

Regulation and distribution of primary production in the northern Gulf of Mexico

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Abstract

As part of the NOAA Nutrient Enhanced Coastal Ocean Productivity program, we are examining the degree to which elevated levels of nutrients in coastal Gulf of Mexico waters associated with the Mississippi River affect phytoplankton production, growth, and photosynthesis-irradiance (P-I) properties. Here, we present results obtained from three cruises including September 1989 and April and July-August 1990 in which we examined (i) the relationships between phytoplankton community physiology, photosynthetic properties and environmental conditions, and (ii) the temporal and spatial patterns of primary production in the northern Gulf of Mexico. Horizontal variations in photosynthetic properties (P^B_{max} / α) were relatively small, despite large differences in phytoplankton community growth rates between the nutrient rich plume waters and low nutrient shelf waters. We concluded that variations in photosynthetic properties were constrained by compensatory changes in carbon-to-chlorophyll ratios. Estimates of integral production from a photosynthesis-irradiance model agreed well with *in situ* and simulated *in situ* incubations. Areal integral production in the vicinity of the river outflow region was apparently coupled to riverine nutrient fluxes.

The primary biological process acting on nutrients introduced into coastal waters is uptake by phytoplankton. Nutrients (e.g. Riley, 1937; Ryther and Dunstan, 1971; Jaworski, 1981; Boynton *et al.*, 1982) and light (e.g. Cole and Cloern, 1984; Pennock, 1985; Pennock and Sharp, 1986; Cloern, 1987) are thought to be the principal factors regulating phytoplankton dynamics. Factors other than light and nutrients (e.g. physical processes and food web interactions) may also contribute to regulation of phytoplankton production and biomass in the complex ecosystems characteristic of estuaries, river plumes and coastal waters. The dynamic and heterogeneous nature of the Mississippi River plume (Thomas and Simmons, 1960; Sklar and Turner, 1981; Lohrenz *et al.*, 1990) has led to uncertainty about the factors controlling primary production in the eutrophic areas of the Mississippi River plume and adjacent shelf waters. Observations of initial limitation of production by light and subsequently by nutrient supply along decreasing turbidity gradients in estuaries might be expected to apply to river plumes (e.g. Xiuren *et al.*, 1988). Indeed, the spatial pattern of high production and biomass at intermediate salinities in the northern Gulf of Mexico (Sklar and Turner, 1981; Lohrenz *et al.*, 1990) encourages such speculation.

Nutrient concentrations associated with freshwater

inputs into our estuarine and coastal ocean environments appear to have increased with population growth and industrial development. For example, nitrate concentrations in the lower Mississippi River have doubled since 1950 (Turner *et al.*, 1987; Turner and Rabalais, 1991). Eutrophication processes have also been demonstrated in Chesapeake Bay (Price *et al.*, 1985) and Altamaha River, Georgia (Walsh *et al.*, 1981). The potential increase in primary production of fixed carbon due to increased nutrient loading could result in significant perturbation of coastal ecosystems (e.g. Nixon *et al.*, 1984). Possible consequences of this nutrient enhanced production include increased sedimentation of organic matter (e.g. Hargrave, 1973, 1975; Smetacek, 1984) resulting in greater likelihood for development of hypoxic conditions in benthic environments and associated reduction in living resource yields. The impact of increased nutrient loading on carbon burial and shelf/sea transport could also have an impact on the global carbon cycle (e.g. Walsh, 1981, 1989).

Prediction of the coupling between nutrient loading, primary production, and export of organic matter from the photic zone requires quantification of these processes and the environmental and ecological factors which regulate them. Large environmental gradients characteristic of river-impacted coastal waters lead to significant variation in phytoplankton community production, growth and the vertical flux of particulate organic matter. The Mississippi River plume and inner Gulf shelf was selected as the initial study area for the Nutrient Enhanced Coastal Ocean Productivity Program (NECOP), part of the NOAA Coastal Ocean Program. As part of this effort, we examined temporal and spatial variation in phytoplankton production, growth and photosynthetic properties. The

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objectives of this portion of our study were as follows:

1. Characterize photoautotrophic community physiology and photosynthesis-irradiance properties in relation to optical conditions, nutrient inputs, and other aspects of the physical/chemical environment.
2. Describe temporal and spatial patterns in primary production using a predictive model based on irradiance and biomass distributions.

Materials and Methods

Data were collected during three cruises in September 1989 and April 1990 aboard the R/V *PELICAN* and July-August 1990 aboard the N/S *BALDRIGE*. Sampling locations for each cruise period are shown in Fig. 1. For R/V *PELICAN* cruises, hydrographic measurements, including profiling of CTD, *in situ* fluorescence, transmissometry, chlorophyll, nutrients and suspended particulate matter were conducted as described in Lohrenz *et al.* (1990) and Dagg *et al.* (1991). Nutrient analyses during the N/S *BALDRIGE* cruise were performed using a Technicon autoanalyzer as described by Whitedge *et al.* (1981). Salinities were determined using an Autosol Model 8400.

Continuous measurements of surface photosynthetic photon flux density (PPFD) were recorded using a Li-Cor system including LI-1000 data logger and a LI-190SA quantum sensor. For underwater profiling during the R/V *PELICAN* cruises, a LI-192SA underwater quantum sensor was used. During the N/S *BALDRIGE* cruise, irradiance profiles were obtained using a Biospherical Instruments QSP-200 underwater quantum scalar irradiance sensor.

