

rently incomplete, it appears that seasonal differences in lipid content are present in the myctophid *Electrona antarctica*, but not in the deeper living (>400 meters) *Bathylagus antarcticus*. Ongoing research will determine if the seasonal trend observed in *E. antarctica* is present in other antarctic micronekton.

References

Clarke, A. 1983. Life in cold water: The physiological ecology of polar marine ectotherms. *Oceanographic Marine Biology Annual Review*, 21, 341–453.

Hopkins, T.L. 1971. Zooplankton standing crop in the pacific sector of the Antarctic. In G.W. Llano and I.E. Wallen (Eds.), *Biology of the Antarctic Seas*. Washington, D.C.: American Geophysical Union.

Hopkins, T.L. 1985. The zooplankton community of Croker Passage, Antarctic Peninsula. *Polar Biology*, 4, 161–170.

Hopkins, T.L. 1987. The midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Marine Biology*, 96, 93–106.

Ikeda, T., and A.W. Mitchell. 1982. Oxygen uptake, ammonia excretion and phosphate excretion by krill and other Antarctic zooplankton in relation to their body size and chemical composition. *Marine Biology*, 71, 283–298.

AMERIEZ 1986: Photoadaptation of phytoplankton and light limitation of primary production in the ice-edge zone of the Weddell Sea

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This group's specific objective was to examine the photoadaptive characteristics of phytoplankton and ice algae in the north-western Weddell Sea in relationship to the optical characteristics of ice and seawater in the marginal ice zone. Of particular interest was the role of ice cover in reducing photosynthetically available irradiance and its influence on the photoadaptive state of microalgae. These studies were carried out as a component of the Antarctic Marine Ecosystem Research at the Ice-Edge Zone (AMERIEZ) project during March, 1986.

Two ships, the *R/V Melville* and the *USCGC Glacier* were used to study the ice-free water in the eastern region of the study area and the ice-covered western portion respectively (for map, see Sullivan and Ainley, *Antarctic Journal*, this issue). Identical measurements were made from both ships. The suitability of available light as a resource for phytoplankton and ice algae was measured in two ways. Diurnal patterns of incident irradiance were recorded throughout the cruise. We also measured vertical profiles of spectral irradiance and photosynthetically available irradiance. Detailed analysis of photosynthetic pigments was carried out with high-performance liquid chromatography according to the method of Mantoura and Llewellyn (1983). Photosynthesis-irradiance curves for 27 samples of both ice algae and phytoplankton were defined using the small-volume, short-incubation method described by Lewis and Smith (1983). Analysis of the photosynthesis-irradiance curves was performed by the methods described by Zimmerman et al. (in press).

The values of daily photosynthetically available irradiance reflect the relatively constant overcast conditions of the study

area during March, 1986 (figure 1). The range of incident photosynthetically available irradiance at noon was 200–2,000 microeinsteins per square meter per second measured from *R/V Melville* and 400–2,000 microeinsteins per square meter per second for *USCGC Glacier*. While the ranges in noontime photon flux are about the same for both ships, notice that overall,

