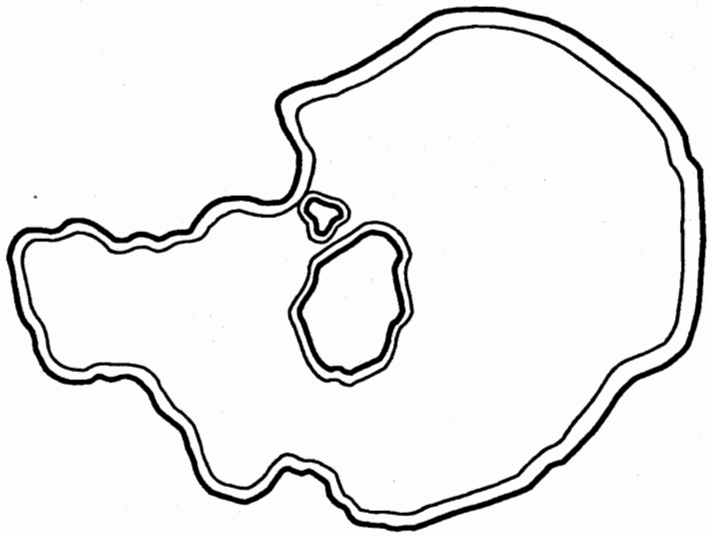
An Auxiliary Report
Prepared for the

MONO BASIN WATER RIGHTS EIR

Algal Photosynthetic Activity and Its Response to Meromixis in Hypersaline Mono Lake, California



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Mono Basin EIR Auxiliary Report No. 16

An Auxiliary Report
Prepared for the
Mono Basin Water Rights EIR Project

This auxiliary report was prepared to support the environmental impact report (EIR) on the amendment of appropriative water rights for water diversions by the City of Los Angeles Department of Water and Power (LADWP) in the Mono Lake Basin. Jones & Stokes Associates is preparing the EIR under the technical direction of the California State Water Resources Control Board (SWRCB). EIR preparation is funded by LADWP.

SWRCB is considering revisions to LADWP's appropriative water rights on four streams tributary to Mono Lake, Lee Vining Creek, Rush Creek, Parker Creek, and Walker Creek. LADWP has diverted water from these creeks since 1941 for power generation and municipal water supply. Since the diversions began, the water level in Mono Lake has fallen by 40 feet.

The Mono Basin water rights EIR examines the environmental effects of maintaining Mono Lake at various elevations and the effects of possible reduced diversions of water from Mono Basin to Owens Valley and the City of Los Angeles. Flows in the four tributary creeks to Mono Lake and water levels in Mono Lake are interrelated. SWRCB's decision on amendments to LADWP's water rights will consider both minimum streamflows to maintain fish populations in good condition and minimum lake levels to protect public trust values.

This report is one of a series of auxiliary reports for the EIR prepared by subcontractors to Jones & Stokes Associates, the EIR consultant, and contractors to LADWP. Information and data presented in these auxiliary reports are used by Jones & Stokes Associates and SWRCB, the EIR lead agency, in describing environmental conditions and conducting the impact analyses for the EIR. Information from these reports used in the EIR is subject to interpretation and integration with other information by Jones & Stokes Associates and SWRCB in preparing the EIR.

The information and conclusions presented in this auxiliary report are solely the responsibility of the author.

Copies of this auxiliary report may be obtained at the cost of reproduction by writing to Jim Canaday, Environmental Specialist, State Water Resources Control Board, Division of Water Rights, P.O. Box 2000, Sacramento, CA 95810.

Running Head: Meromixis and photosynthesis

Algal photosynthetic activity and its response to meromixis in hypersaline Mono Lake, California

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Abstract

Photosynthetic activity was measured in hypersaline Mono Lake during an 8-yr period (1983 through 1990) which spanned the onset (1983), persistence (1984 to 1987), and breakdown of meromixis (1988). Algal biomass during the spring and autumn decreased following the onset of meromixis and annual photosynthetic production was reduced (269–462 g C m^{-2} yr^{-1}; 1984 to 1986) compared to non-meromictic conditions (499–641 g C m^{-2} yr^{-1}; 1989 and 1990). A gradual increase in photosynthetic production occurred even before meromixis was terminated because of increased vertical flux of ammonium due to deeper mixing and the buildup of ammonium in the monimolimnion. Annual production was greatest in 1988 (1,064 g C m^{-2} yr^{-1}) when the weakening of chemical stratification and eventual breakdown of meromixis in November resulted in large fluxes of ammonium into the euphotic zone.

Most of the variation in light-saturated carbon uptake rates normalized to chlorophyll *a* (assimilation numbers) was explained by a regression on temperature (60%); measures of the light and nutrient environments accounted for a further 8% of the observed variation. Estimates of ammonium supply due to vertical mixing and *Artemia monica* excretion indicate nitrogen is most likely to limit photosynthetic production during spring and late autumn when *A. monica* are absent and algal biomass high. Light is also likely to limit production during these periods based on comparisons of the average mixed-layer irradiance to the light intensity at which maximum photosynthetic rates were reached. Light limitation was more pronounced under monomictic conditions when algal biomass was higher.

Measurements of photosynthetic production in saline lakes vary over two orders of magnitude on an areal basis (Hammer 1981) and include some of the highest recorded daily values for natural lakes (Talling et al. 1973; Melack and Kilham 1974). While variation in photosynthetic production among lakes is large and well-documented, few studies of saline lakes are of sufficient duration to assess year to year variation. In several lakes, large interannual differences due to climatic variation have been noted. In shallow Lake Elmenteita (Kenya), photosynthesis declined dramatically as lake levels dropped and salinity increased over a 16-month period (Melack 1981). In large Great Salt Lake (Utah, USA), algal populations increased as lake levels increased and a different zooplankton community became established (Wurtsbaugh 1990). Here, we analyze changes in photosynthetic production during an 8-yr period arising from alteration of the vertical mixing regime due to a climatic perturbation.

At Mono Lake, diversions of freshwater streams out of the basin since 1941 have led to a gradual decline in lake levels. As the surface elevation dropped 14 m the mean depth decreased from 24 m in 1941 to 17 m by 1982, and lake water salinities approximately doubled [Los Angeles Department of Water and Power (LADWP) unpubl. data]. This trend was reversed in 1982 when a 2.6 m rise in surface elevation resulted from spring runoff associated with the 1982/1983 El Niño - Southern Oscillation. This large volume of fresh water mixed into the epilimnion and initiated meromixis. The strong chemical stratification associated with the meromixis reduced vertical mixing and recycling of nutrients from the deeper waters (Jellison et al. 1988).

We analyze the seasonal and year to year variation in phytoplankton production for the period from 1983 through 1990 which includes the onset, persistence, and breakdown of meromixis. We calculate daily integral rates of algal production by combining photosynthetic parameters derived from laboratory incubations with in situ profiles of light attenuation and continuous measurements of insolation. The variation in photosynthetic parameters is examined in relation to several measures of the physical and chemical

environment. A number of authors have found this technique useful in identifying potential determinants of primary production (Platt and Jassby 1976; Harrison and Platt 1980; Fee et al. 1987; Jellison and Melack 1988). This technique also provides an empirical method of interpolating and extrapolating production estimates to periods when rate measurements are absent but environmental and biomass variables are known.

Description of study site

Mono Lake covers 160 km^2 and has a mean depth of 17 m at an elevation of 1943 m. It occupies a tectonic basin on the western edge of the North American Great Basin just east of the Sierra Nevada, California (38°N, 119°W). Sodium is the major cation, and chloride and carbonate are the major anions, while sulfate, borate, silica, and phosphate concentrations are also high (Mason 1967, LADWP unpubl. data). The pH is ca. 10. The lake was monomictic when it was studied in the early 1960s (Mason 1967) and late 1970s through early 1980s (Melack 1983).

The planktonic community of Mono Lake has few species as is typical of hypersaline waters. The phytoplankton is predominantly coccoid chlorophytes (2 - 5 μm diameter) tentatively identified as *Nannochloris* sp., coccoid cyanobacteria, and several bacillarophytes, mainly *Nitzschia* spp. (20 - 30 μm) (Mason 1967; Melack unpubl. data). A brine shrimp, *Artemia monica* Verill, is the only macrozooplankter (Lenz 1982); pelagic ciliates may also be present at times (Mason 1967).

Plankton of Mono Lake have marked seasonal cycles of abundances (Melack 1983). Phytoplankton are abundant throughout the lake during winter, increasing in the epilimnion after the onset of the seasonal thermocline in early spring. The seasonal increase was much reduced during 1984 and 1985, subsequent to the initiation of meromixis (Jellison and Melack 1988). *A. monica* hatch from overwintering cysts from January to May. By mid-May, the first adult *A. monica* are present, grazing the phytoplankton, and causing a rapid decrease in the algal abundance in the upper water

column. During summer, phytoplankton are sparse and *A. monica* abundant in the epilimnion, while the hypolimnion is populated with a dense suspension of phytoplankton and very few *A. monica*. In autumn, the phytoplankton increase in the surface waters as thermal stratification weakens and as the *A. monica* population declines (Jellison and Melack 1988).

Methods

Sampling and analytical measurements -- Plankton samples were collected from 1982 through 1990 at two stations, located in the central portions of the eastern and western halves of Mono Lake. Most samples were collected from the mixed layer with a 9 m integrating tube sampler (diam. 2.5 cm). During early spring, when 9 m would extend below the mixed layer, an opaque Van Dorn water sampler was used to collect samples from 2 m. Discrete depth samples were also collected at 2, 8, 12, 16, and 20 m with additional ones at 5, 14 and 18 m, depending on the thermal structure of the water column. Samples were immediately passed through a 120 μm net to remove all stages of the zooplankter, *Artemia monica*, and a subsample filtered through Gelman A/E glass-fiber filters for analysis of nutrients. Samples were kept chilled (4 to 10°C) and in the dark until returned to the laboratory. *Artemia* abundance was determined from vertical net tows (120 μm net) collected in triplicate at each station.

Incident photosynthetically available irradiance (PAR, 400-700 nm) was recorded continuously on shore with a cosine-corrected quantum sensor and integrated over hour intervals at a site seven kilometers from the southwestern shore of the lake. Attenuation of PAR within the water column was measured at 0.5 m intervals with a submersible quantum sensor. Temperature was measured at 1-m intervals with a thermistor and wheatstone bridge circuit calibrated against a certified thermometer and accurate to 0.05°C.

Ammonium concentrations were measured with the indophenol blue method (Strickland and Parsons 1972) using internal standards for each set of determinations. Nitrate and nitrite concentrations were measured using a modification of the cadmium reduction technique (Strickland and Parsons 1972). After reduction, the pH was lowered to 4.0 with glacial acetic acid for analysis of nitrite. Nitrate and nitrite values were always low (<1 μM) and approximately equal to the analytical error of determination. They are not analyzed here. Phosphate concentrations were determined using the ammonium molybdate method (Strickland and Parsons 1972) on samples that had been diluted 1:99 with distilled-deionized water. The high year-round phosphate values (650 to 1,000 μM) are orders of magnitude greater than half-saturation constants typical for phytoplankton and thus are not considered further here.

Phytoplankton samples were filtered onto Whatman GF/C (1982–1984) or Gelman A/E (1985–1990) filters and kept frozen at -14°C until pigments were analyzed. A comparison of pigment concentrations obtained by the two filter types with samples from different depths did not detect significant differences (Wilcoxon signed-rank, $p < 0.14$). From 1987 to 1990, subsets of samples from various depths were selected on each date and the filtrate from a Gelman A/E filter was filtered through a Whatman GF/F filter; the average retention on GF/F filters was 9% of that collected on the A/E filters. Chlorophyll *a* values given here were not corrected by this amount. Except during periods of low biomass, chlorophyll *a* was determined by spectrophotometric analysis with correction for phaeopigments (Golterman 1969), after a 40-min extraction of the macerated filters in 90% acetone at room temperature in the dark. Low chlorophyll *a* concentrations (<5 mg Chl *a* m^{-3}) were measured on a fluorometer which was calibrated against spectrophotometric measurements using large-volume lake samples.

Carbon uptake rates were measured in laboratory incubations within five hours of sample collection. Samples were kept near lake temperatures and in the dark during transport. Samples in 70 ml borosilicate glass bottles were inoculated with 15–30

microcuries of $NaH^{14}CO_3$. After shaking thoroughly, 0.4-ml samples were removed from five replicate sample bottles and added to scintillation vials containing 1 ml of 0.1 N NaOH and 9 ml of liquid scintillation cocktail to determine total activities. Other samples were inoculated with an equal amount of $NaH^{14}CO_3$ and filtered immediately to provide a zero time control.

Samples were incubated in a water bath and illuminated by cool-white power groove, fluorescent lamps. Temperatures were maintained within 2°C of those from which the samples were taken. Incubator light intensities were measured at the sample with a submersible cosine-corrected quantum sensor. Variation in light levels was achieved by enclosing bottles in neutral density screens. Samples were duplicated at four to eight light levels, ranging from 0 to 300 μEinst m^{-2} s^{-1}. On several dates, samples were only incubated at saturating light levels with dark controls; thus only the light-saturated uptake rates were estimated.

After a 4-h incubation, samples were filtered through a Gelman A/E filter at a pressure not exceeding 125 mm of Hg and rinsed three times with filtered Mono Lake water. The periphery of the filter was rinsed by removing the upper part of the filter holder and pipetting an additional 4–8 ml of filtered lake water around the edge. Filters were then soaked for 12 h in 1 ml of 0.5 N HCl, after which 9 ml of scintillation cocktail were added. Filter activities were then measured on a liquid scintillation counter.