Both *in situ* and simulated *in situ* ^{14}C primary production incubations were conducted. Simulated *in situ* incubations were performed using temperature and irradiance quality/quantity controlled deck incubators (cf. Lohrenz *et al.*, 1988 and 1992). For simulated *in situ* incubations, light levels were adjusted to correspond to *in situ* levels. Samples for simulated *in situ* measurements were incubated in 1 L polycarbonate bottles. After incubation, samples were filtered onto GF/F filters using gentle vacuum, and filters acidified with 0.5 mL 1 N HCl to eliminate inorganic ^{14}C (Lean and Burnison, 1979). For selected samples, determinations were also made of carbon specific growth rates and carbon biomass (labeled chlorophyll technique; Redalje and Laws, 1981; Redalje, 1983; Laws, 1984). Activities of productivity samples were determined by liquid scintillation analysis (Packard Tri-Carb 2000CA). Liquid scintillation counts were corrected for quenching by external standard. Dissolved inorganic carbon samples for specific activity calculations were collected in serum stoppered bottles and preserved with sodium azide (final conc. 0.001 M). Acid-volatilized CO_2 concentrations were determined by infrared absorption spectroscopy (Horriba).

Photosynthesis-irradiance measurements were conducted using a photosynthetron (e.g. Lewis and Smith, 1983). Incubations were less than 1 hour. Samples from

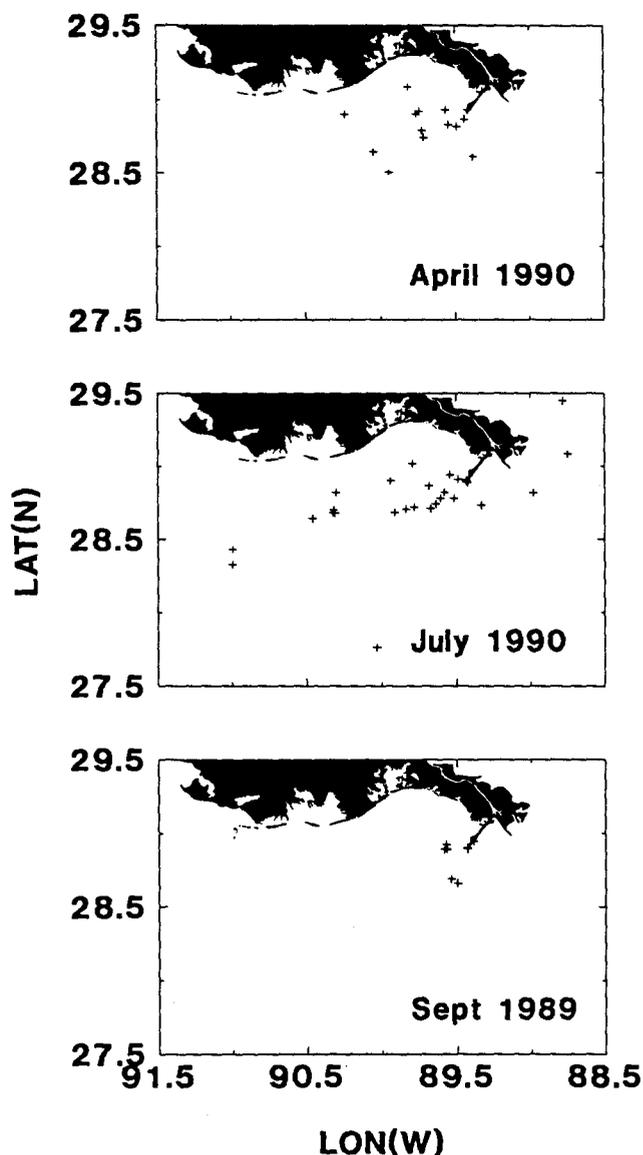


Figure 1. Maps showing station locations during cruises.

the photosynthetron incubations were acidified directly (final conc. 0.3 N H_2SO_4) and counted by liquid scintillation analysis as previously described. The resulting photosynthetic rates, normalized to chlorophyll, were used to construct photosynthesis-irradiance curves. The data were fit to the following equation (Platt *et al.*, 1980):

$$P = B * P_{max}^B * (1 - \exp(-\alpha * I/P_{max}^B)) * (\exp(-\beta * I/P_{max}^B))$$

where P is the primary production rate ($\text{mg C m}^{-3} \text{ h}^{-1}$), B is biomass concentration (mg chl m^{-3}), P_{max}^B is the saturated rate of photosynthesis in the absence of photoinhibition ($\text{mg C mg chl}^{-1} \text{ h}^{-1}$), α is the photosynthetic efficiency ($\text{mg C mg chl}^{-1} (\text{E m}^{-2})^{-1}$), and β is the photoinhibition constant ($\text{mg C mg chl}^{-1} (\text{E m}^{-2})^{-1}$). The photosynthetic capacity (P_{max}^B , $\text{mg C mg chl}^{-1} \text{ h}^{-1}$) was calculated as described by Platt *et al.* (1980). Data were fit using a nonlinear least squares estimation (Systat). In many cases, the photoinhibition parameter was not necessary to adequately model P-I data.

