MacIsaac and Dugdale 1969; Olson 1980). It agrees very well, however, with suggestions that oyster pond algae, a group of diatom species which inhabit an environment similarly high in ammonium, nitrate, and organic nitrogen sources (concentrations of dissolved amino acids were also high in the upper platelet ice, Welborn personal communication), have higher ammonium threshold levels than similar pelagic species so that alternative nitrogen sources may be assimilated when ammonium is high (Collos, Maestrini, and Robert 1989).

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Temperature dependence of the photosynthetic parameter alpha in antarctic sea-ice microalgae

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The environments inhabited by antarctic sea-ice microalgae are characterized by low ambient temperatures near −2.0 °C. Numerous studies have been undertaken to determine which adaptive strategies are employed by antarctic microalgae to cope with such low temperatures and to evaluate to what extent temperature may limit algal growth. In general, these algae are psychrophiles, having optimal growth temperatures below 15 °C, and maximum and minimum temperatures for growth at or below 20 °C and 0 °C, respectively, suggesting that they are adapted to low-temperature environments. Field observations of low photosynthetic rates may indicate, however, that polar microalgae have not overcome limitations imposed by low temperature (Tilzer et al. 1986).

Several studies have reported that both maximal photosynthetic rate (P^bmax) and photosynthetic efficiency (alpha) are temperature dependent (Palmisano, SooHoo, and Sullivan 1987; Tilzer et al. 1986). The temperature dependence of P^bmax (maximum photosynthetic rate obtained at saturating irradiances) is well documented and thought to result from temperature sensitivity of the diffusional or enzymatic processes regulating Pmax. The temperature dependence of alpha (linear portion of the photosynthesis-irradiance curve) is surprising, since it is thought to be regulated by temperature independent photochemical reactions. Consequently, Tilzer et al. (1986) has proposed that at very low temperatures photochemical reactions are replaced by other temperature dependent reactions as rate limiting steps in "light limited" photosynthesis. Alternately, there are other factors that can bring about an apparent change in alpha in response to temperature without proposing a special interpretation of light-limited photosynthesis at low temperature. These factors including light harvest, energy transfer to the reaction center of photosystem II, and carbon fixation pathways.

The aim of our study was to characterize the temperature dependence of alpha and, through a systematic approach, to identify the temperature sensitive steps responsible for the observed effect. Fresh samples of sea-ice microalgae were collected from beneath approximately 2 meters of congelation ice at McMurdo Sound during the 1988–1989 and 1989–1990 field seasons. P^bmax and alpha were determined from isotopic sodium bicarbonate ($NaH^{14}CO_2$) incorporation at 6.0, −2.0, and −6.0 °C. Similarly, assimilation of carbon into proteins, polysaccharides, lipids, and low-molecular-weight compounds was determined by incorporation of $NaH^{14}CO_2$ followed by biochemical fractionation of photosynthetic products. In parallel, measurements of algal absorption, fluorescence, and pigment concentration were taken to calculate mean specific absorption (light harvest), relative energy transfer efficiency from pigments to the reaction center, pigment ratios, and quantum yield. Enzymatic activities were determined for ribulose disphosphate carboxylase (RUBPC) and phosphoenolpyruvate carboxykinase (PEPCK) from −6.0 to 25 °C.

Our data demonstrate that temperature can effect alpha, confirming the observations of other workers (Tilzer et al. 1986; Palmisano et al. 1987). Using the values at 6.0 °C for comparison (0.014 milligrams of carbon per milligram of chlorophyll

a per hour per microeinstein per square meter per second), decreasing temperature decreased alpha by 43 percent at −2.0 °C and 71 percent at −6.0 °C. P^bmax decreased by 66 percent at −2.0 °C and 90 percent at −6.0 °C from the 0.16 milligrams of carbon per milligram of chlorophyll *a* per hour value determined at 6.0 °C. The magnitude of change was greater for Pmax than for alpha suggesting that a different temperature dependent process was regulating each parameter.

