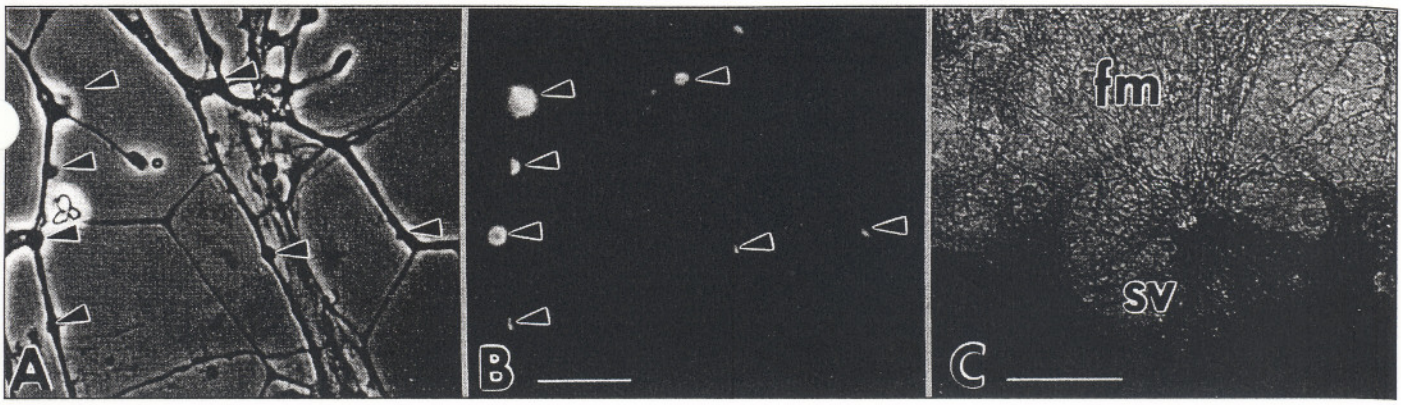

Figure 2. Phase-contrast (*A*) and corresponding fluorescence (*B*) micrographs of *Astrammina* pseudopodia that were first labeled with fluorescein-tagged goat IgG, and then washed free of unbound IgG and fixed. (Arrows denote sites of newly secreted adhesive. Bar = 20 micrometers.) (*C*) High-voltage electron micrograph of a fixed and critical-point dried *Astrammina* pseudopod, showing the extrusion of fibrillar "adhesive matrix" material (fm) from a secretory vesicle (sv). (Bar = 0.25 micrometers.)

with the elastic bioadhesive fibrils representing continuous tension elements and the mineral grains serving as discontinuous, noncompressible struts (Fuller 1961).

The 1994 field program participants included Samuel S. Bowser (7 October to 12 December 1994), Douglas Coons (7 October to 17 December 1994), Lawrence A. Haywood (7 October to 16 December 1994), Roy K. Kinoshita (7 October to 16 December 1994), Neal W. Pollock (1 September to 9 December 1994), and Robert W. Sanders (7 October to 12 December 1994). We are indebted to the Antarctic Support Associates personnel, who helped establish our camp and dive sites at Explorers Cove, as well as the pilots and crew of VXE-6. This work was supported by National Science Foundation grant OPP 92-20146; John H. Hayden was supported in part by an ROA supplement to OPP 92-20146.

References

Bowser, S.S., S.P. Alexander, W.L. Stockton, and T.E. DeLaca. 1992. Extracellular matrix augments mechanical properties of pseudopodia in the carnivorous foraminiferan *Astrammina rara*: Role in prey capture. *Journal of Eukaryotic Microbiology*, 39, 724–732.

Bowser, S.S., and J.M. Bernhard. 1993. Structure, bioadhesive distribution and elastic properties of the agglutinated test of *Astrammina rara* (Protozoa, Foraminiferida). *Journal of Eukaryotic Microbiology*, 40, 121–131.