Table 1. Near surface photosynthesis-irradiance parameters and statistics

Period	P_{max}^a	Standard Deviation	N	α	Standard Deviation	N
September 1989	9.0	3.4	10	8.6	3.2	11
April 1990	7.9	3.8	20	20	14	20
July-Aug 1990	8.9	3.8	40	14	3.5	40

A second model was used to estimate daily integral primary production. Using an approach modified from Fee (1973), the Great Lakes Primary Production Model (GLM) accounted for diel variations in surface irradiance, and depth variations in P-I parameters, extinction coefficients, and chlorophyll concentrations (cf. Fahnensteil *et al.*, 1989). A version of this model has been used to evaluate the effect of internal waves on primary production (Fahnensteil *et al.*, 1988).

Results

Relationship between photosynthetic properties and environmental parameters — The photosynthesis-irradiance curve provides an operational model for quantifying effects of environmental conditions on phytoplankton photosynthesis (Cote and Platt, 1984). In general, variation in near surface photosynthetic parameters within and between cruises was relatively small (Table 1). An exception was the variability observed in α in April 1990, possibly due to higher river discharge conditions leading to greater environmental variability. For the periods sampled, highest flow occurred in April and lowest flow in September (Fig. 2).

Near surface P-I parameters revealed no obvious patterns in relation to salinity in September 1989 (Fig. 3) and April 1990 (Fig. 4). However, there were some consistent trends in nutrient-salinity and light-salinity relationships. In September 1989, nitrate-salinity relationships showed some nonconservative behavior with evidence of depletion occurring around a salinity of 25. Both phosphate and silicate were detectable at all salinities, although there was nonlinearity in the relationships with salinity. The average light level in the mixed layer (expressed as a fraction of surface irradiance) was lowest at low salinity, and became higher and increasingly variable as salinity increased. Nutrient-salinity relationships for nitrate and silicate in April 1990 (Fig. 4) showed evidence of nutrient depletion at salinities greater than 30. Characteristics of the nutrient-salinity relationships were very similar to those reported by Lohrenz *et al.* (1990) for April 1988. Again, the average light level in the mixed layer was lowest at low salinity, and higher and variable as salinity increased.

P_{max}^b and α were negatively correlated with salinities in surface waters during July-August 1990 (P_{max}^b

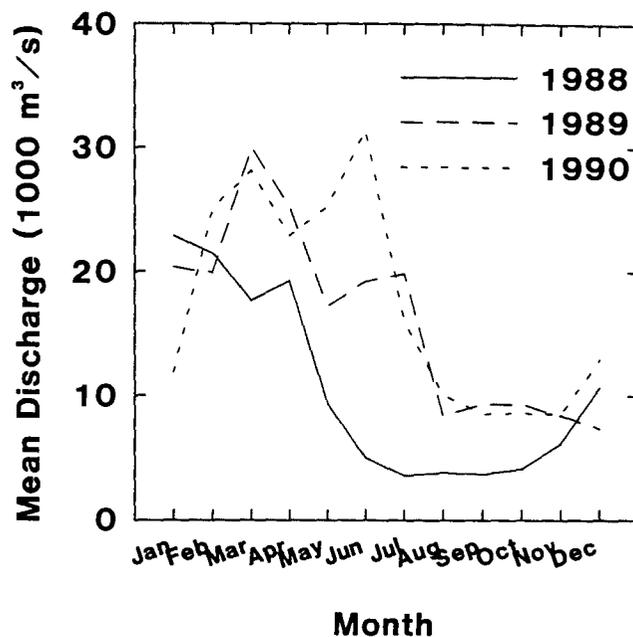


Figure 2. Monthly mean Mississippi River discharge measured at Tarbert Landing, Miss.. (Courtesy Army Corps of Engineers).

Table 2. Near surface growth rates and carbon-to-chlorophyll (C/chl) ratios.