The temperature sensitivity of alpha appears to be at a site effecting the measured values of quantum yield. If reduced light harvest were responsible for the observed decrease in alpha, then a similar decrease in specific absorption and perhaps pigment concentrations would be expected. Over the same temperature range, however, specific absorption remained relatively unchanged, averaging .0043 (±7 percent) per square meter per milligram of chlorophyll *a* for the three temperatures. Similarly, the molar ratios of chlorophyll *c* to chlorophyll *a* and fucoxanthin to chlorophyll *a* were unchanged, averaging .76 (±4 percent) and 1.83 (±2 percent), respectively, for the three temperatures. Quantum yield, derived from alpha and specific absorption, decreased from 0.076 moles of carbon per mole photon at 6.0 °C, by 40 percent and 68 percent at −2.0 °C and −6.0 °C, respectively. Of the factors that may effect quantum yield, both the efficiency of energy transfer in the pigment antenna (ET, fluorescence/absorption) and the efficiency of photochemistry (PC, variable fluorescence/maximum fluorescence) showed no decreasing trend with temperature and values varied by less than 10 percent among the three temperatures tested, far less than needed to explain the 70 percent change in quantum yield over the same temperature range. Consequently, since changes in light harvest, ET, and PC cannot explain the apparent changes in alpha and quantum yield, it is likely that temperature is effecting alpha at the level of carbon incorporation pathways.

We suggest that the temperature sensitivity of alpha may be only an apparent change caused by overlaying carbon fixation from the light independent beta-carboxylation pathway onto the light dependent reductive pentose phosphate (RPP) pathway. In diatoms, the reaction is catalyzed by PEPCK and is accompanied by the conversion of adenosine diphosphate to adenosine triphosphate. The pathway provides carbon skeletons for amino acid and tricarboxylic acid cycle intermediates. When two carbon fixation pathways are operating, then at any light intensity, the measured photosynthetic rate is the sum of carbon fixation rate via both pathways. If we accept that carbon fixation via RPP is controlled by photochemical reactions (at sub-saturating light levels) and beta-carboxylation is controlled by enzymatic (temperature dependent) reactions, then the following extrapolation can be made: alpha, calculated as total photosynthetic rate divided by photosynthetically