The dissolved inorganic carbon (DIC) content of a series of samples collected from 1983 to 1987 was estimated on a gas chromatograph (Shimadzu GC8AT) using a gas stripping procedure (Stainton 1973). The gas chromatograph used a thermal conductivity detector, a 1-ml sample loop, and a column packed with Porapak-Q. Diluted samples were acidified with 0.15 ml of concentrated H_2SO_4, run through the column on the gas chromatograph, and compared with Na_2CO_3 standards. A linear regression of DIC on conductivity was highly significant:

$$DIC\ (g\ liter^{-1}) = 0.7644 + Cond_{25} \times 0.0463 \qquad p < 0.003,\ n=124$$

where $Cond_{25}$ is the conductivity (mS cm^{-1}) at 25°C. Because the replicate error of DIC determination was of the same magnitude as seasonal variations and measurements of conductivity were more precise, the above regression was used to estimate DIC throughout the study. The variation in DIC over the period of study was less than 6%.

Calculation of photosynthetic parameters, error estimates, and regression analyses -- Dark carbon uptake rates were subtracted from the light uptake rates, which were then normalized to chlorophyll *a* and plotted against light intensity. The light-limited (α^B) and light-saturated (P_m^B) rates of photosynthesis were then determined by least-squares fitting of data from each incubation to the hyperbolic tangent equation:

$$P(I) = P_m^B \tanh (\alpha^B I / P_m^B)$$

where I is the light intensity (μEinst m^{-2} s^{-1}), $P^B(I)$ is the specific carbon uptake rate (g C g Chl a^{-1} h^{-1}) as a function of light intensity, P_m^B is the light-saturated or maximum uptake rate (g C g Chl a^{-1} h^{-1}), and α^B is the initial slope of the P-I curve, or the light-limited uptake rate (g C g Chl a^{-1} $Einst^{-1}$ m^2). Moderate to severe photoinhibition was observed in approximately half of the incubations conducted between November and March when ambient chlorophyll *a* concentrations were high and temperature and light low. In these experiments the highest observed uptake was assumed equal to the light-saturated uptake. For these cases the highest observed rates were substituted for those at higher light levels where photoinhibition was observed before applying the fitting algorithm.

During some years in late summer, the P-I curves exhibited little curvature over the range of light intensities and were not fully saturated at the highest incubator light intensity. Although these curves are consistent with much higher P_m^B values, we think higher values are unlikely. Examination of the curvature in experiments with slightly lower P_m^B values which did saturate indicated actual saturation rates were most likely ca. 10% higher than the highest observed rate for these curves. This finding was incorporated into the fitting routine by adding two additional points, 10% higher than the highest

observed rate at a light intensity 200 μEinst m^{-2} s^{-1} above the highest incubator light level. This procedure effectively incorporated a constraint on part of the P-I curve not determined and is justified by two lines of reasoning. It is consistent with an observed continuum of observed α^B and P_m^B values (much higher P_m^B values would leave a gap in the otherwise continuous range of values) and with theoretical analyses which indicate a theoretical maximum P_m^B of ca. 25 (Falkowski 1981). P_m^B values (often termed assimilation numbers) higher than 20 are rarely reported in the literature.

The variance in the estimates of P_m^B and α^B was estimated using a Monte Carlo procedure. The best fit parameters from an individual experiment are used as surrogates for the true parameters. Then synthetic data sets are constructed by adding random errors corresponding to the actual measurement errors of the experiment. Parameters are then estimated for each of these synthetic data sets. The original estimate remains the maximum likelihood estimate, while the distribution of parameters derived from the synthetic data set approximates the distribution of the true values given an appropriate model.

One hundred synthetic data sets which incorporated measurement errors in chlorophyll *a*, the light field, and carbon uptake, were generated for each experimental incubation. Because only duplicate determinations were made at each light level for any experiment, the error distribution for chlorophyll *a* and carbon uptake was based on the mean coefficient of variation of these measurements for the entire suite of experiments. The measurement error was assumed to be normally distributed with zero mean and standard deviation equal to the standard deviation of replicate measurements. The uncertainty in the light measurements was assumed equal to the coefficient of variation of measurements of the incubator light field and was 7.5%. This measure of the uncertainty in the light field may slightly overestimate the actual uncertainty because samples were routinely shifted several times during the 4-h incubations to compensate for non-uniformities in the incubator light field.

The coefficients of variation (C.V.) of the estimated photosynthetic parameters were minimum in incubations yielding P_m^B values between one and five, ranging from 7–17%. In incubations with high P_m^B values, large uncertainty of low chlorophyll *a* determinations coupled with higher carbon uptake rates and fewer points along the saturated portion of the P-I curve led to higher parameter uncertainty (C.V. = 20–50%). In some cases, poor replication or unknown factors led to uncertainty over 100%. The average C.V. associated with the parameter estimates was 38 and 39% for P_m^B and α^B, respectively.

Multiple nonlinear regression analysis of photosynthetic parameters on environmental factors was performed to identify significant trends and derive an empirical description of photosynthesis. Initial analysis of photosynthetic rates versus the chosen environmental factors indicated nonlinear relationships. Because various combinations of nonlinear terms were considered, it was not possible to perform a single transformation to enable multiple linear regression techniques to be used. Three types of model relationships were examined: linear, multiplicative exponential ($y = a_0 a_1^x$), and rectangular hyperbolic (i.e. Monod type).

Four environmental factors were considered: temperature, the ambient light climate, and two measures of the nutrient regime. The ambient light climate was characterized by the average daily irradiance within the mixed layer over the week preceding the sample date. The daily irradiance within the mixed layer was calculated by combining hourly integrated onshore measurements of PAR with vertical attenuation profiles taken on sample dates. Attenuation profiles were linearly interpolated between dates and the hourly photon flux calculated at 1-m intervals. Photon flux was then averaged over the mixed layer and the preceding 7-d period. The depth of the mixed layer was defined as the first depth at which the temperature gradient exceeded 1°C m^{-1}. Because this measure requires numerically intensive calculations and several assumptions about vertical mixing, we also included ambient chlorophyll *a* as an indirect measure of the

light climate. While there are several reasons why ambient chlorophyll *a* might be a poor indicator of light climate, we included it in this analysis to determine if this simpler empirical alternative would serve as well in describing the light environment. In Mono Lake much of the seasonal variation in attenuation is due to changes in chlorophyll *a* concentrations which are also inversely correlated with daylength.

The nutrient regime was characterized by ambient ammonium concentration and a measure based on flux rates. Relative ammonium availability was calculated as the ratio of daily ammonium supply to algal demand assuming optimal uptake rates. Ammonium supply was calculated as the daily sum of *Artemia* excretion and upward ammonium flux through the nutricline and the ambient concentration. Ammonium excretion by the *Artemia* was based on abundance, excretion rates measured in the laboratory, and interpolation to instar specific weights: 0.0002, 0.0071, 0.0094, 0.0136, 0.0222, 0.0365, 0.0833, 0.198, and 0.6 μmol d^{-1} for instars 1, 2, 3, 4, 5, 6, 7, 8 to 11, and adults, respectively (Jellison unpubl. data). Upward ammonium flux was calculated from vertical profiles of ammonium and eddy diffusivities derived using the flux-gradient heat method (Jassby and Powell 1975) corrected for insolation. The upward vertical flux of ammonium showed distinct peaks during periods of winter and spring mixing. Algal demand was based on an optimal uptake rate modified by light, temperature, and algal biomass. The assumed optimal ammonium uptake rate, estimated from observed maximum carbon uptake rates and the Redfield ratio, was 0.19 μmol N (mg Chl *a* $m^{-3})^{-1}$ h^{-1} and the temperature modification assumed a Q_{10} of 2.1.

A significant problem in applying multiple regression analyses to field measurements is the covariation of independent variables. In Mono Lake, with a marked regular seasonal pattern, covariation of environmental variables is expected. We addressed this problem in two ways. First, we included only one measure of the light climate (ambient chlorophyll *a* or average mixed-layer irradiance) and one measure of the nutrient environment (ambient ammonium or relative ammonium availability) in any

regression. Second, we considered all possible combinations of these variables in step-wise fashion and examined changes in parameter estimates. Regression parameters were estimated by minimizing the sum of the squared errors between observed and predicted values.

Estimates of daily integral production were made using a numerical interpolative model and assuming the photosynthetic parameters (P_m^B and α^B) estimated for the mixed-layer sample were representative of the euphotic zone. Other inputs to the model included the vertical attenuation of photosynthetically available irradiance and vertical water column structure as measured by temperature at 1-m intervals and chlorophyll *a* from samples collected at 2–4 m intervals. Chlorophyll-specific uptake rates were multiplied by ambient chlorophyll *a* concentrations interpolated to 1-m intervals, and modified by temperature assuming a Q_{10} of 2.1. The photosynthetically available light field was calculated from hourly integrated values at the onshore monitoring site, measured water column attenuation, and a calculated albedo. The albedo was calculated based on hourly solar declinations (Jassby and Powell 1975). All parameters, except insolation which was recorded continuously, were linearly interpolated between sampling dates. Daily integral production was calculated by summing hourly rates over the upper 18 m. The interpolative model and incubator technique used here are similar to those developed by Fee (1973). Harrison et al. (1985) found agreement between areal production rates derived with similar incubator/model techniques and more traditional in situ measurements. A further test of the incubator/model method was conducted by comparing estimates derived from laboratory incubations with whole-lake ^{14}C additions (Bower et al. 1987); the two methods were in close agreement when the model ignored photoinhibition.

Results

Photosynthetic parameters -- Chlorophyll-normalized light-saturated carbon uptake rates (assimilation numbers) had a strong and regular seasonal pattern during all 8 yr (Fig. 1A). Values ranged from 0.08 to 15.0 g C g Chl a^{-1} h^{-1} with a mean of 4.3 g C g Chl a^{-1} h^{-1} (n=194). The overall coefficient of variation was 74%. Minimum rates coincided with the seasonal temperature minima during February. Peak rates occurred during July and August, coinciding with peak epilimnetic water temperature (ca. 20°C) and minimum chlorophyll *a* levels (<2 mg Chl *a* m^{-3}). The two stations had similar rates. While on any given day there were significant station to station differences, the overall pattern and mean rates were nearly identical [mean: 4.25±0.37 (1 SE) at the eastern station versus 4.43±0.36 (1 SE) at the western station]. A pair-wise comparison on 72 dates did not yield a significant difference between the two stations (p-value = 0.71).

There were several year-to-year differences, however, statistical tests are weak due to strong seasonality and differences in sampling dates. Winter months were not sampled from 1983 to 1985 and in 1988 measurements of carbon uptake were not begun until July. A subset of the data consisting of monthly averages from March through September was used to compare years. Because temperature explains approximately 60% of the observed variation, an analysis of covariance with temperature as a covariate was performed on this subset. The variation between years was significant with 1985 being higher than other years. Winter (November through February) uptake rates were similarly compared for years in which measurements were made (1986 to 1990). There was a significant decline in winter chlorophyll-specific uptake rates from 1986 to 1990.

The light-limited uptake rates showed a seasonal pattern similar to the P_m^B (Fig. 1B). Rates ranged from 1.7 to 31.9 g C g Chl a^{-1} $Einst^{-1}$ m^2 with a mean of 10.0. While the overall coefficient of variation (56%) was smaller than for P_m^B, the seasonal pattern

was less regular and station to station differences were often larger. No significant station or year-to-year differences could be detected.

Environmental covariates -- Temperatures ranged from 1°C in February to over 20°C during July. Algal biomass varied over two orders of magnitude, from less than 1 to near 100 mg Chl *a* m^{-3} (Fig. 2). Despite the marked increase in chlorophyll *a* following the breakdown of meromixis, midsummer concentrations were always low due to intense grazing by *Artemia* (Lenz 1982). Midsummer minima were lower in 1989 coinciding with a summer *Artemia* population which was approximately double that seen between 1983 and 1990.

Average irradiance within the mixed layer varied from 0.007 to near 11.4 Einst m^{-2} d^{-1}. The low values resulted from high chlorophyll *a*, low insolation, and a deep mixed layer during the winter. Midsummer values were mostly 3 to 6 Einst m^{-2} d^{-1} which, assuming a 12-h photoperiod, is equivalent to an average intensity of 70 to 140 μEinst m^{-2} s^{-1}. Rising lake levels in 1986 following a large spring runoff resulted in a secondary chemocline located above the deeper persistent one which led to higher average light levels in the mixed layer. Following the loss of meromixis, the midwinter irradiance within the mixed layer was smaller due to deeper mixing associated with winter holomixis.

The derived photosynthetic saturation parameter, I_k ($P_m{}^B$ / α^B), indicates the light intensity at which the maximum photosynthetic rate is virtually attained. Comparisons between I_k and the average irradiance within the mixed layer (I_m) were employed to estimate whether algal cells are light-limited. The period over which the average irradiance should be calculated (e.g. the entire day, the daylight period, midday period) for comparison with the photosynthetic saturation parameter depends not only on the question being posed but on the light regime of individual cells and their response to variations within this light regime. We chose to consider the average irradiance in the mixed layer calculated over a five-hour period around midday. If the ratio of I_m to I_k is less than one, photosynthesis is light-limited during the midday period. The photosynthetic saturation

parameter ranged from 22 to 340 μEinst m^{-2} s^{-1} and exhibited a strong seasonal trend of higher values during midsummer conditions of high insolation and water transparency (Fig. 3A). The average midday mixed-layer irradiance showed a similar seasonal pattern with larger amplitude. Thus, the ratio of I_m to I_k varied seasonally (Fig. 3B). Saturating midday light intensities ($I_m / I_k > 1$) are indicated during all of 1983, 1984, and through August 1985. Midday light intensities were subsaturating briefly during winter 1985/1986 as mixing deepened and algal biomass increased. Light intensities remained saturating during most of 1986 and 1987. Following the breakdown of meromixis in 1988, subsaturating midday light conditions prevailed during the winter periods of deep mixing, low insolation, and high algal biomass.