Bowser, S.S., and T.E. DeLaca. 1985. Rapid intracellular motility and dynamic membrane events in an antarctic foraminifer. *Cell Biology International Reports*, 9, 901–910.

DeLaca, T.E. 1986. The morphology and ecology of *Astrammina rara*. *Journal of Foraminiferal Research*, 16, 216–223.

DeLaca, T.E., D.M. Karl, and J.H. Lipps. 1981. Direct use of dissolved organic carbon by agglutinated benthic foraminifera. *Nature*, 289, 287–289.

DeLaca, T.E., J.H. Lipps, and R.R. Hessler. 1980. The morphology and ecology of a new large agglutinated antarctic foraminifer (Textulariina: Notodendrodiidae Nov.). *Journal of the Linnean Society London, Zoology*, 69, 205–224.

Fuller, R.B. 1961. Tensegrity. *Portfolio Artnews Annual*, 4, 112–127.

Gooday, A.J., L.A. Levin, P. Linke, and T. Heeger. 1992. The role of benthic foraminifera in deep-sea food webs and carbon cycling. In G.T. Rowe and V. Pariente (Eds.). *Deep-sea food chains and the global carbon cycle*. Netherlands: Kluwer Academic Publishers.

Statistical analyses of environmental predictors for phytoplankton photosynthetic parameters and productivity in an antarctic time series database

MARK A. MOLINE *and* BARBARA B. PRÉZELIN, *Department of Biological Sciences, University of California, Santa Barbara. Santa Barbara, California 93106*

OSCAR SCHOFIELD, *Institute of Marine and Coastal Studies, Rutgers University, New Brunswick, New Jersey 08903-0231*

From 3 December 1991 to 27 February 1992, 249 discrete water samples were collected at the Palmer Long-Term Ecological Research (LTER) program's station B (Waters and Smith 1992). For each discrete sample, physical, biological, and chemical measurements were made including incident irradiance, *in situ* irradiance, temperature, density, and nitrate, phosphate, silicate, particulate organic carbon, and particulate organic nitrogen levels. In addition, 15 distinct algal pigments were determined by high-performance liquid chromatography (HPLC), and the algal pigments were classified into groups based on their functionality (i.e., photoprotective carotenoids and photosynthetic carotenoids). In addition,

photosynthesis-irradiance (P-I) relationships were determined for each sample from which the photosynthetic parameters P_{max} (photosynthetic capacity) and alpha (the light-limited photosynthetic efficiency) were derived. Further details of sample collection and analyses are described elsewhere (Prézelin et al. 1992; Moline et al. in press).

The dynamics of the physical, chemical, and biological components of the system were highly coupled at station B over the 1991–1992 season (Moline et al. in press). In early December 1991, freshwater input from melting fast ice and nearby coastal glaciers and low wind speeds permitted the water column to stratify. This enhanced stability allowed a large bloom [approximately 30 milligrams of chlorophyll-*a* per cubic meter (mg chl-*a* m^3)] to develop, a size that depleted macronutrients to detection levels (Moline and Prézelin 1994). This bloom accounted for 75 percent of the integrated productivity over the season (Moline and Prézelin in preparation). A period of high wind advected the water mass out of the area, and for the following 2 months, the water column was well mixed. The phytoplankton community varied over the season with diatoms, chrysophytes, cryptophytes, or prymnesiophytes dominating at any given time. This study examines the predictive capability of the environmental variables measured over this dynamic period at station B in determining the temporal variability in the P-I parameters.