Region	Salinity	Growth rate (d ⁻¹)	C/chl
Plume	12	2.7	12
Inner Shelf	25	0.34	125

SEPT 1989

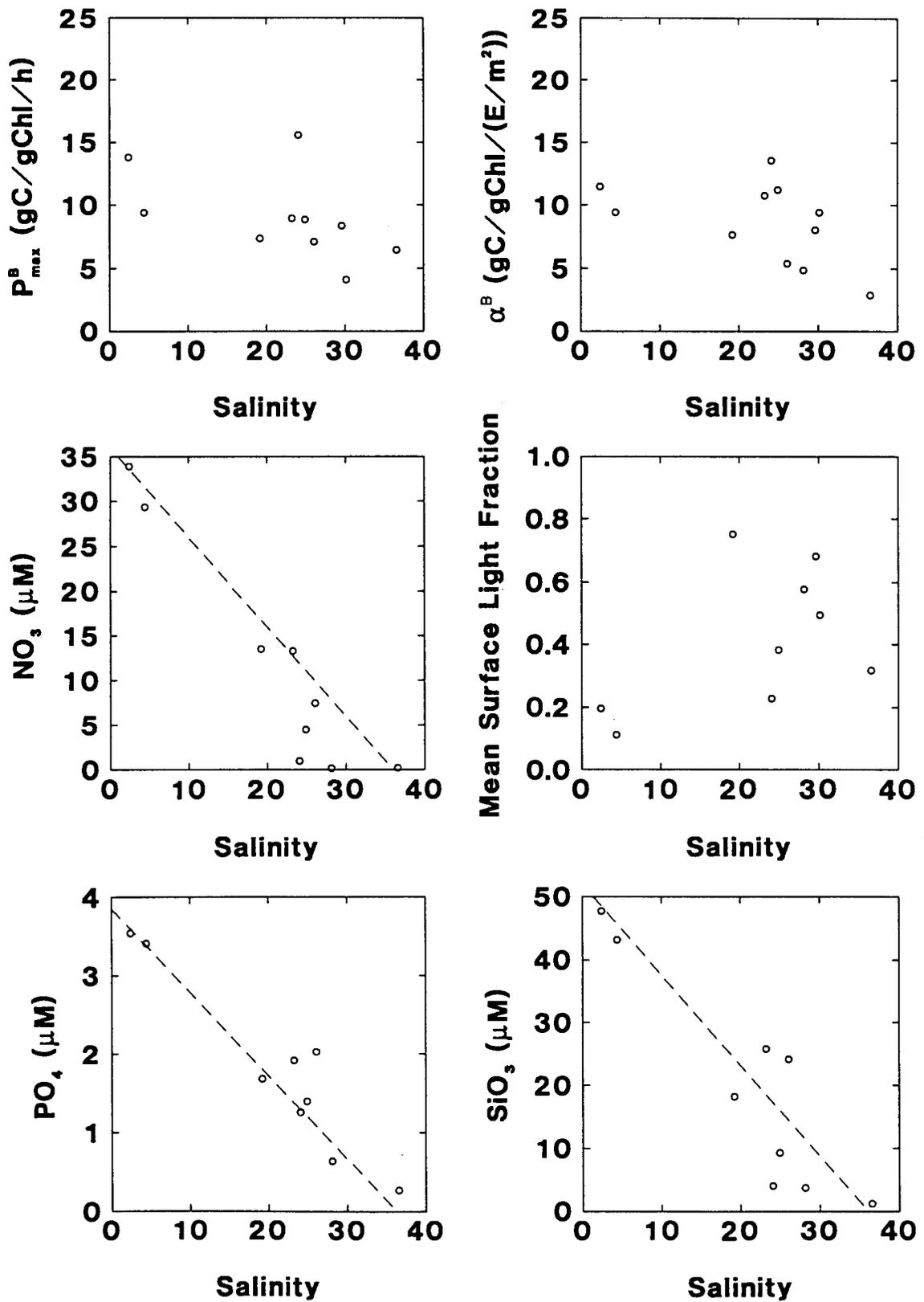


Figure 3. Near surface property-salinity relationships for September 1989. Dotted lines indicate possible conservative mixing relationship between river and Gulf of Mexico endmembers.