Ambient ammonium concentrations in the mixed layer were mostly low (<5 μM) during meromixis (Fig. 4A). Ammonium-rich water was entrained into the euphotic zone during late 1987 due to deep mixing leading to slightly elevated values seen in 1988. When meromixis terminated in November 1988, epilimnetic ammonium concentrations abruptly increased. Despite the large pulse of ammonium into the euphotic zone, there were brief periods of low ambient concentrations in 1989 and 1990. Low ammonium concentrations occurred in late spring when water temperatures had warmed and algal biomass increased but before the spring generation of *Artemia* matured. Estimates of peak midsummer rates of *Artemia* ammonium excretion were 20–30 mmol m^{-2} d^{-1}, except in 1989 when a much larger summer generation led to even higher estimates (Fig. 4B). During the stratified period when *Artemia* were present, excretion of ammonium was nearly always much larger than the calculated upward flux.

Relative ammonium availability was calculated as the ratio of daily supply to algal demand at optimal growth rates under the observed temperature and biomass conditions. During most of the meromictic period supply and demand were similar (Fig. 4C). Supply exceeded demand in late 1985 due to deeper mixing. Supply, which in this calculation includes ambient ammonium, increased again in late 1987 with further deepening of the

thermocline and even more following the breakdown of meromixis. The ratio of supply to demand during the meromictic period varied from 1 to 4 and increased to above 25 afterwards. This estimate suggests the algae are only limited by nitrogen for brief periods during the spring when peaks in biomass occur.

Due to the strong seasonality in Mono Lake, there were significant correlations among nearly all of the chosen environmental variates (Table 1). Temperature, light, and relative ammonium availability were all positively correlated with each other and negatively correlated with ambient ammonium and chlorophyll *a*. The only pair not significantly correlated were ambient ammonium and relative ammonium availability. Overlain on the strong seasonal pattern were significant year-to-year differences. Winter and spring chlorophyll *a* was much lower during meromixis than after, and nutrient levels were much higher throughout the year following holomixis. The year-to-year differences observed in this long-term data set increase the chance of determining the effects of individual factors, even in the presence of strong seasonal covariation.

Temperature explained a significantly larger portion of the variation in P_m^B than any of the other variates (Table 2, Fig. 5A). The multiplicative exponential and linear regressions both explained over 60% of the total variance. The linear regression predicted lower than observed values and sometimes negative values during the coldest water temperatures, while the exponential regression slightly overestimated these same rates. The maximum rates predicted with the exponential relationship were slightly higher than those predicted with the linear regression.

Chlorophyll *a* could account for 48% of the total variation in an exponential regression. However, most of the explained variation is due to the covariation of chlorophyll *a* with temperature. When the effect of temperature is considered, the addition of chlorophyll *a* only adds a few percent in explained variance. Because P_m^B is already normalized to chlorophyll *a*, this amounts to a secondary dependence. The coefficient less than one indicates P_m^B is lower at higher chlorophyll *a* levels and may be

indicative of self-shading within algal cells. The average attenuation of PAR per unit chlorophyll *a* was calculated from the attenuation of PAR over the 2-m interval from which discrete samples were collected. During periods in which chlorophyll *a* exceeded 6 mg Chl *a* m^{-3}, the chlorophyll *a*-specific attenuation coefficient was only 0.008 m^{-1} compared to 0.024 m^{-1} when chlorophyll *a* was less than 6 mg Chl *a* m^{-3}.

Nonlinear regressions were performed with all possible combinations of two environmental variables including linear, exponential, and Monod type functional forms (Table 3). Only combinations of factors including temperature could predict as well as temperature alone. While including the average mixed-layer irradiance increased the explained variance from 1 to 4 percent, no improvement was obtained by including a measure of nutrients. Three combinations of nutrients, light, and temperature explained slightly more of the total variance (up to 67.7%). The data here do not allow a definitive choice between the various formulations and an examination of the residuals across time for the three formulations showed them to be nearly identical. A formulation based on a linear relationship between (Temp) and ambient light climate (Light) with a Monod type multiplicative effect of relative ammonium availability (Rel) was used for further analysis. The equation:

$$P_m^B = [-0.848 + (0.3863 \times \text{Temp}) + (0.264 \times \text{Light})] \times [\text{Rel} / \text{Rel} + 0.181]$$

explained 67.7% of the total variance in assimilation numbers.

The problem of highly correlated variables can be partially addressed by noting the change in coefficients when a highly correlated variable is entered into the regression. If the coefficient of a variable in the previous regression does not change in sign or magnitude greatly when the new variable is added, the effect of the correlation between variables is probably negligible. The linear temperature regression coefficient decreased slightly when ambient light climate and then relative ammonium availability were added to the regression equation (Table 4). The regression coefficient of ambient light climate increased when relative ammonium availability was added to the regression, but retained

the same sign. Similarly, the coefficient of relative ammonium availability increased when ambient light was added to the regression. The main effect of entering ambient light climate into the regression was to predict slightly lower rates during periods of high chlorophyll *a* from 1988 to 1990 relative to the same periods in 1983 to 1987 when chlorophyll *a* was lower. Adding relative ammonium availability into the regression increased predicted values during 1988 to 1990 relative to those in 1983 to 1987 when ammonium availability was lower. As described earlier, most of the explained variance (60% of 68%) is due to temperature and only slightly better predictions are obtained by including other environmental variables. The major differences can be seen by comparing predicted versus observed P_m^B for the regression including only temperature to the one including temperature, ambient light climate and relative nutrient availability (Fig. 5A, B). Winter minima and the spring transition to higher rates in 1989 and 1990 are better predicted in the full regression.

Less of the overall variance in α^B could be explained on the measured environmental variables. Temperature, in either a linear or exponential form, was the best predictor, but explained only 23% of the total variance. Adding relative ammonium availability resulted in a slight improvement to 27.6%. Light-limited rates were highly correlated with assimilation numbers. Forty-six percent of the total variance in α^B could be explained by a linear regression on P_m^B (Fig. 6):

$$\alpha^B = 4.54 + (1.24 \times P_m^B) \qquad n=132,\ r^2=0.46$$

Ambient light and chlorophyll variations -- Daily insolation varied from an annual minimum of ca. 17 Einst m^{-2} d^{-1} to an annual maximum of ca. 63 Einst m^{-2} d^{-1}. Insolation data were not available for 25% of the days over the eight-year period. On these days, which occurred mostly in mid-winter, the average insolation for the same day during the other years was used. In situ attenuation varied inversely with chlorophyll *a*. The 1% light level varied from about 5 m during the winter and spring period to 15 m in the summer. The winter and spring value was higher in 1984 and 1985 due to low

chlorophyll *a* concentrations and lower in winter 1988/1989 due to high chlorophyll *a* concentrations. Chlorophyll *a* increased below the mixed layer due to the absence of *Artemia* grazing. Therefore, changes in the depth of the mixed layer affect the depth of the euphotic zone. The euphotic zone was slightly deeper in summer 1985 (16 to 17 m) due to a deeper mixed layer and in 1989 due to exceptionally low chlorophyll *a* concentrations.

Ambient chlorophyll *a* concentrations showed strong seasonal variation and marked differences between meromictic and monomictic conditions (Fig. 2). Epilimnetic concentrations were high during the winter (10 to 20 mg Chl *a* m^{-3}), increased during the spring (>50 mg Chl *a* m^{-3}) and sharply reduced (<5 mg Chl *a* m^{-3}) in the summer as the first generation of *Artemia* reached maturity and grazing pressure increased. As stratification weakened in the autumn and *Artemia* declined, an autumn bloom occurred. Superimposed on this general pattern was a strong effect due to meromixis. Chlorophyll *a* concentrations remained low from mid-1983 through late 1985. An increase to 10 to 20 mg Chl *a* m^{-3} occurred in winter-spring 1985/1986 and a slightly larger one in 1986/1987. A much larger increase (30 to 40 mg Chl *a* m^{-3}) followed deep mixing in autumn 1987. Following the breakdown of meromixis in late 1988, winter and spring values were elevated further with spring concentrations exceeding 70 mg Chl *a* m^{-3}.

Daily and annual primary production -- Measurements of P_m^B and α^B were not as frequent as those of chlorophyll *a*, light, and temperature. When not available, P_m^B and α^B were linearly interpolated between adjacent measurements. However, in the winter of 1983 and 1984, this would overestimate production because no measurements were made during the coldest months; there were also no measurements made from January through June in 1988. For these periods, P_m^B and α^B were estimated from the regression equation utilizing temperature, average mixed-layer irradiance and relative ammonium availability.

Daily integral production calculated on sampling days ranged from 0.1 to 10.0 g C m^{-2} d^{-1} (Fig. 7). During the spring period of peak biomass in 1982 when no measurements

of carbon uptake are available, a slightly higher maximum estimate (ca. 12 g C m^{-2} d^{-1}) was derived based on the derived regression equations. During December 1983, when no measurements were performed, production estimates using photosynthetic parameters based on the nonlinear regression yielded values near zero. The strong seasonal pattern observed in P_m^B due to temperature is largely obscured in estimated integral production due to the inverse relationship of algal biomass and temperature. Although there was marked variation throughout the season, there were some general patterns. Integral production usually increased during the spring as algal biomass, water temperature, and insolation increased. Then integral production often decreased as *Artemia* grazed the algae to low levels. A second seasonal increase was observed in the autumn from 1987 through 1990. Peak rates of integral production were higher from late 1987 through 1990 (4–10 g C m^{-2} d^{-1}) compared to the meromictic period (2–4 g C m^{-2} d^{-1}).

The year-to-year differences can best be seen by comparing estimates of annual production (Fig. 8). There was a four-fold difference between production in 1984 (269 g C m^{-2} yr^{-1}) following the onset of meromixis and estimated production in 1988 (1064 g C m^{-2} yr^{-1}) during the breakdown of meromixis. Because actual measurements of carbon uptake measurements were not made from January to June in 1988, the annual estimate employed uptake rates predicted from the regression analysis of ambient conditions (temperature, light, and nutrients). Annual production during meromixis (1984 to 1987) averaged 375 g C m^{-2} yr^{-1} compared to 554 g C m^{-2} yr^{-1} during monomictic conditions in 1983, 1989, and 1990. Annual estimates indicate a decline between 1983 and 1984 followed by a slight increase in 1985, 1986, and 1987. The large increase in 1988 during the breakdown of meromixis was followed by lower values in 1989 and 1990. Although daily production often varied between the two stations in opposite halves of the lake, the corresponding annual estimates were similar. The C.V. of the annual estimates from the two stations ranged from 0 to 21% (mean = 13%, n = 8).

Annual production for the entire period from 1982 to 1990 was also estimated based on P_m^B and α^B predicted from regressions on temperature, ambient light climate, and relative ammonium availability. Estimates of annual production based on the regression equations compared well with those based on measured uptake rates (Fig. 8) except in 1989 and 1990 when they overestimated annual production by 37% and 44%, respectively. For 1983 through 1988, the average relative error between annual estimates based on measurements of carbon uptake versus those based on the regression equations ranged from 2 to 23%.

Discussion

Photosynthetic rates and environmental variables -- Maximum daily rates of production among the eight-years for Mono Lake (3–10 g C m^{-2} d^{-1}) were slightly higher than those reported for other salt lakes in the Great Basin (0.13–6.15 g C m^{-2} d^{-1}) (Walker 1975; Stephens and Gillespie 1976; Galat et al. 1981; Cloern et al. 1983). The range of light-limited and light-saturated (assimilation number) carbon uptake rates are within the range of those found in a variety of studies in many different aquatic systems (Table 5, see Harrison and Platt 1980 and Keller 1988 for values from other studies). Both summer assimilation numbers (5–15 g C g Chl a^{-1} h^{-1}) and light-limited carbon uptake rates (1.7–31.9 g C g Chl a^{-1} $Einst^{-1}$ m^2) are at the high end of the range observed in other studies. In laboratory cultures, light-limited rates are usually between 5 and 9 g C g Chl a^{-1} $Einst^{-1}$ m^2 (cf. Langdon 1988).

Numerous studies have examined, with varying degrees of success, the relationship between environmental variables and P-I curves normalized to some measure of biomass. Difficulties arise because algae show a variety of responses to fluctuating light, temperature, and nutrient regimes. Changes in the size of the photosynthetic unit which may include changes in the ratio of various photosynthetic pigments, the number of photosynthetic pigments, dark enzyme activity, and thylakoid membrane state are among

identified responses (Prézelin 1981). These responses affect the observed P-I curve in different nonlinear ways depending on complex interactions within the algal cells. Also, responses vary across species. Without detailed physiological data on individual species, the interpretation of P-I curves is limited to empirical generalizations for a specific set of environmental conditions and species.

In the current study, our primary goal of studying the relationship between environmental variables and photosynthetic parameters was empirical. The regression analysis enabled estimates of primary production to be made during periods in which nutrient, light, and biomass data were available but not photosynthetic rates. The probability that empirical relationships will remain true under new or different conditions depends on having captured essential determinants of a system's behavior. This is increased by observations of the system over a wide range of environmental conditions. Here, not only were photosynthetic parameters measured throughout eight years but also during different mixing and nutrient regimes. Empirical relationships can be further enhanced if known causal interactions with temperature, light, or nutrient conditions are incorporated into their formulation.