Stepwise forward and backward multiple linear regression analyses were used with the above variables to generate algorithms to predict the P-I parameters. The statistical (enter/remove) constraint for the analyses was $p<0.015$. This approach was similar to that used by Schofield et al. (1993) within the Southern California Bight. Once significant variables and their coefficients were determined, the algorithms were verified using nonparametric randomization regression techniques. Results of these analyses are presented in the table. A majority of the variance in both alpha and P_{max} were explained by density and the concentration phosphate and nitrate, respectively. The relationship improved with the addition of the biomass indicator, chlorophyll-*a*. Full pigmentation information provided only a slightly stronger relationship, suggesting that over the season, despite large variations in nutrient concentration, water column stability, and community composition, the capacity of light harvesting by phytoplankton changed little. The P_{max} and alpha values predicted from these regressions were then used to estimate the *in situ* productivity (Ps) using the following relationship (Platt and Gallegos 1980),

$$P(z, t) = P_{max} \cdot \left(\frac{Q_{pPAR}(z, t)}{I_k(z, t)} \right)$$

where I_k is equal to P_{max}/alpha and Q_{par} is the *in situ* light field [400–700 nanometers (nm)]. Once the *in situ* productivity based on the *predicted* P_{max} and alpha variables had been estimated, the productivity estimated from the *measured* P-I parameters was determined using the same approach. The predicted productivity and measured productivity from station B were then compared (figure 1). Sixty-five percent of the variance in productivity could be explained by the P-I parameters predicted from density and the nutrient concentrations (figure 1*A*). The relationship, however, was biased toward the higher

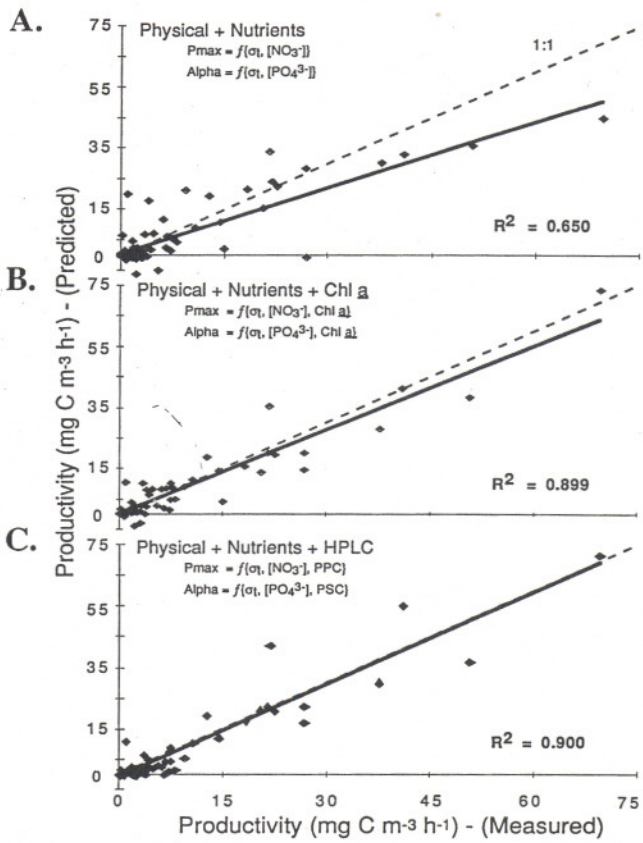

Figure 1. Comparison of *in situ* primary productivity calculated from predicted P_{max} and alpha and measured P_{max} and alpha. Variables used to predict P_{max} and alpha are included in the figure. R^2 values are indicators of how well the predictor variables were for P_{max} and alpha. The closeness of the regression line (solid) to the 1:1 line (dashed) indicates how well the regression calculated the variable coefficients. (mg C m^{-3} h^{-1} denotes milligrams of carbon per cubic meter per hour.)