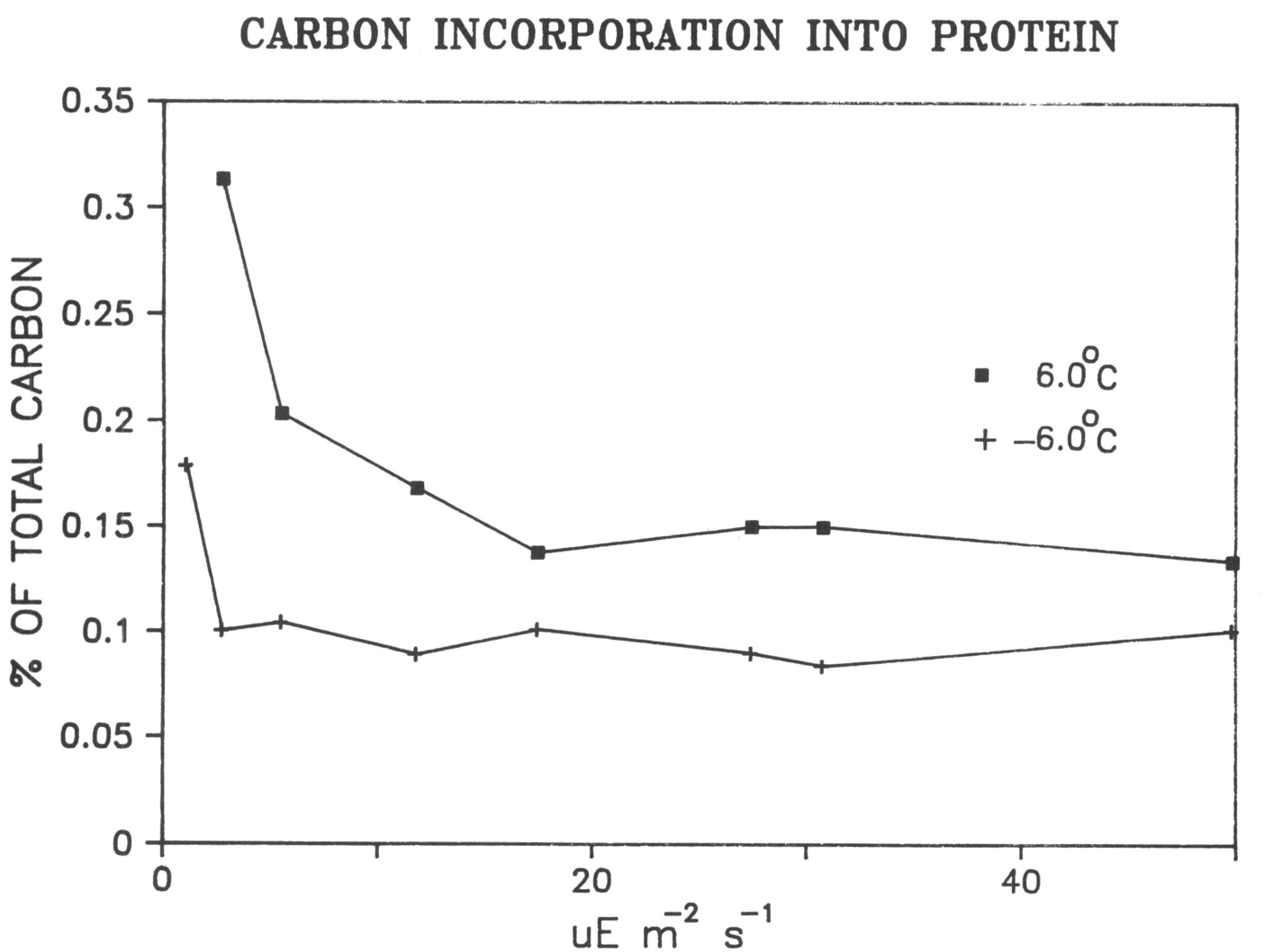

Figure 1. Assimilation of carbon into protein as a function of irradiance. Values are reported as a percentage of total carbon incorporated. (uE m^{-2} s^{-1} denotes microeinsteins per square meter per second.)

available irradiance, would be larger at higher temperatures and smaller at lower temperatures due to the relative contribution of beta-carboxylation to total carbon fixation.

If this hypothesis is true, then algae-exhibiting, temperature-dependent alpha would have high rates of carbon assimilation via the beta-carboxylation pathway relative to the RPP pathway, and as light becomes limiting (i.e., RPP fixation is limiting) the relative contribution of beta-carboxylation to total carbon assimilation rate would increase. Evidence that sea-ice microalgae in this study satisfied these condition comes from two sources. First, PEPCK activity *in vitro* responded to temperature change by increasing activity from −6.0 °C to 6.0 °C with a temperature coefficient (Q_{10}) of approximately 3. The ratio of RUBPC to PEPCK activity was low, averaging 1.5, indicating high beta-carboxylation activity relative to RPP (Mortain-Bertrand, Descolas-Gros, and Jupin 1988). Second, the fraction of assimilated carbon flowing into protein was 50 percent higher at 6.0 °C (0.15) than at −6.0 °C (0.10) undersaturating light. At limiting light levels, the fraction of carbon assimilated into the protein fraction increased to 0.30 at 6.0 °C and 0.18 at −6.0 °C (figure 1). Increased activity of beta-carboxylation pathway has been associated with an increased flow of assimilated carbon into the protein fraction (Morris 1980). These results are consistent with our proposed mechanism for the apparent temperature dependence of alpha.

The ecological significance of these results may have more to do with light limitation than temperature limitation. The occurrence of high rates of beta-carboxylation in algae has been associated with organisms from low-light environments (Morris 1980). In McMurdo Sound, irradiance reaching the bottom of the sea ice can be as low as 0.1 percent of surface irradiance. Despite these low irradiance conditions, standing stocks of seaice microalgae can reach concentrations of 2 to 5 (grams of chlorophyll *a* per liter) (Arrigo et al., *Antarctic Journal*, this issue). To produce high biomass under such low-irradiance conditions, highly efficient energy acquisition and utilization would seem to be a necessary requirement. Appleby et al. (1980) and Kremer (1981) suggest that an energetic advantage of the beta-carboxylation pathway, catalyzed by PEPCK, to growth in low light environments is the generation of an adenosine triphosphate with each carbon incorporated. In light of this suggestion, it is interesting to note that during the 1988 season at our study site, where maximum irradiance available to microalgae at the bottom of the sea ice ranged from 30 microeinsteins per square meter per second in early October to 11 microeinsteins per square meter per second late November, the occurrence of temperature dependent alpha (presumably active beta-carboxylation) coincided with the lowest irradiances (figure 2). This observation suggests that beta-carboxylation activity may be regulated by light