Temperature is a major factor controlling rates of growth and photosynthesis in algae (Eppley 1972). Short-term responses of light-saturated rates to changes in temperature typically show a Q_{10} of ca. 2.0 (cf. Davison 1991). Raven and Geider (1988) list a large number of Q_{10} values associated with various growth processes and many are near 2. Several continuous culture studies of marine and freshwater algae indicate Q_{10} values for growth of about 2 (cf. Eppley 1972). Paired samples collected throughout the season from Mono Lake and incubated at two different temperatures yielded a Q_{10} for carbon uptake of 2.0 (Jellison and Melack 1988).

Variation in temperature often explains a significant portion of the observed variation in assimilation numbers in natural populations (37%, Harrison and Platt 1980; 40%, Platt and Jassby 1976; 53%, Côte and Platt 1984). In the present study,

temperature accounted for 60% of the observed variation. Q_{10} values derived from seasonal measurements of phytoplankton often exhibit a wider range than those derived from laboratory studies because in addition to the direct effects of temperature, a "seasonal Q_{10}" will reflect species differences and changes in the light and nutrient environments. In this study, the seasonal temperature regression coefficient yielded a "seasonal Q_{10}" of 5.0, when only temperature was considered. This high value reflects the coincidence of low temperature with other suboptimal factors. When measures of ambient light climate and nutrient availability were included, the temperature regression coefficient yielded a "seasonal Q_{10}" of 3.86. While still high, it is closer to the value expected from laboratory studies (1.9–2.3).

While temperature strongly affects enzymatic rates, a strong correlation between photosynthetic parameters and temperature is not always found in natural populations. In Hamilton Harbour, Harris et al. (1980) found any temperature affect to be obscured by stronger effects of physical variations in the mixing regime. In Mono Lake, several factors likely contribute to the strong correlation. The plankton is dominated by only a few species of phytoplankton and one zooplankton, and nutrients and mean mixed-layer irradiance covary with temperature.

Algae acclimate to changes in spectral irradiance by changing the size or number of photosynthetic units and pigment ratios (cf. Falkowski and LaRoche 1991). When cells acclimate to low light conditions, maximum photosynthetic rates normalized to chlorophyll *a* will often decrease due to less efficient absorption per unit chlorophyll *a* (Falkowski 1981; Prézelin 1981; Geider 1987). Several authors have noted that light-saturated and light-limited uptake rates in natural populations often decline under conditions of low light (Platt and Jassby 1976; Jellison and Melack 1988; Heyman 1986). In the current analysis, ambient chlorophyll *a* and average mixed-layer irradiance entered significantly in a multiple regression of assimilation numbers on environmental factors. Assimilation numbers were slightly depressed during periods of higher chlorophyll *a* and

low light. The ratio of the mixed-layer irradiance averaged over five hours around noon to the light intensity at which photosynthesis saturated indicated light-limiting conditions for winter through spring during late and post-meromictic conditions. A chloroplast packaging effect was evidenced by decreasing attenuation per unit chlorophyll *a* at low light or high chlorophyll *a* levels. However, consideration of the mixed-layer irradiance only reduced the unexplained variance in light-saturated uptake rates from 1 to 5%. Heyman (1986) concluded that rates normalized to cell carbon are much more useful in interpreting physiological responses. We agree, but while potentially more useful, cellular carbon is much more difficult to measure due to methodological problems of separating algal carbon from other particulate carbon.

The direct effect of nutrient limitation is a decrease in nitrogenous photosynthetic pigments and enzymes of photosynthetic carbon metabolism (see Turpin 1991). Low assimilation numbers in natural populations have been assumed to indicate nutrient limitation (Curl and Small 1965). However, the light and dark reactions of photosynthesis are affected differently by nitrogen stress in different species. While assimilation numbers declined with decreasing growth rates in nutrient-limited chemostats, both absolute and relative declines were species-specific (Glover 1980).

Neither of our measures of the nutrient regime, ambient ammonium or relative ammonium availability based on supply and demand rates, explained more than a few percent of the overall variation in assimilation number. Our estimates of supply and demand suggest that nitrogen limitation is only likely during short periods occurring predominantly in the spring when algal biomass is high and water temperatures are increasing. Therefore at Mono Lake, periods of low light coincide with those most likely to experience nitrogen stress. Because both adaptation to low light and conditions of nitrogen stress cause a decline in assimilation number, it is not possible to separate these two effects in the current study.

Seasonal patterns of primary production -- The estimates of photosynthetic production we present were based on photosynthetic rates from integrated samples of the mixed layer assuming no photoinhibition. These rates were modified by the changes in the vertical profiles of chlorophyll *a*, temperature, and light attenuation. Several times during the summer a chlorophyll *a* maximum was located at the bottom of the mixed layer. This region is exposed to low light levels, but is below the depth to which *Artemia* graze because of low oxygen levels. In some meromictic lakes, chemoautotrophic production is a significant portion of the overall production (see Cloern et al. 1983). Our estimates only include algal planktonic production. Previous estimates of annual production utilizing samples from three to four depths including the deep chlorophyll *a* maximum were similar to the present ones (540 and 340 for 1983 and 1985 according to Jellison and Melack 1988 compared to 523 and 399 g C m^{-2} d^{-1} in the present study).

The regular annual cycle in temperature and insolation are not evident in seasonal patterns of primary production due to variation in photosynthetic parameters, light attenuation, and algal biomass. The predominant effect of temperature is evidenced by its ability to explain sixty percent of the variation in P_m^B. However, unlike many temperate lakes, the annual cycle of algal biomass is out of phase with temperature due to the seasonal dynamics of the brine shrimp, *Artemia monica*. *Artemia* overwinters as a dormant cyst and hatches out in the spring. In the low spring water temperatures it matures slowly, reaching maturity in late May. Grazing pressure steadily increases as individuals mature and water temperatures warm; algal biomass and daily production also increase. The algal increase was less pronounced under meromictic conditions from 1983 to 1987 compared with 1988 through 1990. Increasing algal demand and thermal stratification results in declines in ambient ammonium concentrations to near zero. For brief periods in April or May calculations of daily algal ammonium demand, assuming optimal uptake rates exceed supply rates. Algal ammonium demand declines as *Artemia* grazing results in a clearing phase in which algal biomass is reduced to less than 1 mg Chl

a m^{-3}. The rapid clearing phase occurs over a 2–3 week period and is accompanied by an increase in ambient ammonium as particulate nitrogen in algae is converted to dissolved inorganic nitrogen through *Artemia* excretion. A second generation of *Artemia*, produced ovoviviparously (live birth) from the first, matures in about 3 weeks at the higher water temperatures. Individuals from both generations switch almost entirely to cyst production at the low chlorophyll *a* levels found during the summer. Although assimilation numbers are high throughout the summer, algal biomass and production are held low by the large summer generation of shrimp. Algal biomass increases in the autumn as the shrimp population declines rapidly when water temperatures decline to below 10°C. Superimposed on the annual patterns imposed by stratification and *Artemia* dynamics were changes due to the onset of meromixis.

Neither direct physical effects (bottom-up) nor grazing (top-down) are sufficient by themselves to explain the year-to-year differences in the seasonal pattern of primary production. The patterns of primary production can only be understood by examining both changes in the *Artemia* dynamics and those in the vertical mixing regime accompanying the onset, persistence, and breakdown of meromixis. The *Artemia* dynamics can be summarized by the spring and summer peaks of adult abundance (Fig. 9). Exceptionally large second generations occurred when the spring generation was small as seen in 1982 and 1989. *Artemia* fecundity is strongly dependent on ambient chlorophyll *a* levels (Jellison unpubl. data) and high recruitment into the second generation results when chlorophyll *a* levels remain high under reduced grazing pressure associated with a small first generation.

Spring *Artemia* abundance of adults in 1983 and 1989 were low and similar to each other. However, when coupled with different nutrient regimes, similar spring *Artemia* abundance led to quite different plankton dynamics. In 1989 under nutrient replete conditions and low grazing pressure, a significantly larger algal bloom (80–90 mg Chl *a* m^{-3}) occurred than in 1983 when ammonium concentrations and vertical mixing

were reduced (15–20 mg Chl *a* m^{-3}). High food availability for the first generation led to midsummer *Artemia* abundances which were over twice as large as in 1983 and higher than any observed during meromixis. High *Artemia* abundances resulted in depressed algal levels and lower production rates late in the summer compared to 1983.

In 1988 an exceptionally large number of *Artemia* reached adulthood in the first generation. The large spring hatch was most likely due to accumulated dormant cysts being exposed to oxygenated conditions during deep winter mixing in early 1988. The relative sizes of the two *Artemia* generations were opposite those observed in 1989, as the spring generation was much larger than the summer generation. As in 1989, algal levels and production were depressed due to heavy grazing, but this occurred much earlier. During meromixis from 1984 through 1987 the two generations of *Artemia* were more similar and the seasonal variation in algal production less.

Annual production -- There are no comparable long-term studies of algal production in other large, deep hypersaline lakes. The annual estimates of planktonic photosynthesis found in this study (269–640 g C m^{-2} yr^{-1}, 1063 g C m^{-2} yr^{-1} estimated in 1988) are somewhat higher than other hypersaline lakes in the Great Basin: Great Salt Lake (southern basin), 145 g C m^{-2} yr^{-1} (Stephens and Gillespie 1976); Soap Lake, 391 g C m^{-2} yr^{-1} (Walker 1975); and Big Soda, 500 g C m^{-2} yr^{-1} (350 g C m^{-2} yr^{-1} phototrophic production)(Cloern *et al.* 1983). Previously reported estimates for Mono Lake, 340–540 g C m^{-2} yr^{-1} (Jellison and Melack 1988), were all taken during the period of meromixis and are lower than the maximum estimates reported here which include monomictic conditions.

The effect of changes in nutrient cycling accompanying meromixis were clear in this study. While the *Artemia* strongly affect the seasonal patterns of production through grazing, ammonium excretion, and nitrogen export via fecal pellets, the year-to-year differences in annual production closely followed the vertical flux of nutrients associated with different stages of meromixis. Ambient ammonium concentrations in the

mixolimnion were low during the six-year period of meromixis (Fig. 10). Low nutrient availability was mirrored in the annual production estimates and clearly indicates the "bottom-up" control of annual phytoplankton production in Mono Lake.

The differences in annual phytoplankton production resulted primarily from changes in the amount of standing biomass; year-to-year changes in assimilation numbers were not correlated with annual production. During periods of increased vertical mixing and low grazing, algal biomass increased significantly compared to periods of strong chemical stratification. When chemical stratification was weak in the autumn, a significant algal bloom developed and was nearly always followed by higher algal biomass in the spring. Thus, patterns of annual production calculated from 1 July to 30 June (Fig. 11) show more clearly the effects of the onset, persistence and breakdown of meromixis than those based on the calendar year. Vertical mixing was nearly to the bottom during winter 1982/1983 and annual production from mid-1982 to mid-1983 was estimated to be 699 g C m^{-2} yr^{-1}. Strong chemical stratification and decreased vertical fluxes of ammonium resulted in a large decline to 251 g C m^{-2} yr^{-1} in 1983/1984. Production increased during 1984 and 1985 as vertical ammonium flux increased due to both deeper mixing and the monimolimnetic buildup of ammonium. In 1986 large freshwater inflows resulted in a secondary chemocline becoming established over the then deeper persistent one formed in 1983. This resulted in decreased production in 1986/1987. Production subsequently increased in 1987/1988 as mixing deepened and reached its maximum for the period of study in 1988/1989 as meromixis was terminated in November 1988 and a large pulse of ammonium was injected into the euphotic zone. In 1989/1990 annual production declined slightly presumably due to the observed lower ammonium levels.

Annual photosynthetic production provided much clearer evidence of the ecosystemic effects of changes in vertical mixing and nutrient availability than the analysis of assimilation numbers. Assimilation numbers actually decreased slightly from 1985 to 1988 and then increased in 1989 and 1990, opposite the trend of annual photosynthetic

production. This apparent contradiction illustrates one limitation of using assimilation numbers to assess the physiological state of algae. At Mono Lake, the largest response to changes associated with meromixis occurred during the spring and autumn as both daily integral production and chlorophyll *a* increased. Because increased chlorophyll *a* resulted in lower average irradiance, an algal response of increasing chlorophyll *a* per cell and consequent decreases in assimilation number, may have masked increased algal growth rates. The extent to which changes in chlorophyll *a* per cell will mask nutrient effects depends on a suite of factors including species composition and the degree of nutrient and light limitation before and after nutrient enrichment. A different response to increased nutrients was observed in phosphorus-limited Southern Indian Lake, Canada (Hecky and Guildford 1984). Nutrient enrichment due to impoundment led to a general increase in photosynthetic rates (assimilation number and light-limited uptake) and integral production.

The effect of El Niño-Southern Oscillation events on marine systems is well-documented (Glynn 1988). We document a dramatic effect on photosynthetic production in an inland lake due to changes in nutrient cycling as a result of alterations in vertical mixing associated with changes in snowmelt runoff. While a "bottom-up" effect was primarily responsible for changes in annual primary production, the *Artemia* played an important role in determining the details of the seasonal production pattern. Jassby et al. (1990) found a similar interaction of "bottom-up" and "top-down" effects in Castle Lake, California. A deep productivity maximum was dependent on the timing of ice breakup and the amount of hydraulic flushing, both of which varied with El Niño events. "Top-down" effects determined by trophic interactions between algae, *Daphnia* and trout were observed in August-September with primary production being reduced when trout were scarce and *Daphnia* abundant.