APRIL 1990

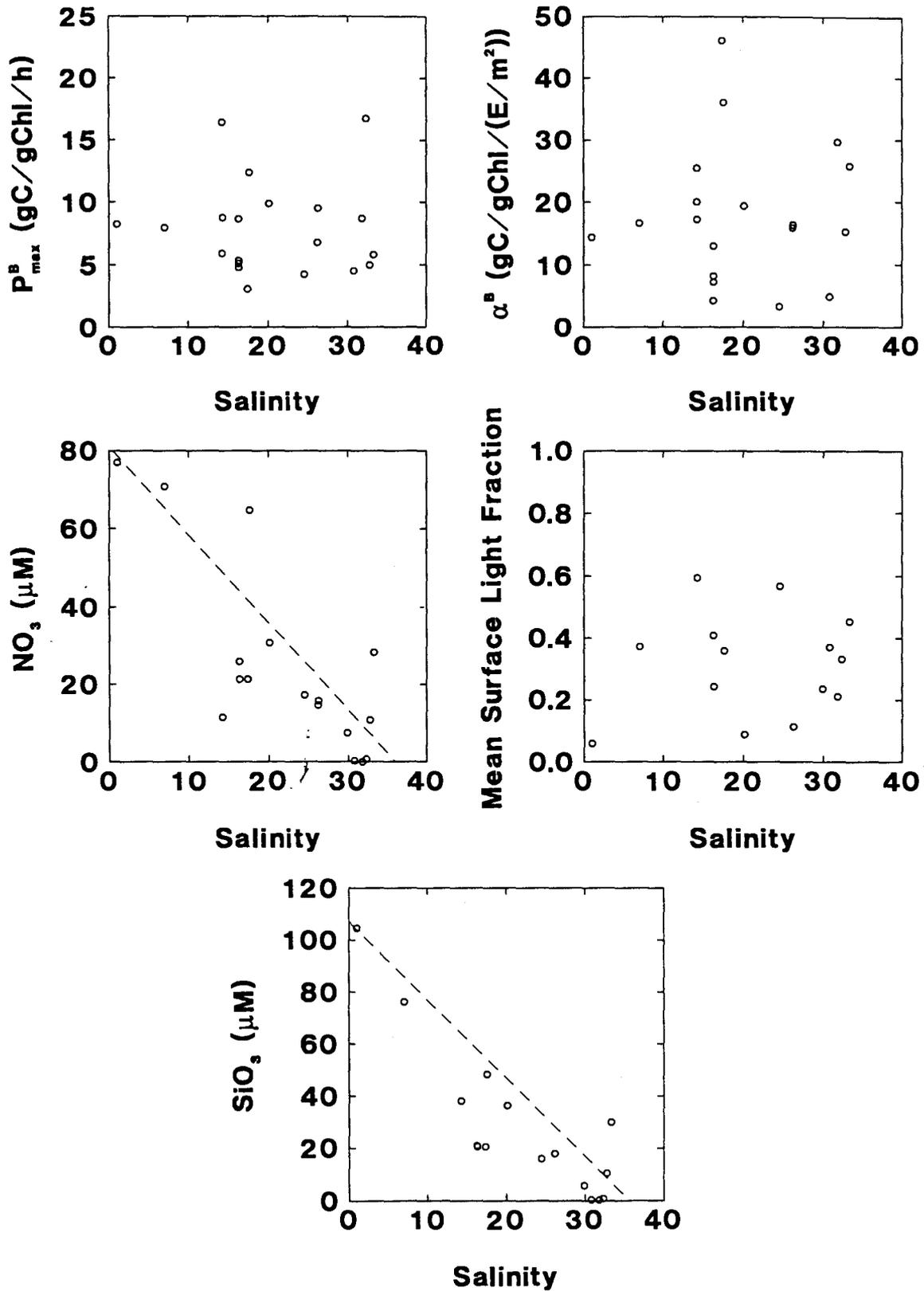


Figure 4. Near surface property-salinity relationships for April 1990.

JUL-AUG 1990

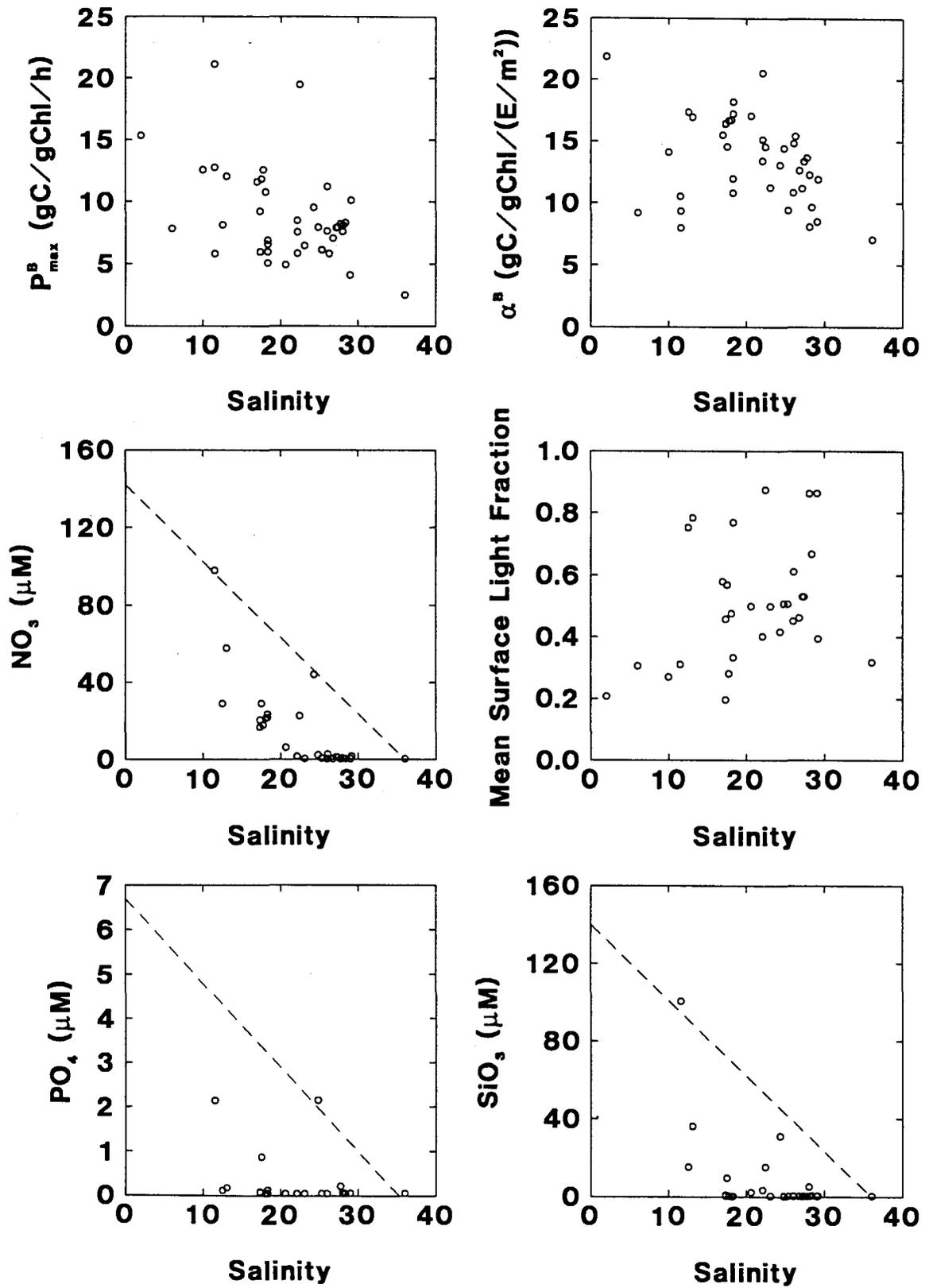


Figure 5. Near surface property-salinity relationships for July-August 1990.