Results of multiple linear regression analyses from Palmer LTER station B (p-value for regression is <0.00001 in all cases)

Category of variables	Photosynthetic parameter variables	Significant independent	R^2
Physical + nutrient	P_{max}	σt, NO_3	0.65
	Alpha	σt, PO_4	0.59
Physical + nutrient + chl-*a*	P_{max}	σt, NO_3, chl-*a*	0.84
	Alpha	σt, PO_4, chl-*a*	0.83
Physical + nutrient + HPLC	P_{max}	σt, NO_3, PPC[a]	0.86
	Alpha	σt, PO_4, PSC[b]	0.85

[a]Photoprotective carotenoids
[b]Photosynthetic carotenoids

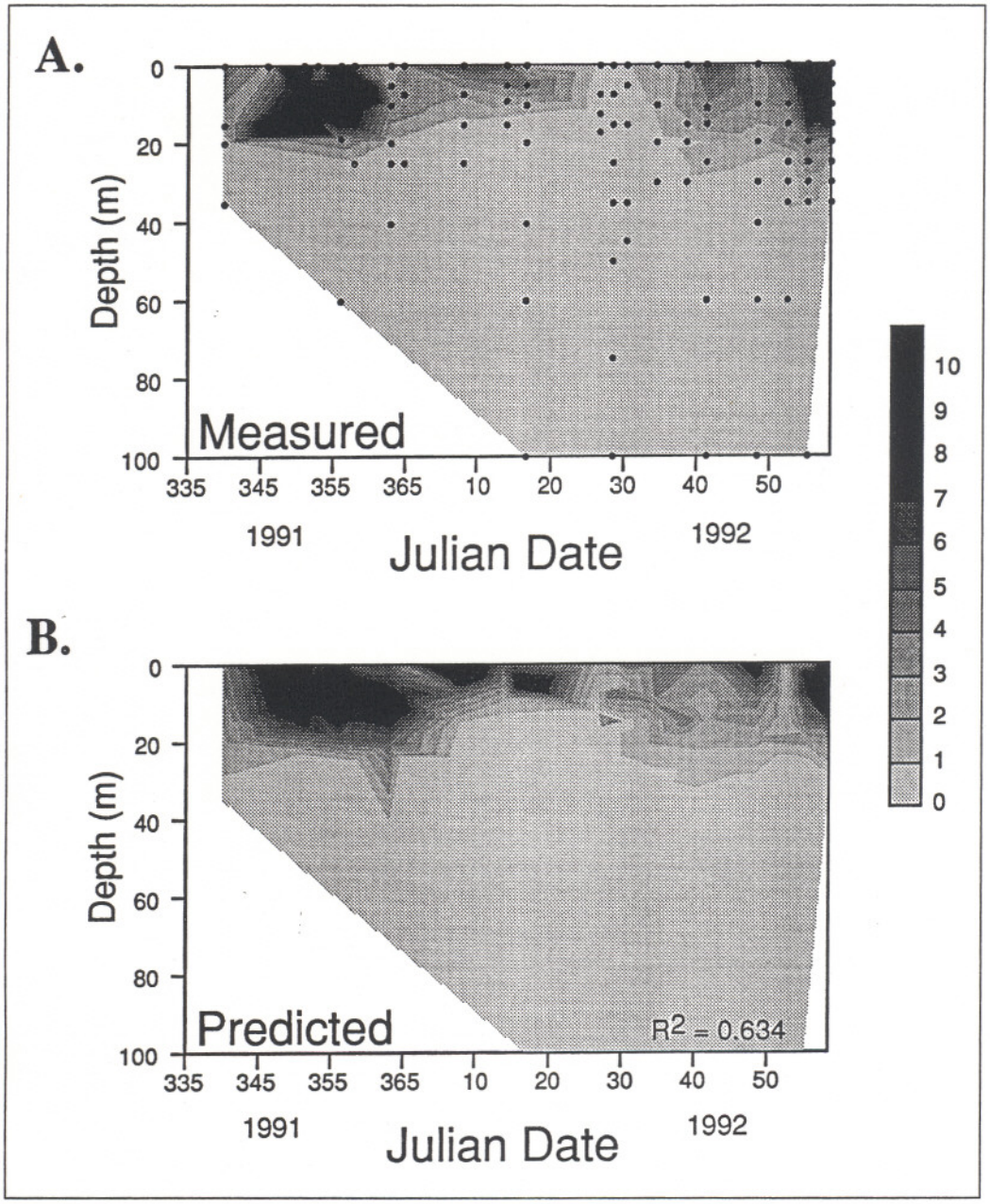

Figure 2. Contours of (*A*) the 1991–1992 *in situ* productivity measured at station E and (*B*) the productivity predicted from the regressions derived for station B in figure 1*C*. Closed circles indicate the discrete sampling points. (m denotes meter.)