Long-term effects of the recent 6-yr period of meromixis at Mono Lake were not evident in this study. During meromixis, increasing monimolimnetic concentrations of

ammonium and mixed-layer deepening contributed to increasing vertical fluxes of ammonium. The rapid buildup of ammonium in the monimolimnion during meromixis is partly a function of the small monimolimnetic volume. Subsequent to the initial decline in photosynthetic production observed at the onset of meromixis, annual production increased and by 1985/1986 was nearly equal to that estimated for 1982/1983. This suggests a relatively rapid return to monomictic levels of photosynthetic production. However, the effect of meromictic events on losses (e.g. burial, volatilization) or gains (e.g. nitrogen fixation) from the lake was not assessed in this study. Increased volatilization of ammonium is likely due to the high surface concentrations observed following the breakdown of meromixis and could result in increased losses of nitrogen from the lake if the frequency of meromictic events were to increase.

The frequency of meromictic episodes in Mono Lake is unknown. The recent episode resulted from a record high snowfall in the Sierra Nevada. Accurate measurements of surface levels in Mono Lake beginning in 1912 (LADWP unpubl. data) show previous single year changes in elevation to be smaller than that which occurred in 1983. However, since diversion of inflowing streams began in 1941 the lake level has dropped 14 m and thus variation in snowmelt and runoff are larger relative to the volume of Mono Lake. Also, as the lake declines it becomes more saline, leading to a larger density difference between lake water and inflowing streams. These factors could increase the frequency of meromictic episodes with consequent effects on this ecosystem.

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Table 1. Correlation between environmental variates: temperature of incubation (Temp, °C), light within the mixed layer averaged over depth and the preceding week (Light, Einst m^{-2} d^{-1}), chlorophyll *a* (Chl, mg Chl *a* m^{-3}), ambient ammonium concentration (NH_4^+, μM), and relative ammonium availability (Rel, ratio of calculated supply to calculated optimal demand, see methods).

	Temp	Light	Chl	NH_4^+	Rel
Tmp	1.00	0.64	-0.54	-0.26	0.66
Lit	-	1.00	-0.54	-0.39	0.35
Chl	-	-	1.00	0.34	-0.41
NH_4^+	-	-	-	1.00	0.13*
Rel	-	-	-	-	1.00

*The only correlation which is not significant ($p > 0.05$).

Table 2. Regressions of assimilation numbers (P_mB) on single environmental variates: temperature of incubation (Temp, °C), light within the mixed layer averaged over depth and the preceding week (Light, Einst m-2d-1), chlorophyll *a* (Chl, mg Chl *a* m-3), ambient ammonium concentration (NH4+, µM), and relative ammonium availability (Rel, ratio of calculated supply to calculated optimal demand, see results).

Equation	Total variance explained (%)
$P_m^B = (Temp \times 0.496) - 1.493$	60.1
$P_m^B = 0.834 \times (1.132^{Temp})$	62.0
$P_m^B = (Light \times 0.3007) + 1.923$	37.8
$P_m^B = 10.54 \times [Light / (Light + 8.172)]$	43.6
$P_m^B = (-0.108 \times Chl) + 5.826$	30.9
$P_m^B = 8.364 \times (0.818^{Chl})$	48.0
$P_m^B = (-0.063 \times NH_4^+) + 4.969$	6.8
$P_m^B = 4.55 \times [NH_4^+ / (NH_4^+ + 0.040)]$	0.0
$P_m^B = (-0.00418 \times Rel) + 4.52$	1.3
$P_m^B = 5.173 \times [Rel / (Rel + 0.219)]$	6.0

Table 3. Percent of variation explained in nonlinear regressions including two independent variables. Functional relationships included linear , exponential (Exp.), and Monod type forms.

		Chlorophyll *a*		*Light		NH_4^+		*Rel	
		Linear	Exp.	Linear	Monod	Linear	Monod	Linear	Monod
Temperature:	Linear	62.8	65.7	63.2	63.4	60.5	60.5	60.1	62.2
	Exp.	65.5	65.8	62.9	59.3	62.8	62.0	62.1	60.7
Chlorophyll *a:*	Linear	-	-	44.7	48.9	31.5	32.8	31.8	-
	Exp.	-	-	51.0	52.6	51.4	47.1	50.1	48.6
Light:	Linear	-	-	-	-	37.9	43.1	37.9	55.6
	Monod	-	-	-	-	45.2	50.9	44.2	61.8

*See text for calculation of ambient light climate (Light) and relative ammonium availability (Rel).

Table 4. Relative change in regression coefficients as new variables are included. Variables are temperature of incubation (Temp, °C), light (Einst m^{-2} d^{-1}), and relative ammonium availability (Rel, ratio of calculated supply to calculated optimal demand, see methods).

	Temp	Temp/Light	Temp/Rel	Temp/Light/Rel
a_0	-1.493	-1.330	-1.319	-0.848
Std. Err.	0.458	0.515	0.459	0.502
p-level	<0.005	<0.01	<0.05	0.093
a_1	0.496	0.524	0.415	0.386
Std. Err.	0.035	0.041	0.045	0.050
p-level	<0.001	<0.001	<0.001	<0.001
a_2		0.152		0.264
Std. Err.		0.067		0.095
p-level		<0.05		<0.01
a_3			0.094	0.181
Std. Err.			0.035	0.048
p-level			<0.01	<0.001
Variance explained (%)	60.0	63.2	62.2	67.7

Equations are:

$$P_m^B = a_0 + a_1 \times \text{Temp}$$

$$P_m^B = (a_0 + a_1 \times \text{Temp} + a_2 \times \text{Light})$$

$$P_m^B = [a_0 + a_1 \times \text{Temp}] \times [\text{Rel} / (\text{Rel} + a_3)]$$

$$P_m^B = [a_0 + a_1 \times \text{Temp} + a_2 \times \text{Light}] \times [\text{Rel} / (\text{Rel} + a_3)]$$

Table 5. Photosynthetic parameters derived from studies of various aquatic systems: chlorophyll *a*-specific light-saturated uptake (P_m^B, g C g Chl a^{-1} h^{-1}) and light-limited uptake (a^B, g C g Chl a^{-1} $Einst^{-1}$ m^2).

Region	P_m^B	a^B	Reference
Nova Scotia coast	0.9–19.1	3.3–42.8	Platt and Jassby 1976
Bedford Basin, Nova Scotia	2.0–8.4	4.7–15.8	Côte and Platt 1983
Southern Indian Lake, Canada	1.7–4.5	3.0–6.7	Hecky and Guildford 1984
Chesapeake Bay	1.0–12.0	2.8–52.8	Harding et al. 1985
Delaware Estuary	1.0–22.7	5.6–17.8	Pennock and Sharp 1986
ELA Lakes	1.3–3.6	2.5–6.9	Fee et al. 1987
MERL mesocosm (estuarine)	1.0–25.6	1.7–46.7	Keller 1988
Mono Lake, California	0.2–19.9	1.7–31.9	present study

Figure Captions

Fig. 1. Assimilation numbers (P_m^B, g C g Chl a^{-1} h^{-1}) (A) and light-limited (α^B, g C g Chl a^{-1} Einst^{-1} m^2) carbon uptake rates (B) at an eastern (o) and western (•) pelagic station from 1983 to 1990.

Fig. 2. Seasonal variation in chlorophyll *a* (mg Chl *a* m^{-3}) of mixed-layer samples collected from 1983 to 1990 at an eastern (o) and western (•) pelagic station.

Fig. 3. Photosynthetic saturation parameter, I_k (μEinst m^{-2} s^{-1}) at an eastern (o) and western (•) pelagic station (A). Ratio of average mixed-layer irradiance from 0930–1430 hours (I_m, μEinst m^{-2} s^{-1}, see text for calculation) to I_k (B).

Fig. 4. A. Ambient ammonium concentration (μM) in mixed-layer samples collected from 1983 to 1990 at an eastern (o) and western (•) pelagic station . B. *Artemia* ammonium excretion (•, mmol m^{-2} d^{-1}) and upward fluxes of ammonium (o, mmol m^{-2} d^{-1}) at a western pelagic station. C. Comparison of daily ammonium supply (•, mmol m^{-2} d^{-1}) (defined as the sum of *Artemia* excretion, upward flux, and ambient ammonium) to algal demand (o, mmol m^{-2} d^{-1}) at optimal rates of photosynthesis at a western pelagic station.

Fig. 5. A. Observed assimilation numbers (•) at a western pelagic station versus those predicted (o) from a linear regression on temperature (Temp): $P_m^B = -1.493 + 0.496 \times \text{Temp}$. B. Observed assimilation numbers at a western pelagic station versus those predicted from a nonlinear regression on temperature, ambient light climate (Light, see text) and relative ammonium availability (Rel, see text): $P_m^B = (-0.848 + 0.3863 \times \text{Temp} + 0.652 \times \text{Light}) \times (\text{Rel} / (\text{Rel} + 0.264))$.

Fig. 6. Linear regression of α^B [g C (g Chl *a* Einst)$^{-1}$ m^2] on P_m^B [g C (g Chl *a* h)$^{-1}$]; $\alpha^B = 4.54 + (1.24 \times P_m^B)$; n=132, r^2=0.46.

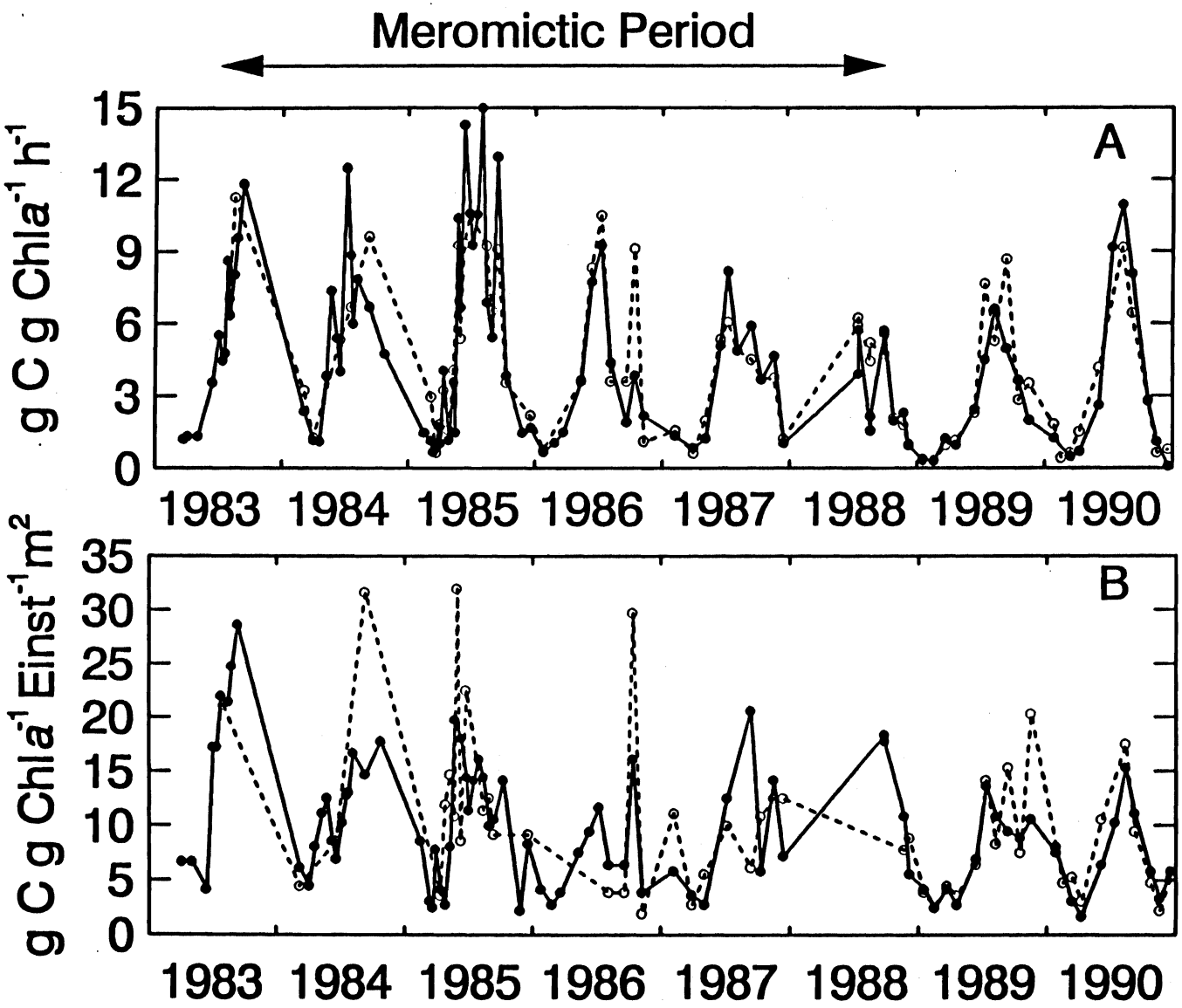
Fig. 7. Daily phytoplankton production (g C m^{-2} d^{-1}) at an eastern (A) and western (B) pelagic station, 1982–1990. Points indicate dates when photosynthetic parameters were derived from laboratory incubations (•), interpolated between adjacent dates (o), or based on nonlinear regression (Δ).