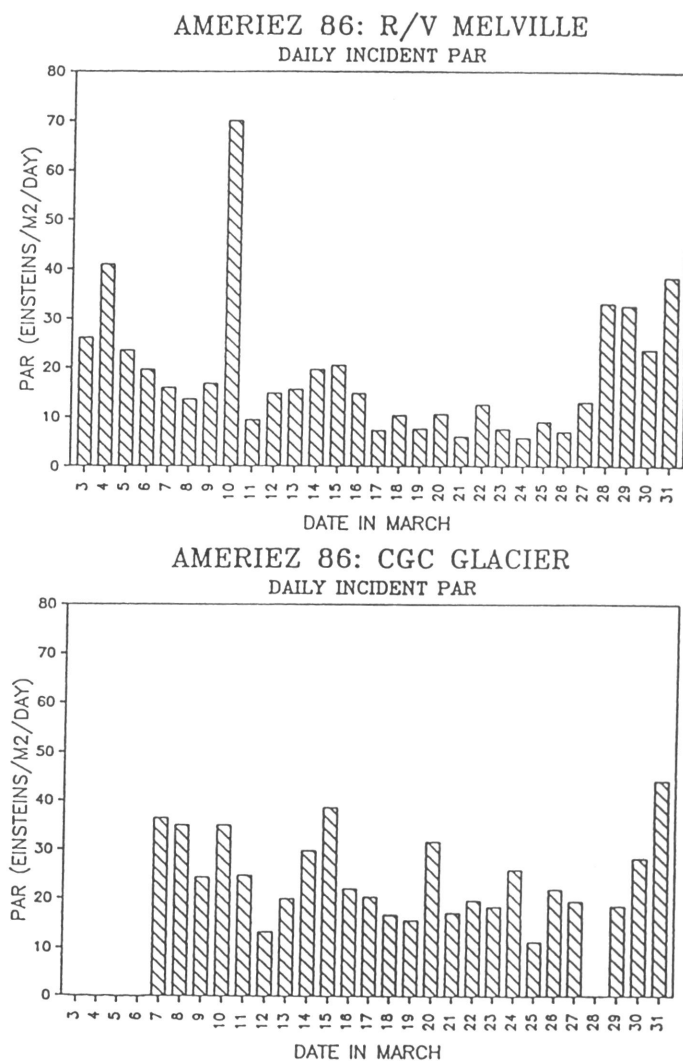


Figure 1. Daily photosynthetically available radiation (PAR) in einsteins per square meter (M^{-2}) as measured on both the *Melville* and *Glacier*.

incident photosynthetically available irradiance was less over the open ocean for R/V *Melville* and is probably attributable to variations in cloud and fog cover. The mean noontime irradiance for the month of March, 1986, measured from R/V *Melville* was 560 microeinsteins per square meter per second—only about one-third to one-fourth that found on clear days at temperate latitudes.

A summary of spectral irradiance data is presented in figure 2. Irradiance spectra narrow with increasing depth. However, both in open water and in water with variable degrees of ice cover, the irradiance spectra are dominated by blue light with peak transmittance at 440 nanometers. The deep penetration of blue light is the result of the low chlorophyll *a* concentrations (Nelson et al., *Antarctic Journal*, this issue) present during this study.

The transmittance of the open water column along the transects was quite uniform from east-to-west. The bottom of the

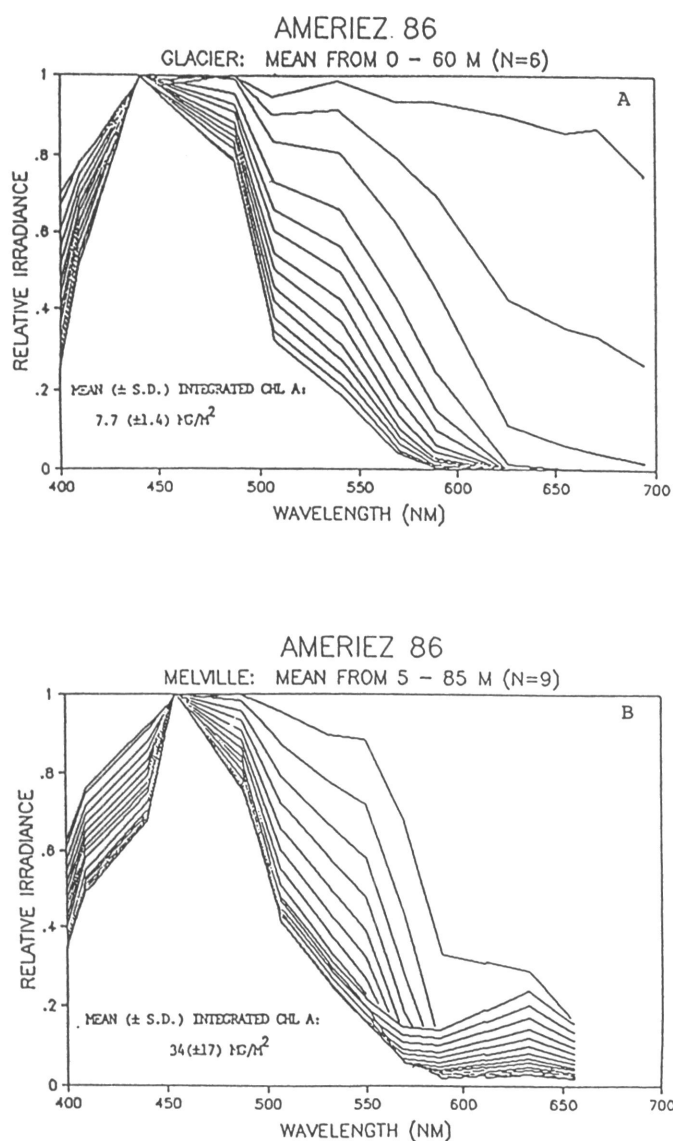


Figure 2. a. Vertical profile of mean relative spectral irradiance at 5-meter depth intervals for six *Glacier* stations. Each spectrum was normalized to its maximum at 440 nanometers (nm). **b.** Same as in a, but for nine *Melville* stations. (“S.D.” denotes “standard deviation.” “MG/M²” denotes “milligrams per square meter.” “NM” denotes “nanometer.” “CHL A” denotes “chlorophyll a.”

euphotic zone, operationally defined as the depth to which 1 percent of surface irradiance penetrates, ranged from 75–85 meters except at the easternmost end of the study site where Nelson et al. (*Antarctic Journal*, this issue) report a maximum in chlorophyll *a*. At this point, the depth of the euphotic zone was only 65 meters.