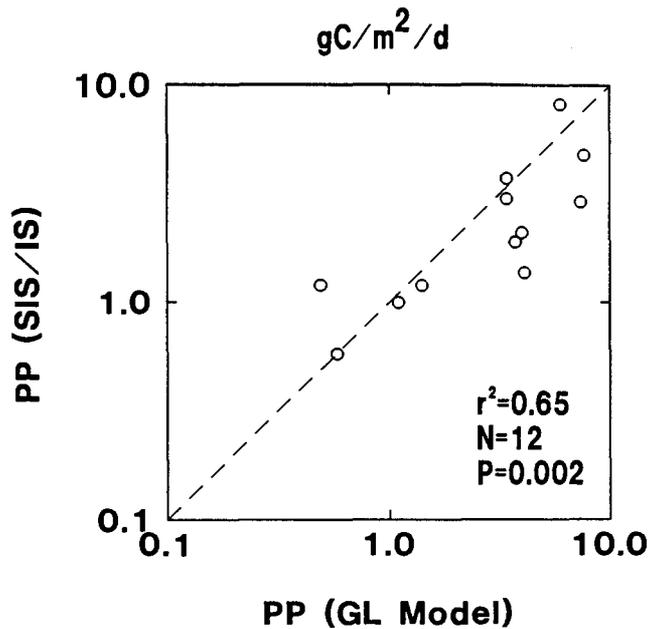


Figure 6. Comparison of integral production estimated using the Great Lakes Model with estimates from simulated *in situ* and *in situ* (SIS/IS) incubations.

versus salinity: $r^2=0.20$, $P=0.004$, $N=40$; α versus salinity: $r^2=0.13$, $P=0.022$, $N=40$; see Fig. 5). P_{max}^B was also negatively correlated with temperature ($r^2=0.21$, $P=0.003$, $N=40$) and positively correlated with nutrient concentrations ($r^2>0.13$, $P<0.03$, $N>25$). It was during the July-August 1990 period that strongest evidence of nutrient depletion was observed. Nitrate, phosphate and silicate all deviated from conservative mixing lines. In fact, phosphate and silicate were found to be at or below detection limits at salinities between 15 and 20. The pattern of light availability was similar to that observed on the other cruises, although the maximum levels were higher.

Despite the large environmental gradients in surface light and nutrients, variations in P-I parameters (Table 1 and Figs. 3-5) were generally small relative to variations in primary production (see below). In contrast, we observed substantial differences in phytoplankton community growth rates (Table 2), with highest growth rates observed in the river plume and lower growth rates in the inner Gulf shelf region. The relatively small differences in P-I parameters could be partially attributed to compensating differences in carbon-to-chlorophyll ratios between regions (Table 2).

Using photosynthesis-irradiance relationship to model primary production: the Great Lakes Model — The fact that variations in P-I parameters were relatively small justified the use of a photosynthesis-irradiance modeling approach to estimation of primary production. A comparison of integral production estimated by *in situ* and simulated *in situ* techniques with estimates obtained using the Great Lakes Primary Production Model (GLM) indicated good agreement (Fig. 6). Relationships between integral production and surface salinity were similar for all periods examined (Fig. 7). Low