productivity values; it predicted the bloom accurately (75 percent of the seasonal productivity) but performed poorly when predicting the periods of low productivity. As before, when chlorophyll-*a* was added as a predictor variable for P_{max} and alpha, the relationship greatly improved (figure 1*B*). The addition of algal pigmentation in the regressions shifted the relationship to nearly 1:1 and was a better predictor than chlorophyll-*a* for the periods of low productivity (figure 1*C*).

The regressions used in figure 1*C*, derived from station B, were then used to predict *in situ* productivity at station E, 3 kilometers from station B within the same LTER nearshore grid (Waters and Smith 1992). The measured production is shown with depth over the 3-month sampling period in figure 2*A*. The calculated production, based on the regressions from station B, is shown in figure 2*B*. Even though the regressions overestimated productivity by approximately 10 percent over the season, the main features of production could be detected and the relationship was significant.

Results from this study show that for 1991–1992, the physical- and nutrient-based regression model described the majority of the spring/summer variation in productivity; however, the predictive linkages were strongly dependent on the occurrence of a bloom in stratified, nutrient-depleted waters. For periods of water column instability, the physical- and nutrient-based regression model was not adequate to predict variability in primary productivity, unless knowledge of phytoplankton pigmentation was incorporated into the regression. Lastly, primary productivity at station E could be significantly predicted using the outcome of the regression analyses from station B. This suggests the dynamics of these antarctic coastal stations are closely coupled and exhibit similar processes controlling primary production.

Special thanks go to K. Seydell, K. Scheppe, P. Handley, T. Newberger, and B. Frank for assistance in the field. This work was supported by National Science Foundation grant OPP 90-11927 awarded to B.B. Prézelin. This is Palmer LTER contribution 90.

References

Moline, M.A., and B.B. Prézelin. 1994. Palmer LTER: Impact of a large diatom bloom on macronutrient distribution in Arthur Harbor during austral summer 1991–1992. *Antarctic Journal of the U.S.*, 29(5), 217–219.

Moline, M.A., and B.B. Prézelin. In preparation. High resolution time series data for *in situ* carbon fixation at the Palmer LTER site and its implications for modeling primary production in the southern ocean. *Polar Biology.*

Moline, M.A., B.B. Prézelin, O. Schofield, and R.C. Smith. In press. Temporal dynamics of coastal antarctic phytoplankton: Environmental driving forces through a 1991–1992 summer

diatom bloom on the nutrient and light regime. In B. Battaglia, J. Valencia, and D.W.H. Walton (Eds.), *Antarctic Communities.* Cambridge: Cambridge University Press.

Platt, T., and C.L. Gallegos. 1980. Modeling primary productivity. In P.G. Alkowski (Ed.), *Primary production in the sea.* New York: Plenum Press.

Prézelin, B.B., M.A. Moline, K. Seydel, and K. Scheppe. 1992. Palmer LTER: Temporal variability in HPLC pigmentation and inorganic nutrient distribution in surface waters adjacent to Palmer Station, December 1991–February 1992. *Antarctic Journal of the U.S.*, 27(5), 245–248.

Schofield, O., B.B. Prézelin, R.R. Bidigare, and R.C. Smith. 1993. *In situ* photosynthetic quantum yield. Correspondence to hydrographic and optical variability within the Southern California Bight. *Marine Ecology Progress Series*, 93, 25–37.

Waters, K.J., and R.C. Smith. 1992. Palmer LTER: A sampling grid for the Palmer LTER program. *Antarctic Journal of the U.S.*, 27(5), 236–238.