Mean ratios of chlorophyll *c/a* and fucoxanthin/chlorophyll *a* were 0.48 (± 0.14) and 0.88 (± 0.19), respectively, for phytoplankton from the open water and 0.51 (± 0.10) and 0.63 (± 0.13 for phytoplankton from under the ice. Bidigare et al. (1986) found chlorophyll *c/a* ratios of 0.23 ± 0.08 for southern ocean plankton dominated by diatoms. The higher values we report for this ratio may reflect a photoadaptive response to low values of incident photosynthetically available irradiance or may be due to differences in species composition.

The parameters derived from photosynthesis-irradiance curves from ice algae and phytoplankton from representative samples are shown in the table and typify the variations in photoadaptive state we observed. In figure 3a, the photosynthesis-irradiance curve for algae contained in snow-free pancake ice floating at the surface is shown. These algae are physically constrained to the sea’s surface and therefore, receive full photosynthetically available irradiance. They demonstrate a high assimilation number, P_m^B (chlorophyll *a*-specific rate of photosynthesis at saturating irradiance), high I_k (the irradiance at which photosynthesis becomes saturated), a low value of the slope of the light-limited portion of the photosynthesis-irradiance curve (where irradiance $\leq I_k$), α , and have characteristics of algae adapted to relatively high light levels. The photosynthesis-irradiance curve for phytoplankton from USCGC *Glacier* station 29 is shown in figure 3b. The photosynthesis-irradiance parameters of phytoplankton from the water column at station 29 near the ice edge show predictable trends. Assimilation numbers decrease with depth, I_k decreases with depth. The values of α are the same at 3 meters and 33 meters, but significantly higher at 70 meters, enabling the deep algae to photosynthesize at higher rates for the same low irradiance than those from shallower depths. The two upper samples come from above the pycnocline as described by Muench and Husby (*Antarctic Journal*, this issue) but the 70-meter sample is from well below the pycnocline and its characteristics are representative of algae adapted to low light. *Melville* station 17

Selected photosynthesis-irradiance parameters for ice algae and phytoplankton samples

Sample	α^a	P_m^B ^b	I_k ^c
Pancake ice	0.032	2.60	81
<i>Glacier</i> station 29			
3 meters	0.025	1.48	59
33 meters	0.025	0.91	36
70 meters	0.071	0.82	12
<i>Melville</i> station 17			
0 meters	0.034	2.72	110
56 meters	0.063	2.10	50

^a Units are milligrams of carbon per milligram of chlorophyll *a* per micro-einstein per square meter per second.

^b Units are milligrams of carbon per milligram of chlorophyll *a* per hour.

^c Units are microeinsteins per square meter per second.