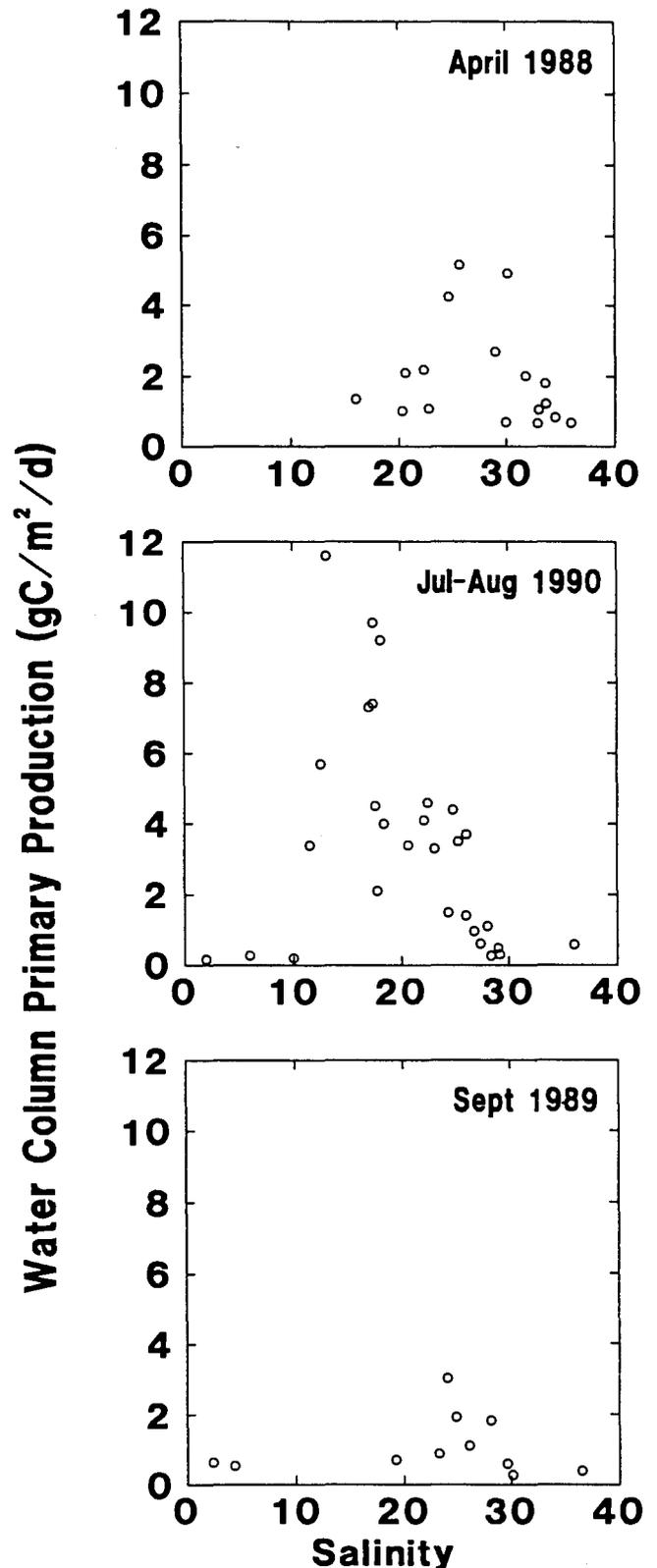


Figure 7. Relationship of integral production versus salinity. The Great Lakes Model was used to estimate integral production for September 1989 and July-August 1990. As model output was not yet available for April 1990, simulated *in situ* data from April 1988 (Lohrenz *et al.*, 1990) were used instead for comparison.

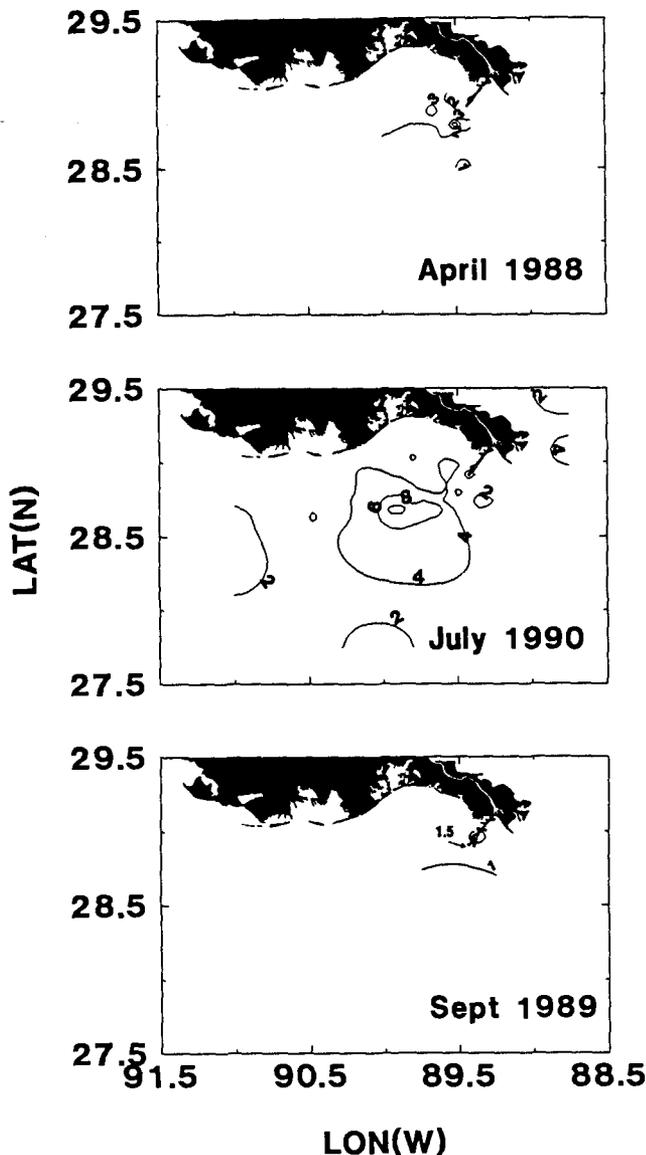


Figure 8. Contour maps of areal integral production using production data as described in Fig. 7.

integral production was generally observed at high and low salinities with highest values occurring at intermediate salinities. The salinity region of high integral production generally also corresponded to the region where depletion of nutrients was observed (cf. Figs. 3-5). Highest integral production values among cruises were observed in July-August 1990. Consistent with the results in Fig. 7, contour maps of areal integral production (Fig. 8) show localized regions of high primary production in regions of mixing of plume and oceanic waters.