Excluding connectivity leads to inaccurate estimates of the PSII absorption cross section of an antarctic macrophyte using "pump and probe" fluorometry

BERND M.A. KROON, *Amsterdam Research Institute for Substances in Ecosystems (ARISE), University of Amsterdam, The Netherlands*

BARBARA B. PRÉZELIN, *Department of Biological Sciences, University of California at Santa Barbara, Santa Barbara, California 93106*

During *Icecolors '93*, we used the Pulse-Amplitude-Modulated (PAM) fluorescence technique to locate the target site at photosystem II (PSII) for solar ultraviolet-B (UV-B) radiation in antarctic ice-algae (Kroon, Schofield, and Prézelin in preparation). Furthermore, we began to explore how PAM and its ability to simulate "pump and probe" fluorescence (PPF) might be applied to derive photobiologically relevant parameters in other groups of antarctic algae. Here, we report an experiment designed to evaluate the accuracy to derive the absorption cross section of a macrophyte brown alga isolated from Arthur Harbor, Antarctica, using the PAM to simulate the PPF.

Theoretically, photosynthetic rates are determined by just three parameters: incident light, light absorption, and the photochemical quantum yield. The latter two are biological parameters and nonlinearly related to many ecosystem variables. The recent development of PAM and PPF techniques allows us to quantitatively determine light absorption and quantum yield, albeit by different principles and with different underlying assumptions to interpret data. The critical difference between PPF and PAM lies in the derivation of optical cross sections for photosynthesis and, thus, the bio-optical derived estimate of *in situ* photosynthesis. The PPF analysis assumes that variable fluorescence is a direct measure for the amount of closed PSII reaction centers, and consequently, the absorption cross section has a fixed value and is independent on the amount of closed PSII. Under this assumption, the cross section can be derived by a target function describing the increase in variable fluorescence with increasing light energy. If, however, antennae pigments of different PSII's share energy (connectivity; *see* Hipkins 1978), it is then possible for absorbed photons to be trapped by an open reaction center that belongs to a PSII that is different from the PSII whose antennae absorbed the photons. Consequently, fluorescence varies less than linearly with the amount of closed PSII. The absorption cross section will be variable, depending on the amount of closed PSII. The PAM analysis allows connectivity, and its quantification is possible. Hence, PAM-derived cross sections will differ from those derived by the PPF method. We adapted the PAM method to simulate the PPF method accurately and assessed the impact of connectivity in the data analyses to quantify the absorption cross section in a low-light adapted antarctic macrophyte.

We collected an antarctic macrophyte from 40 meters depth near Arthur Harbor, Antarctica, on 1 September 1993, maintaining it in the laboratory under low light and incubating it for 1.5 hours in darkness prior to the fluorescence measurements. The average of nine fluorescence decay curves at 20-second (s) intervals were monitored at 25-microsecond resolution during 20 milliseconds after a single turnover flash of 5-microsecond duration and of variable intensity. Decay profiles were deconvoluted into fast and slow kinetic components. Complete methodology for simulating PPF with a PAM fluorometer is presented in Kroon (1994). The fast component amplitude varied nonlinearly with increasing flash intensity as a result of PSII closure, but the fraction of PSIIs with fast kinetics was constant (figure 1). It was impossible to fit the relation between variable fluorescence and flash intensity with a target function having a single value for the cross section (figure 2), in contrast to common PPF analysis procedures (Kolber and Falkowski 1993). Our data revealed the cross section of the low-light adapted kelp varied 27-fold from 0.0003, when almost all PSII were open, to 0.008, when all PSII's were closed (figure 2).We were not surprised to observe that a dependency of the cross section on the fraction of open PSII existed in antarctic kelp, though the extent of the variation was dramatic with significant implications for future fluorescence probing of aquatic photosynthesis in polar environments. The excited state of an absorbed photon (exciton) has a lifetime of several picoseconds. Assume the exciton can visit N pigment mole-