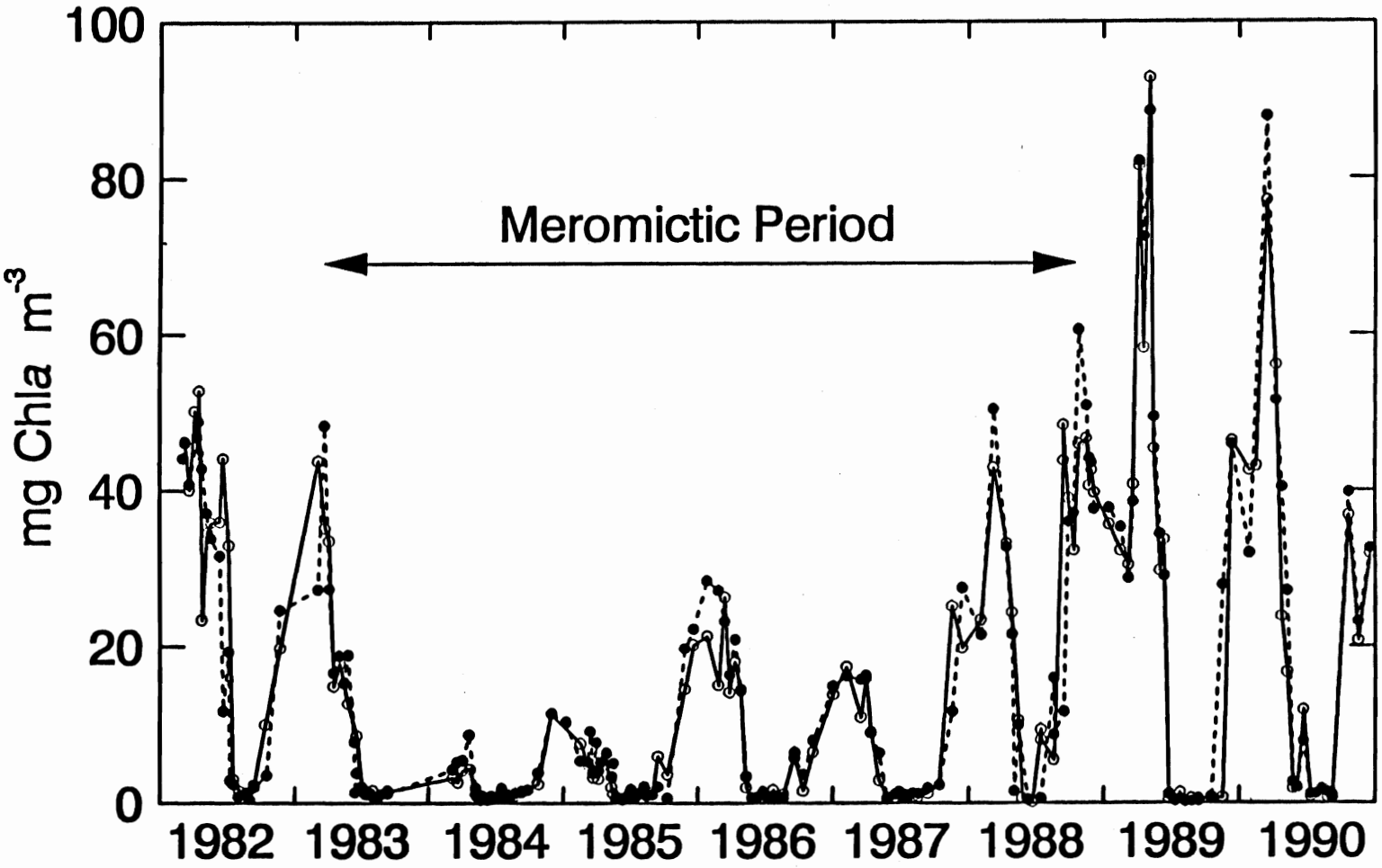
Fig. 8. Comparison of annual phytoplankton production estimates (g C m^{-2} yr^{-1}) at an eastern and western pelagic station from 1982–1990 based on photosynthetic parameters derived from laboratory incubations versus those predicted from a nonlinear regression equation.

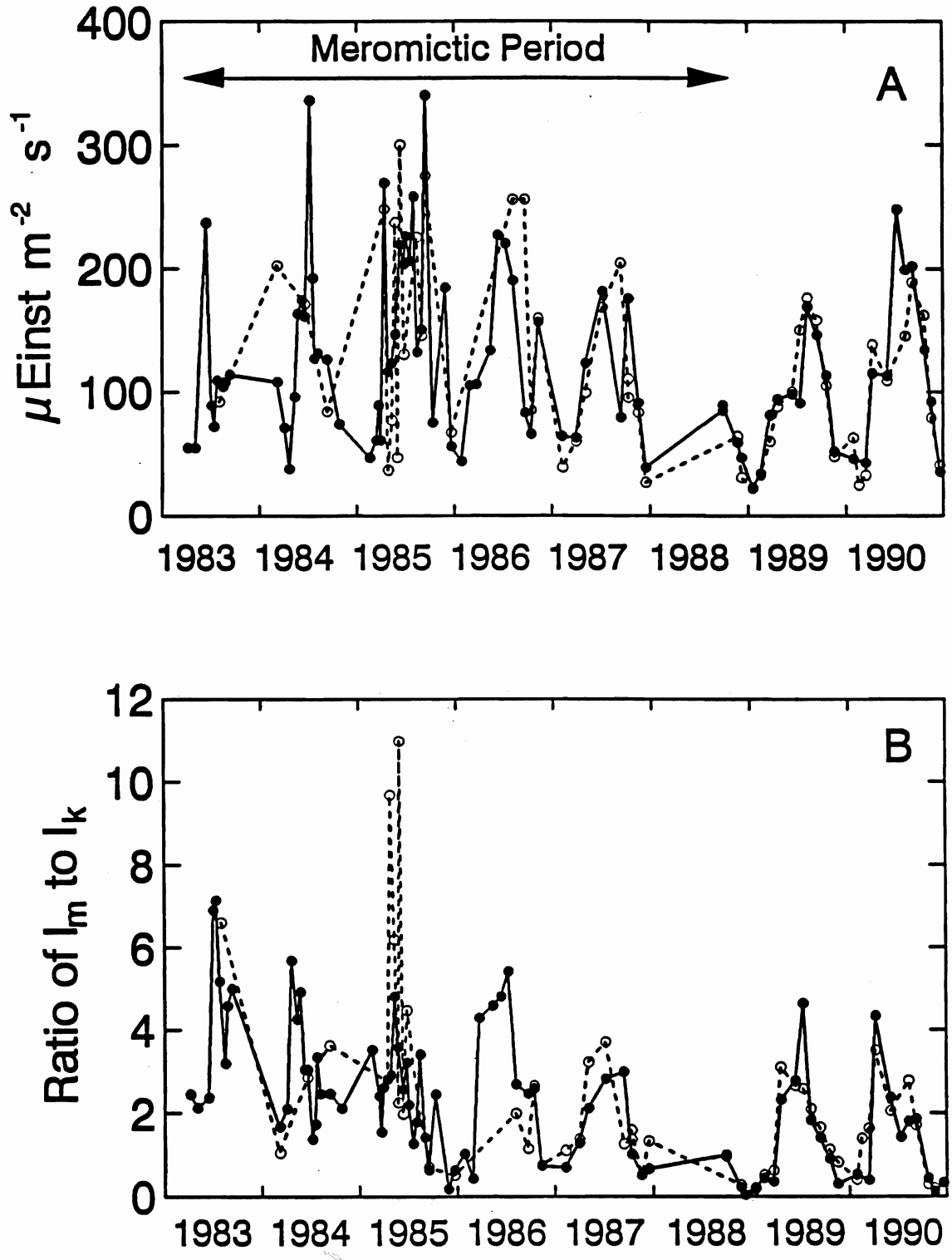
Fig. 9. Spring (solid) and summer (hatched) *Artemia* peak adult abundances, 1982 to 1990. Error bars indicate 1 SE of lakewide means based on ten stations.

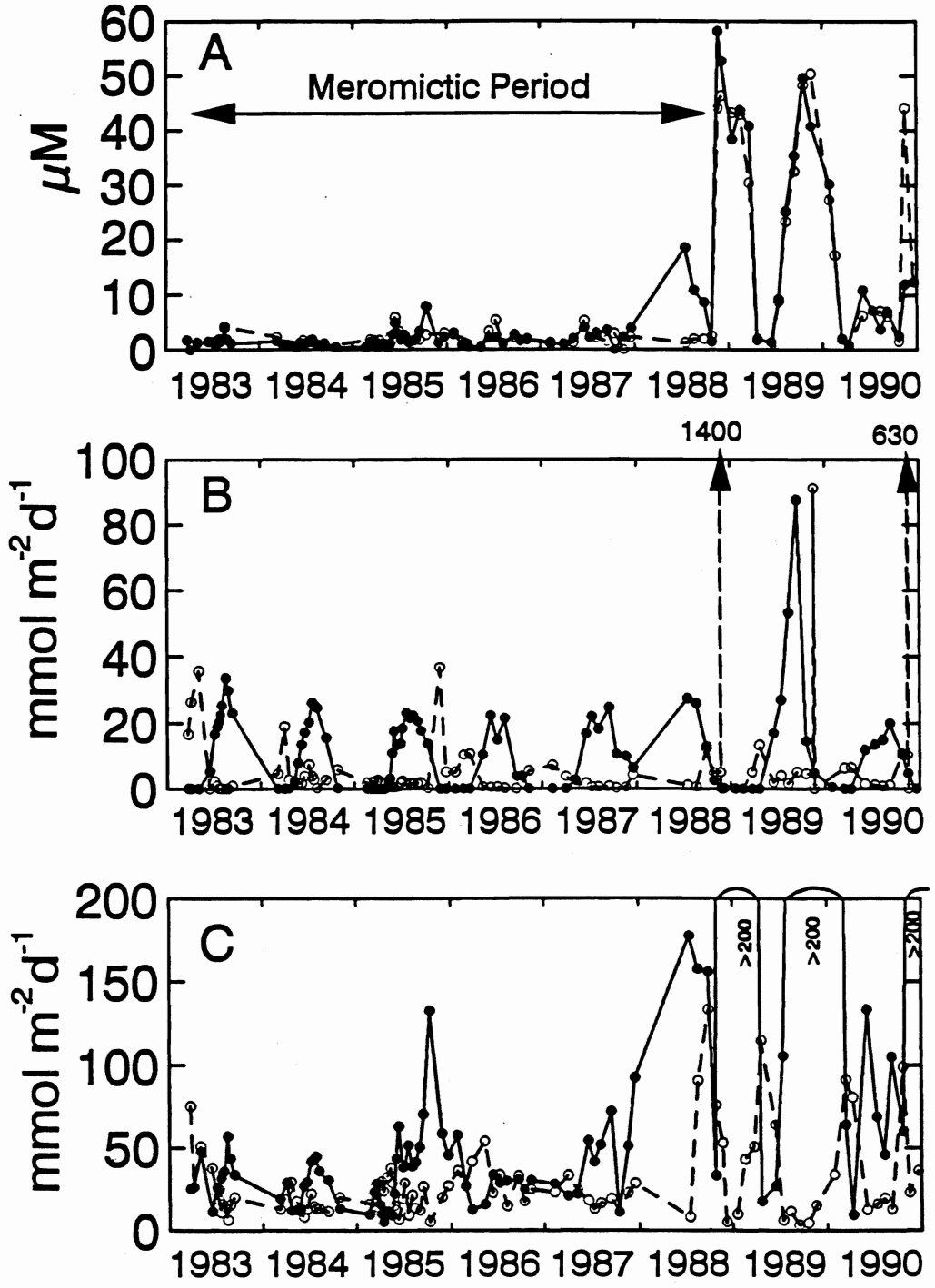
Fig. 10. Ambient ammonium concentration (μM) during the onset, persistence and breakdown of meromixis in Mono Lake, 1982 to 1990.

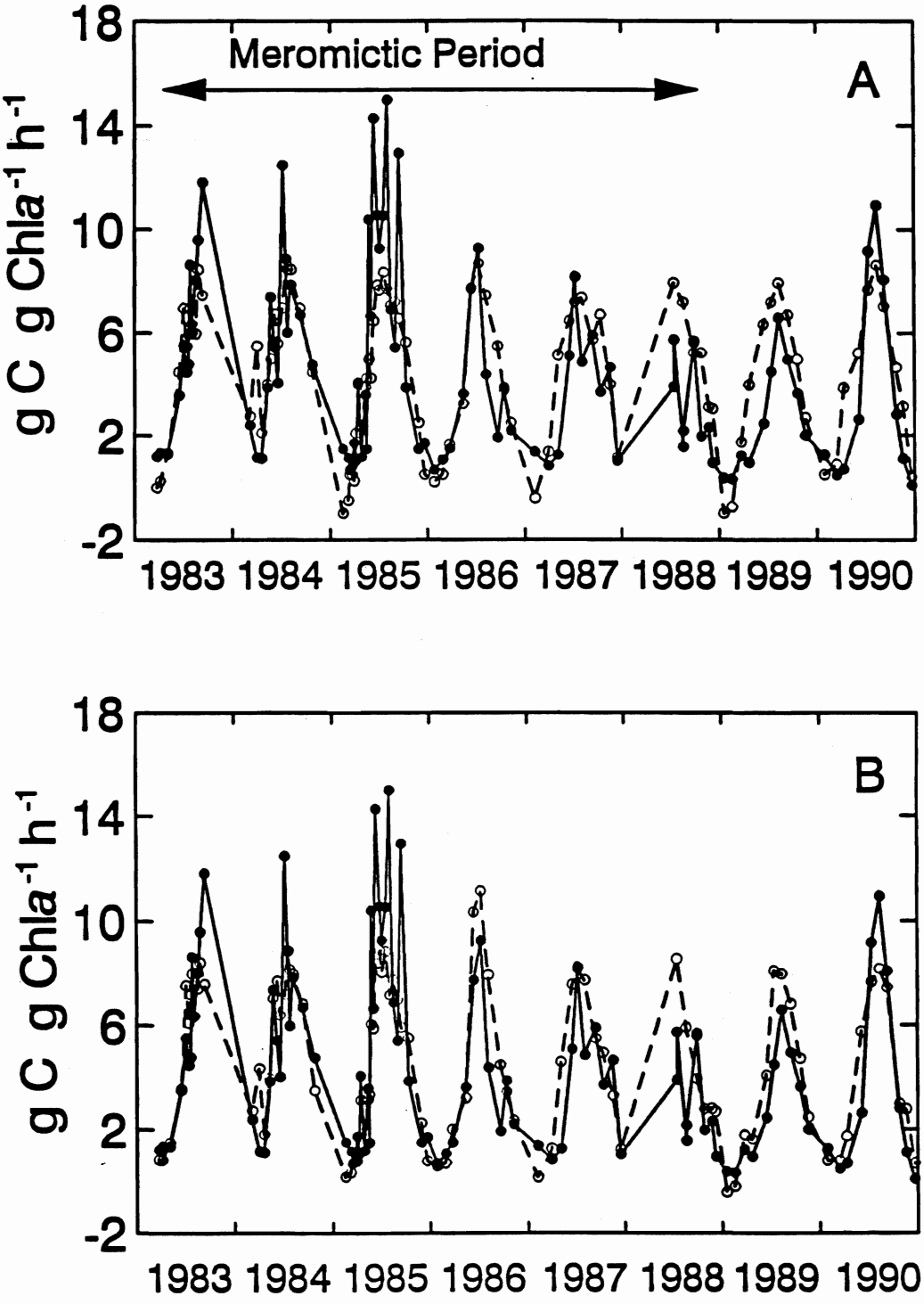
Fig. 11. Eight-year trend of annual phytoplankton production (g C m^{-2} yr^{-1}) calculated from 1 July to 30 June during the onset, persistence and breakdown of meromixis. Error bars indicate one standard error of estimate derived from two pelagic stations located in opposite sides of the lake. During 1982 and the first half of 1988 photosynthetic parameters were estimated from regression equations.