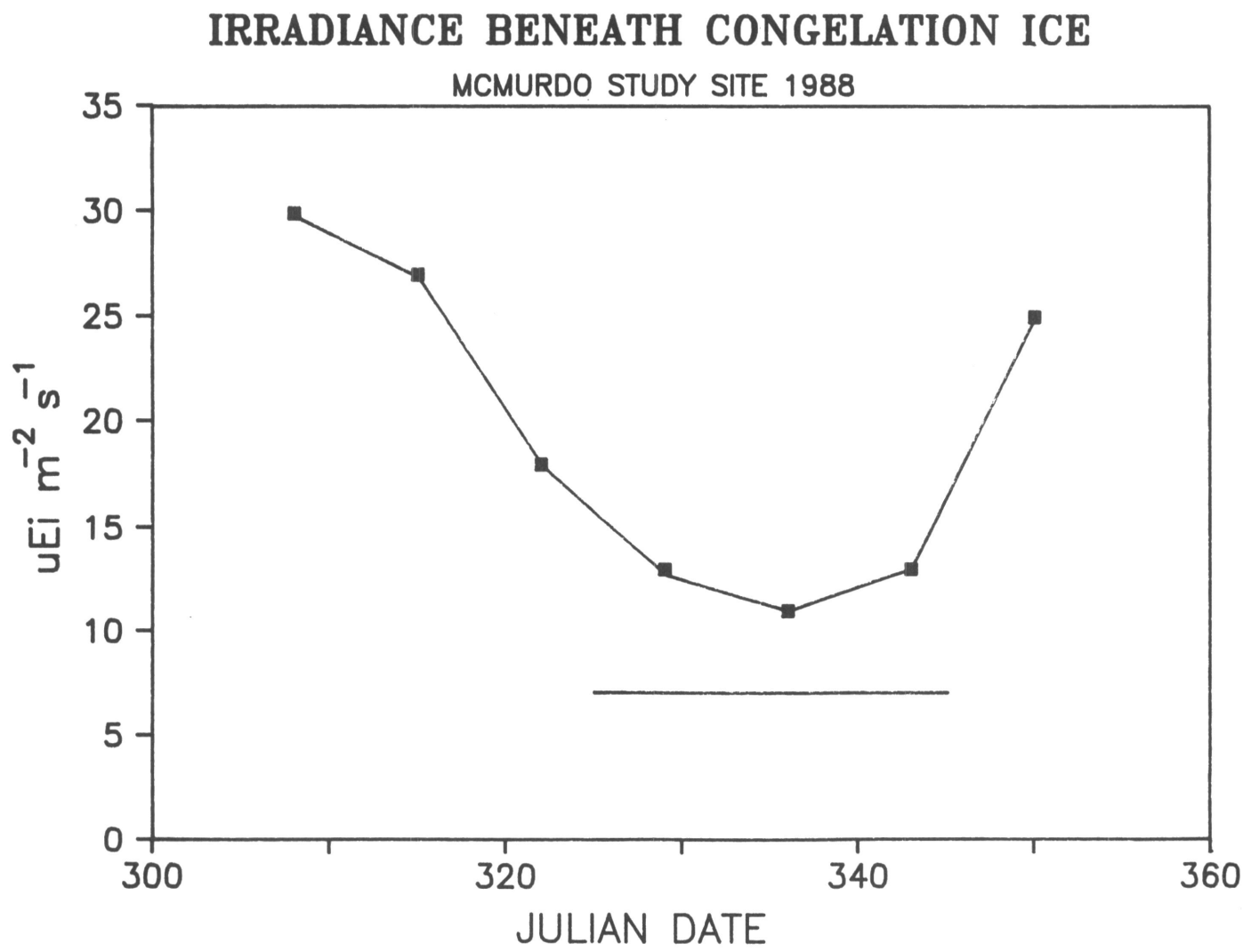

Figure 2. Maximum underice irradiance for the 1988 field season at the study site in McMurdo Sound. Horizontal bar indicates period of time over which temperature dependence of alpha was observed. (uE m^{-2} s^{-1} denotes microeinsteins per square meter per second.)

availability, possibly as an adaptive response to low-light conditions.