Discussion

High growth rates of the phytoplankton community in the plume region (Table 2 and Fahnenstiel *et al.*, 1992) are evidence that populations were able to efficiently utilize available light. Thus, it may be necessary to re-evaluate the hypothesis that primary production is primarily light-limited in the plume. The relatively

high growth rates in the plume suggested that growth rates were neither light nor nutrient limited. The lack of large variations in photoadaptive characteristics (Figs. 3-5) implies that much of the variation in photosynthetic rates can be explained on the basis irradiance and biomass distributions (cf. Lohrenz *et al.*, 1990; Cullen *et al.*, 1991). Thus removal mechanisms which constrain biomass, such as sedimentation, grazing, and advective and diffusive losses, may place an upper limit on rates of primary production. Lohrenz *et al.* (1990), using a light-limitation model (Wofsy, 1983), inferred high loss rates of phytoplankton in the Mississippi River plume. Scavia and Fahnenstiel (1987) found that sedimentation and zooplankton grazing were the major losses accounting for approximately 70 percent of phytoplankton growth in a Lagrangian study in Lake Michigan. However, phytoplankton losses due to sinking were generally small for most species in the Mississippi River plume in July-August 1990 (Fahnenstiel *et al.*, 1992). In contrast, microzooplankton grazing losses may have been important (Fahnenstiel *et al.*, 1992). Other evidence that grazing may be important in the northern Gulf of Mexico comes from estimates of mesozooplankton grazing (Dagg and Ortner, 1992) and high zooplankton abundance (Dagg *et al.*, 1987; Ortner *et al.*, 1989; Dagg *et al.*, in press). Losses of fixed carbon to the dissolved organic carbon pool, either through direct release from phytoplankton (e.g. Mague *et al.*, 1980) or through mediation by zooplankton (e.g. Corner *et al.*, 1984; Jumars *et al.*, 1990) may represent a significant flux. Some of the dissolved organic carbon would be available for consumption by microheterotrophs (e.g. Williams, 1984), thus re-entering the particulate carbon pool. Evidence that this may have been occurring during July-August 1990 comes from measurements of high dissolved organic matter concentrations and high rates of bacterial production at intermediate salinities (Benner *et al.*, 1992). Advective losses also may have been important. Lohrenz *et al.* (1990) estimated a mean turnover time of two days for Mississippi River plume waters, based on river flow volume and observed salinity distributions during April 1988. Although the calculation is approximate, it nonetheless illustrates that physical transport of materials can be significant in these waters.

Although phytoplankton community growth rates were high in the plume, it is likely that the supply of nutrients constrained growth rates at higher salinities. We observed lower growth rates in the inner Gulf shelf region, and concentrations of dissolved nitrate, phosphate and silicate were near detection levels at intermediate salinities (Figs. 3-5). The importance of each of these nutrients as limiting to phytoplankton along the plume/oceanic gradient has been suggested (Sklar and Turner, 1981; Thomas and Simmons, 1960; Dortch and Whitedge, in press; Dortch *et al.*, 1992; Ammerman *et al.*, 1992).

Spatial and temporal patterns of primary production — In addition to supporting the view that anthropogenic nutrient inputs from the Mississippi River produce

elevated levels of primary production in the northern Gulf of Mexico (cf. Riley, 1937; Thomas and Simmons, 1960; Sklar and Turner, 1981; Lohrenz *et al.*, 1990), our results suggest large temporal and spatial variability in the distribution of primary production in the northern Gulf of Mexico (Fig. 8). This is not surprising in view of the large changes in river flow and corresponding nutrient outputs. Previous investigators have suggested that seasonal variations in the extent of the river-influenced region were likely to be substantial (e.g. Sklar and Turner, 1981). To compare areal primary production in Fig. 8 to riverine nutrient inputs, we computed the approximate fluxes of nutrients at Southwest Pass, assuming a discharge of 30 percent of that measured at Tarbert Landing (Fig. 2). River endmember concentrations were extrapolated from the conservative mixing lines (Figs. 3 and 5 and Lohrenz *et al.*, 1990). We estimated nitrate fluxes of 3×10^7 mol N d⁻¹ for April 1988, 5×10^7 mol N d⁻¹ for July-August 1990, and 0.8×10^7 mol N d⁻¹ for September 1989. Comparison to Fig. 8 reveals that trends in areal production appeared to be closely related to riverine nutrient inputs. Based on these preliminary data, it is expected that the ecosystem of the plume environs will be eutrophic, with an abundant supply of new nutrients and production limited by other factors. As distances from the outflow region increase, the role of heterotrophic nutrient regeneration will become more important. Turner *et al.* (1987) noted that primary production beyond the plume was primarily nitrogen-limited, and hypothesized that increases in riverine nutrient inputs will result in increased inputs of phytoplankton carbon to bottom waters in those areas. However, Redalje *et al.* (1992) found that the relationship between primary production and the sinking of particulate organic matter may be quite variable. Thus, it may not be appropriate to assume a constant relationship between areal primary production and inputs of organic matter to the bottom.

Conclusions

1. Variations in near surface values of P_{max}^8 and α were relatively small both within and between cruises. In contrast, there were large differences in growth rates between the plume and inner Gulf shelf regions.
2. Surface nutrient concentrations displayed nonconservative mixing patterns, with evidence of depletion at higher salinities.
3. There was large variability in the spatial and temporal patterns of integral primary production. This could at least partially be related to riverine nutrient fluxes.

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