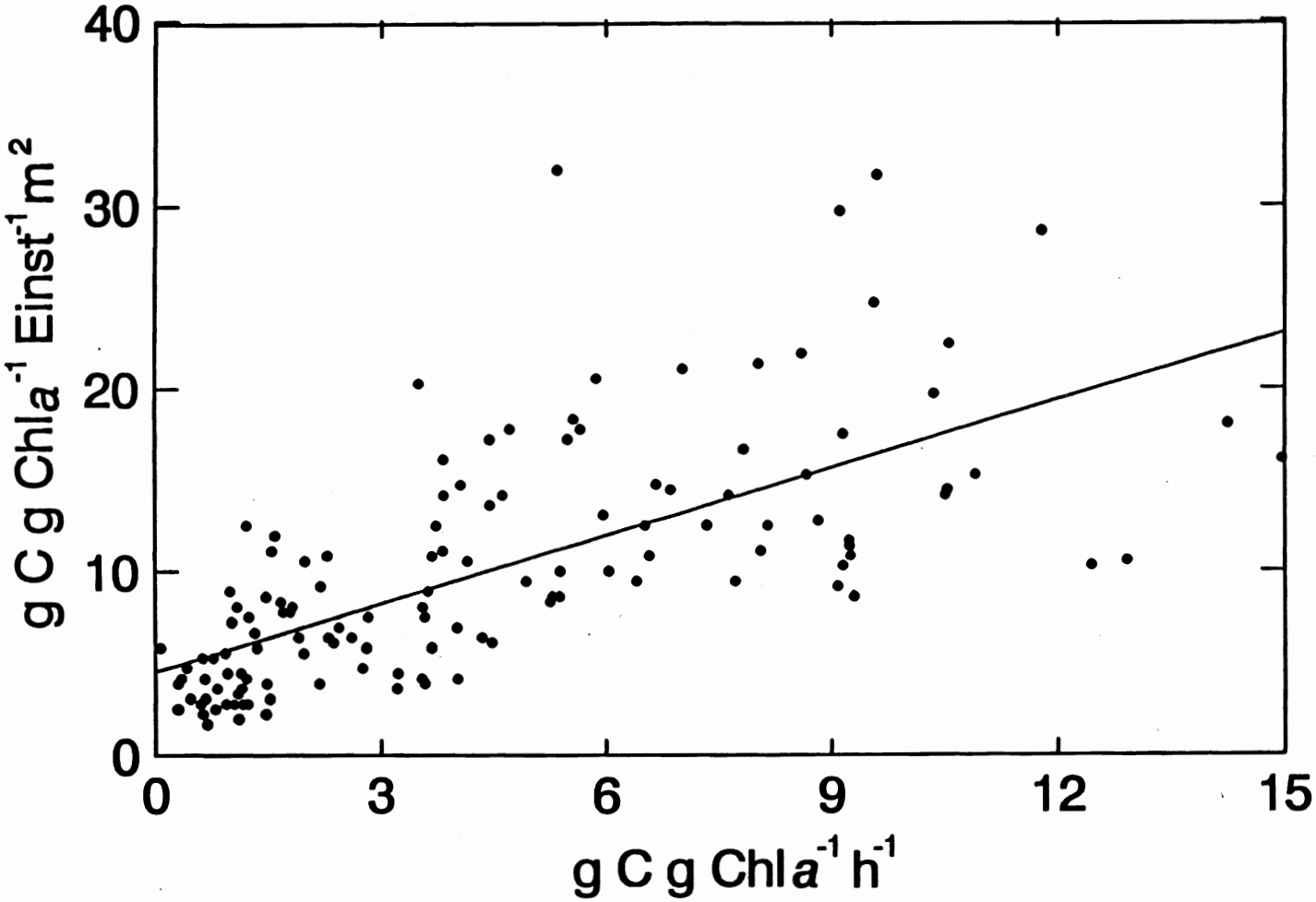

Meromictic Period
A
B
g C g Chla-1 h-1
g C g Chla-1 Einst-1 m2
0
3
6
9
12
15
0
5
10
15
20
25
30
35
1983
1984
1985
1986
1987
1988
1989
1990

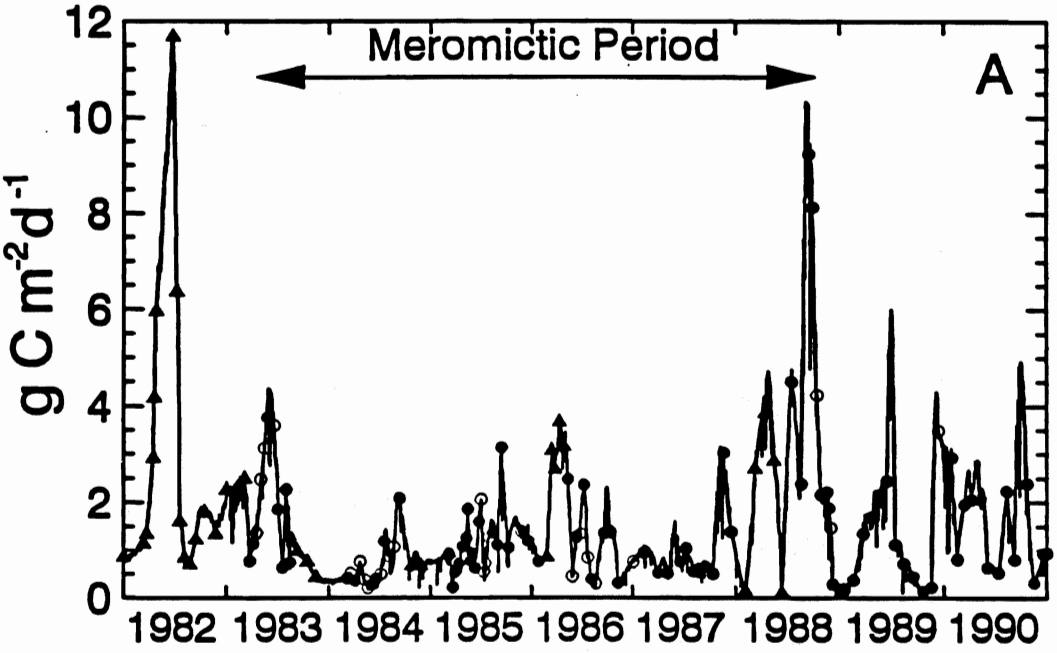

100
80
60
40
20
0
mg Chla m-3
Meromictic Period
1982
1983
1984
1985
1986
1987
1988
1989
1990

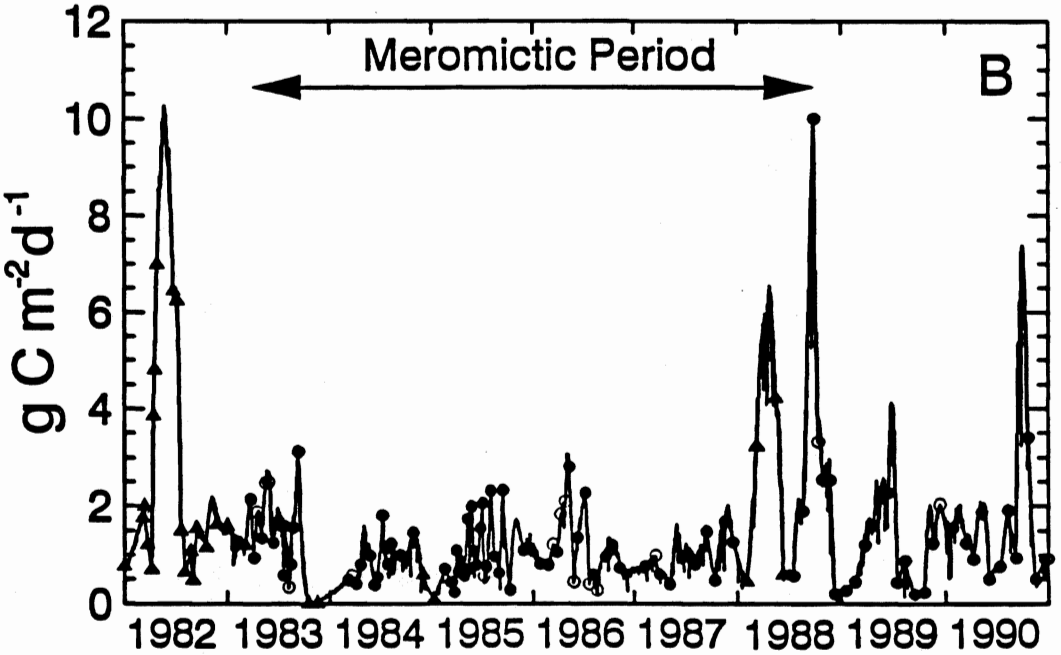

Meromictic Period
A
B
μEinst m-2 s-1
Ratio of Im to Ik
0
100
200
300
400
0
2
4
6
8
10
12
1983 1984 1985 1986 1987 1988 1989 1990
1983 1984 1985 1986 1987 1988 1989 1990

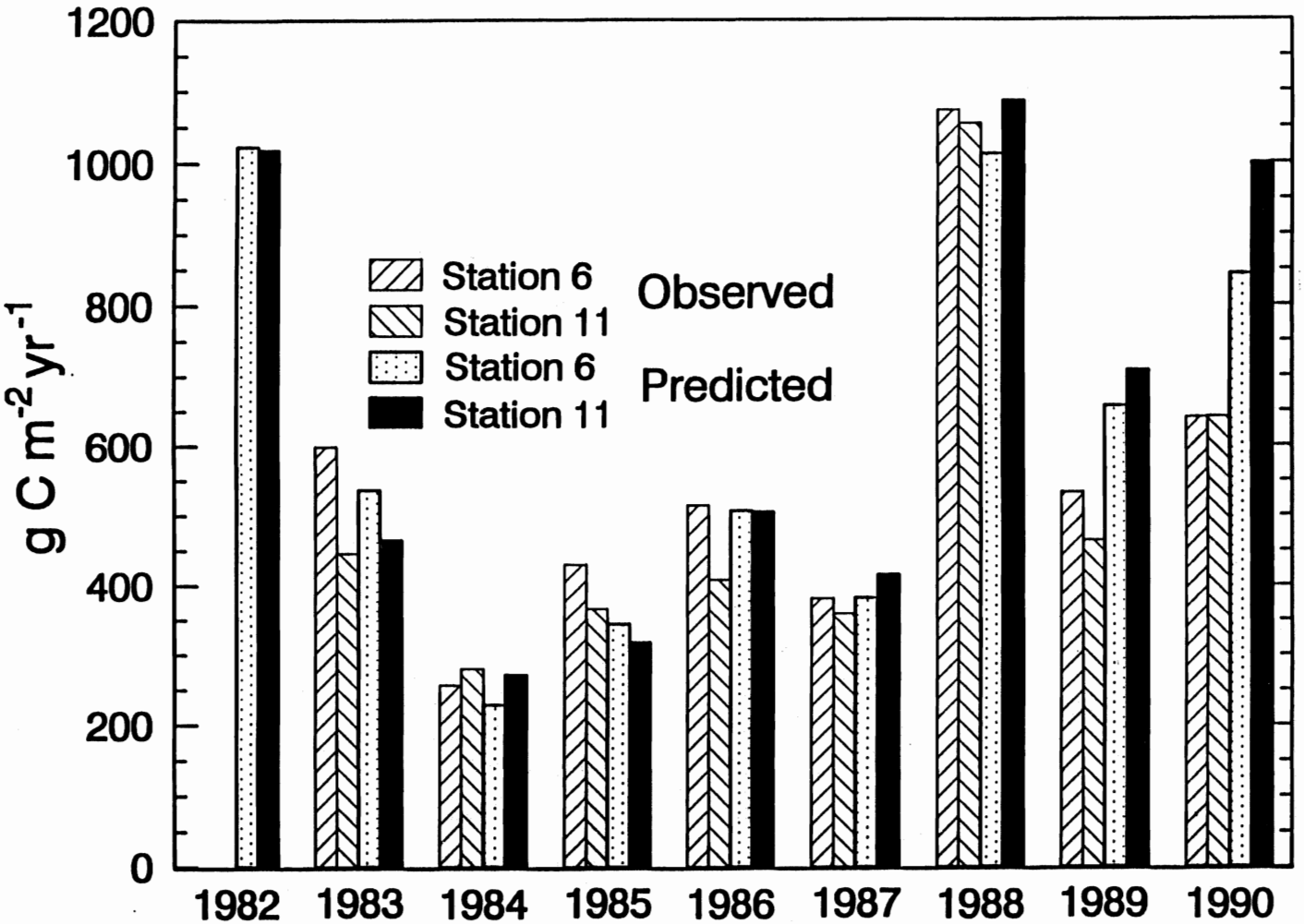

A
Meromictic Period
μM
60
50
40
30
20
10
0
1983 1984 1985 1986 1987 1988 1989 1990
B
1400
630
mmol m-2d-1
100
80
60
40
20
0
1983 1984 1985 1986 1987 1988 1989 1990
C
>200
>200
>200
mmol m-2d-1
200
150
100
50
0
1983 1984 1985 1986 1987 1988 1989 1990

