.180	1/14/94	2	64.74°	68.00°
500.200	1/14/94	2	64.61°	68.29°
600.200	1/15/94	3	63.97°	66.86°
600.180	1/15/94	3	64.09°	66.56°
600.160	1/15/94	3	64.21°	66.26°
600.140	1/16/94	4	64.33°	65.96°
600.120	1/16/94	4	64.45°	65.65°
600.100	1/17/94	5	64.58°	65.34°
600.080	1/17/94	5	64.70°	65.03°
600.040	1/17/94	5	64.93°	64.40°
600.060	1/17/94	5	64.81°	64.72°
Palmer D[b]	1/24/94	12	64.81°	64.05°
Palmer J[b]	1/24/94	12	64.77°	64.13°
620.015	1/25/94	13	64.94°	63.72°
602.017	1/25/94	13	65.06°	64.00°
585.010	1/26/94	14	65.21°	64.13°
575.010	1/26/94	14	65.28°	64.27°
550.005	1/27/94	15	65.48°	64.54°
510.000	1/27/94	15	65.78°	65.04°
440.015	1/28/94	16	66.15°	66.32°
382.010	1/29/94	17	66.56°	67.13°
375.020	1/29/94	17	66.54°	67.40°
400.040	1/31/94	19	66.25°	67.34°
400.060	1/31/94	19	66.13°	67.66°
400.080	1/31/94	19	66.00°	67.97°
400.100	2/1/94	20	65.88°	68.28°
400.120	2/1/94	20	65.75°	68.59°
400.140	2/1/94	20	65.62°	68.90°
400.160	2/2/94	21	65.50°	69.20°
400.180	2/2/94	21	65.37°	69.50°
400.200	2/2/94	21	65.24°	69.80°
300.200	2/3/94	22	65.85°	71.38°
300.180	2/3/94	22	65.98°	71.08°
300.160	2/3/94	22	66.11°	70.78°
300.140	2/4/94	23	66.24°	70.48°
300.120	2/4/94	23	66.38°	70.18°
300.100	2/4/94	23	66.51°	69.87°
300.080	2/6/94	25	66.63°	69.55°
300.060	2/6/94	25	66.76°	69.24°
300.040	2/6/94	25	66.89°	68.92°

[a]Days from 12 January 1994.
[b]The designations "D" and "J" correspond to two of 10 stations in Arthur Harbor. Their exact positions are shown in Waters and Smith (1992).

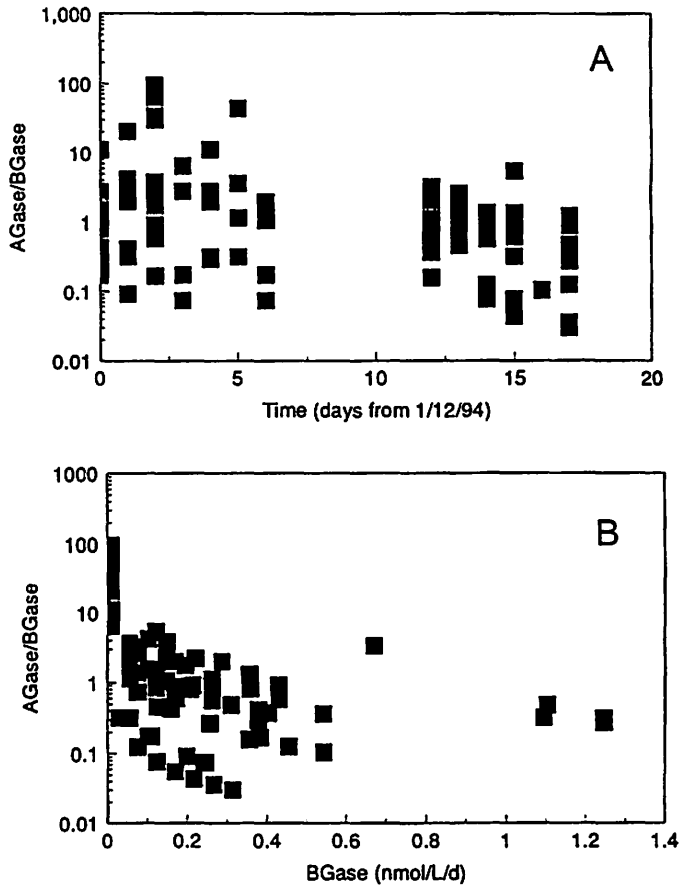

Figure 2. *A.* Ratio of α-glucosidase (AGase) to β-glucosidase (BGase) at stations sampled from 12 January 1994 through 29 January 1994 (see table for names and locations of stations sampled each day). *B.* Ratio of α-glucosidase (AGase) to β-glucosidase (BGase) relative to β-glucosidase (BGase) (in nanomoles per liter per day), at same stations shown in *A*.

composition of the bacterioplankton community, because BGase is dominant in the ice. On the 500 line, there are a number of samples in which BGase is very low but AGase is present at average to high levels, resulting in extremely high AGase/BGase ratios. This may indicate either the presence in the water column of fecal matter from swarms of krill or bacterial commmunities that have evolved from earlier inputs of fecal matter.

The BGase/LAPase ratio at the surface is significantly correlated (r^2=0.46, P<0.001) with BGase (figure 3). It appears that waters with significant ice melt influence are enriched in BGase relative to both AGase and LAPase. LAPase/BGase ratios in brown ice are higher than in other enriched microenvironments such as fecal pellets but lower than in the water column on this cruise. Water column LAPase/BGase ratios on this cruise were among the highest we have encountered on four cruises in this region. Near-surface LAPase/BGase at the ice-covered stations was at the low end of the range, but a number of stations far from the ice exhibited comparable ratios.

The relative activities of these three enzymes expressed by bacterioplankton on this cruise suggest that the bacterial community goes through several as yet poorly defined stages of succession as the annual pack ice recedes. The water is initially seeded with bacteria and receives substantial inputs of organic matter that may be quite different in its chemical composition than the autochthonous organic matter in the water column. Phytoplankton blooms at the receding ice edge will provide additional sources of organic matter, through

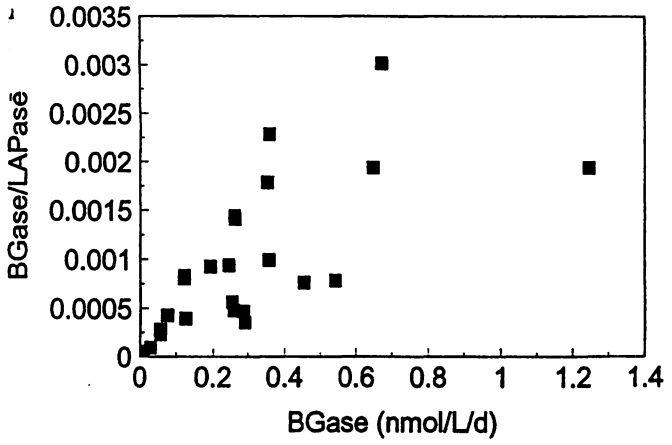

Figure 3. Ratio of β-glucosidase to leucine aminopeptidase (BGase/LAPase) vs. β-glucosidase (BGase) (in nanomoles per liter per day) in surface samples from all stations.

excretion, lysis, and grazing, that are likely to be present only for a short time. These processes are likely to play an important role in the adaptation of marine bacteria to this seasonally variable environment, and the biochemical characteristics of the bacteria may change rapidly.

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