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Bacterioplankton abundance and productivity at the ice-edge zone of McMurdo Sound, Antarctica

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The ice edge is a transition zone from land fast ice or dense pack ice to open water. These are regions of intense biological activity (see reviews by Smith and Nelson 1986; Smith 1987; Sullivan and Ainley 1987). The ice edge has been extensively studied in the Weddell Sea, however, the McMurdo Sound ice edge has, for the most part, been neglected. Several hydrographic studies have suggested that there is a southerly net nontidal flow of water along the east side of McMurdo Sound and a northerly counter current along the western side of the sound (Barry 1988; Barry and Dayton 1988). This southerly flow typically transports *Phaeocystis* sp. from the Ross Sea into McMurdo Sound in mid to late December. This delivery of allochthonous phytoplanktonic biomass may account for the rich benthic faunal assemblage on the east side of McMurdo Sound (Dayton and Oliver 1977) and may sustain heterotrophic food chains throughout the aphotic austral winter (Rivkin in press).

Metazoan and protozoan zooplankton and the planktotrophic larvae of numerous antarctic benthic invertebrates have been identified from McMurdo Sound (Foster 1987, 1989). These grazers require sufficient nutritional resources for growth and development. High-latitude regions, such as McMurdo Sound, are characterized by highly seasonal yet persistently low phytoplankton biomass (Bunt and Lee 1970; Rivkin in press). Our study was a part of a multidisciplinary study of the ecology and nutrition of polar and temperate planktotrophic echinoderm larvae, and we measured the abundance and rates of production of potential autotrophic and heterotrophic prey. These and other invertebrate larvae from temperate and high-latitude regions appear to ingest both phytoplankton and bacterioplankton as potential food resources. Here, we report on the distribution of bacterioplankton and phytoplankton at the ice edge during the late austral spring and early summer, prior to the delivery of *Phaeocystis* sp. into McMurdo Sound.

Vertical profiles of planktonic biomass were collected during late October and late November 1989 at four stations along an east-west transect at the ice edge (figure 1). These samples were immediately returned to our field station for processing. Chlorophyll *a* was measured fluorometrically after extracting, in 90 percent acetone, the particulate material collected onto Whatman GF/F filters. Bacteria were preserved in glutaraldehyde (1 percent final concentration) and abundances were measured by counting cells stained with acridine orange using epifuorescence microscopy (Hobbie, Daley, and Jasper 1977).

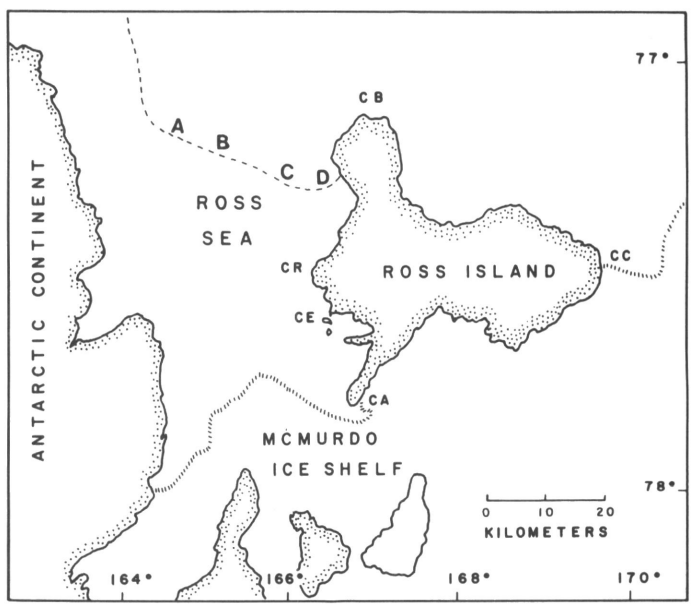

Figure 1. Map of McMurdo Sound, Antarctica, showing the location of the ice edge stations A, B, C, and D. (Other geographic features: CA denotes Cape Armitage, CB denotes Cape Bird, CC denotes Cape Crozier, CE denotes Cape Evans, and CR denotes Cape Royds.)