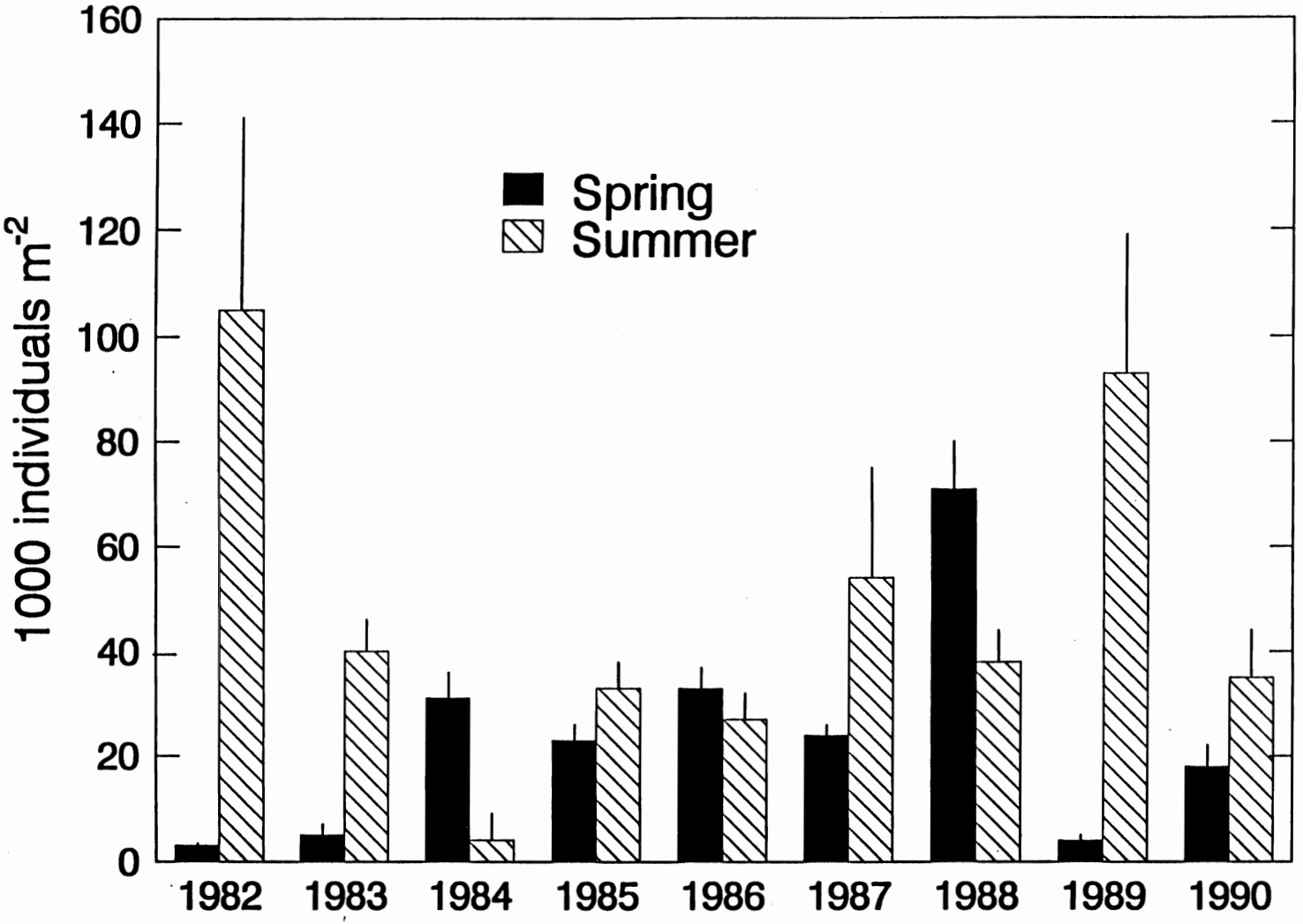

Meromictic Period
A
B
g C g Chla^{-1} h^{-1}
18
14
10
6
2
-2
1983 1984 1985 1986 1987 1988 1989 1990

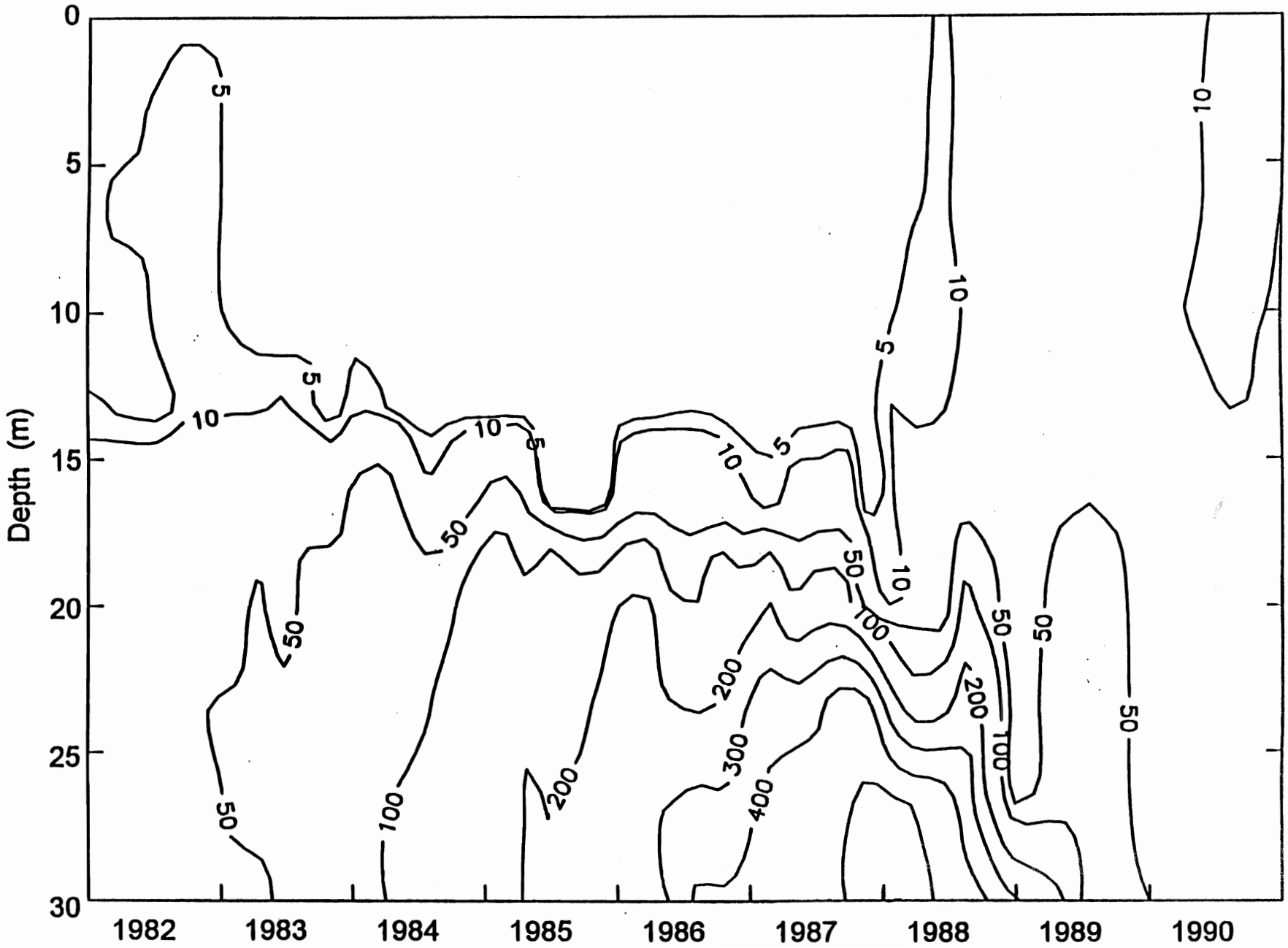

40
30
20
10
0
0
3
6
9
12
15
g C g Chla-1 Einst-1 m2
g C g Chla-1 h-1

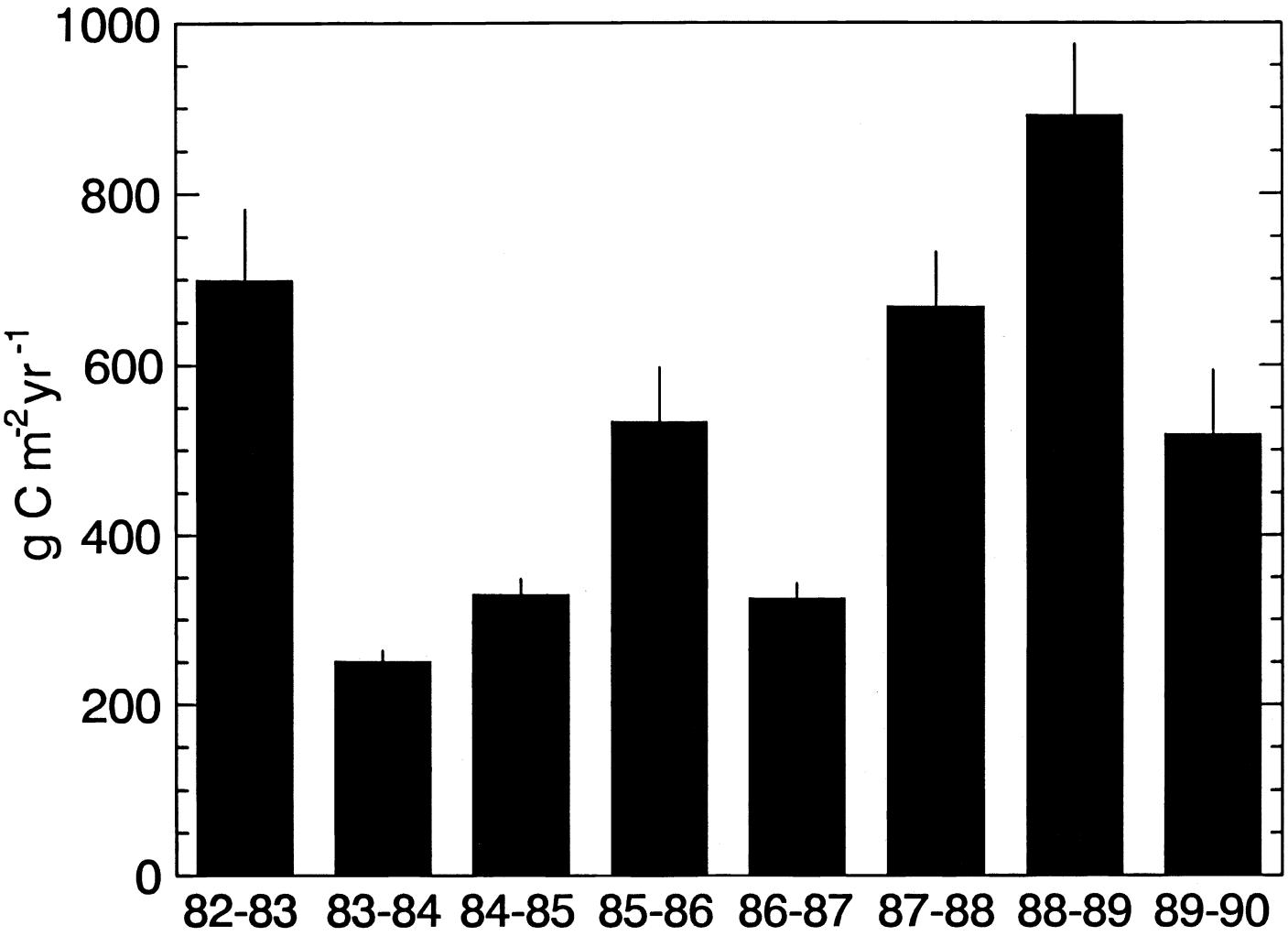

Meromictic Period
A
12
10
8
6
4
2
0
g C m-2d-1
1982 1983 1984 1985 1986 1987 1988 1989 1990


Meromictic Period
B
12
10
8
6
4
2
0
g C m-2d-1
1982 1983 1984 1985 1986 1987 1988 1989 1990


1200
1000
800
600
400
200
0
g C m-2 yr-1
Station 6
Station 11
Station 6
Station 11
Observed
Predicted
1982
1983
1984
1985
1986
1987
1988
1989
1990


160
140
120
100
80
60
40
20
0
1000 individuals m-2
Spring
Summer
1982
1983
1984
1985
1986
1987
1988
1989
1990


Depth (m)
0
5
10
15
20
25
30
1982
1983
1984
1985
1986
1987
1988
1989
1990
5
10
50
100
200
300
400


1000
800
600
400
200
0
g C m-2yr-1
82-83
83-84
84-85
85-86
86-87
87-88
88-89
89-90