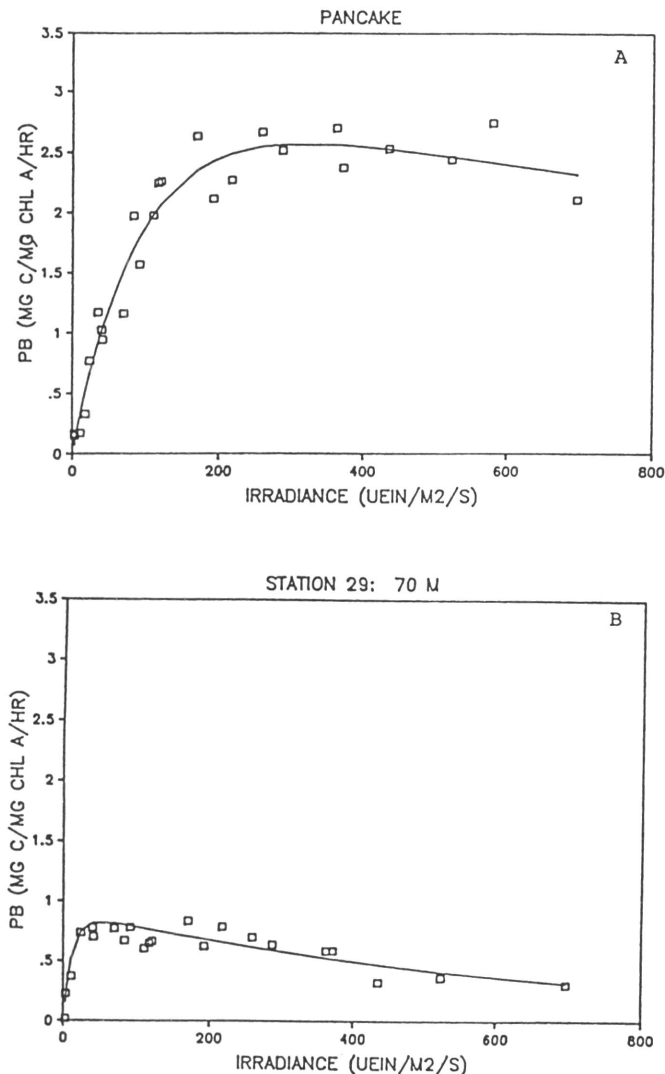


Figure 3. a. Photosynthesis-irradiance curve for pancake ice. b. Photosynthesis-irradiance curve for phytoplankton from a depth of 70 meters at Glacier station 29. ("MG C/MG CHL A/HR" denotes "milligrams of carbon per milligram of chlorophyll a per hour." "UEIN/M2/S" denotes "microeinsteins per square meter per second.")

was in open water. The photosynthesis-irradiance parameters demonstrate photoadaptive differences between the surface sample and a sample from 56 meters (the 1 percent light penetration depth)—below the pycnocline. Note that values of P_m^{PB} for open-water phytoplankton are higher than for even surface phytoplankton under the ice, and that while I_k decreases with depth at both stations, it is higher for the sample from the open water. Similarly, although α increases with depth at both stations, its value for the deep sample at the under-ice station is greater than that for the deep sample at the open-water station, reflecting the lower availability of light for phytoplankton under the ice cover.

We have used the values of incident irradiance, the patterns of transmittance of the water column and ice, and the photosynthesis-irradiance parameters of the phytoplankton along transects of the marginal ice zone to define the regions of the water column where algae are able to photosynthesize at maximal rates. For the case of a static water column at times of

highest incident irradiance (2,000 microeinsteins per square meter per second), the upper 40 meters of the open water column are able to support maximal photosynthetic rates. When incident irradiance is low (200 microeinsteins per square meter per second), only the upper 5–10 meters of the open water column will support maximal rates of photosynthesis. When the incident irradiance is characteristic of the mean noon-time value we observed during our study (560 microeinsteins per square meter per second), phytoplankton in the upper 15–30 meters of the open-water column would be able to photosynthesize at maximal rates. Because of the high attenuation of light by ice (K_T values of about 1.61 per meter; Palmisano et al. 1987), phytoplankton under the ice cover are never able to photosynthesize at maximal rates. Light limitation of phytoplankton photosynthesis at the ice-edge zone during this autumn period was evidenced by lower productivity of the region relative to that observed during a spring cruise in 1983 (Sullivan and Ainley, *Antarctic Journal*, this issue).

Incident irradiance in the northwestern Weddell Sea was low during the month of March, 1986, and a variety of physiological parameters indicates that phytoplankton were low-light adapted and had very low assimilation numbers. We have demonstrated that phytoplankton photosynthesis in the open water of the ice-edge zone was light limited in approximately one-half to seven-eighths of the euphotic zone and that phytoplankton photosynthesis beneath the ice was always light limited. Data collected enable us to develop a simple but physiologically realistic model of primary production in the marginal sea-ice zone.

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References

- Bidigare, R.R., T.J. Frank, C. Zastrow, and J.M. Brooks. 1986. The distribution of algal chlorophylls and their degradation products in the Southern Ocean. *Deep-Sea Research*, 33, 923–937.
- Lewis, M.R., and J.C. Smith. 1983. A small volume, short incubation time method for measurement of photosynthesis as a function of incident irradiance. *Marine Ecology*, 13, 99–102.
- Mantoura, R.F.C., and C.A. Llewellyn. 1983. The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse-phase high-performance liquid chromatography. *Analytical Chimica Acta*, 151, 297–314.
- Muench, R.D., and D.M. Husby. 1987. AMERIEZ 1986: Physical oceanographic conditions in the northwestern Weddell Sea marginal ice zone. *Antarctic Journal of the U.S.*, 22(5).
- Nelson, D.M., W.O. Smith, Jr., and L.I. Gordon. 1987. AMERIEZ 1986: Nutrient and phytoplankton biomass distributions in the ice-edge zone of the northwestern Weddell Sea. *Antarctic Journal of the U.S.*, 22(5).
- Palmisano, A.C., J. Beeler SooHoo, R.L. Moe, and C.W. Sullivan. 1987. Sea ice microbial communities. VII. Changes in under-ice spectral irradiance during the development of Antarctic sea ice microalgal communities. *Marine Ecology*, 35, 165–173.
- Sullivan, C.W., and D.G. Ainley. 1987. AMERIEZ 1986: A summary of activities on board the R/V *Melville* and USCGC *Glacier*. *Antarctic Journal of the U.S.*, 22(5).
- Zimmerman, R.C., J. Beeler SooHoo, J.N. Kremer, and D.Z. D'Argenio. In press. Evaluation of variance approximation techniques for non-linear photosynthesis-irradiance models. *Marine Biology*.