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Relationships Between Phytoplankton Standing Crop and Physical, Chemical, and Biological Gradients in the Suwannee River and Plume Region, U.S.A.

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ABSRACT: The Suwannee River (USA) is an amber stained, nutrient rich, blackwater river which flows into relatively clear oceanic waters resulting in the formation of a coastal region with unique physical, chemical, and biological gradients. The intent of this study was to describe the spatial and temporal variability of phytoplankton as it relates to these gradients. Ten stations along a transect ranging from 5 km up river to 31 km offshore, were sampled during four different flow regimes. All four sampling periods included in our study of the Suwannee River and plume region exhibited a similar pattern of phytoplankton abundance; low phytoplankton biomass in the Suwannee River and offshore stations with an area of elevated biomass seaward of the Suwannee River outflow. The results of our analysis of light and nutrient limitation in the region support the hypothesis that this spatial pattern of phytoplankton abundance is strongly influenced by color dependent light limitation in the river and outflow area, combined with nutrient limitation offshore. Our results suggest that both light and nutrient availability control abundance and composition of phytoplankton in this coastal area.

Introduction

The chemical and physical gradients, which characterize many estuaries and plume regions, influence the abundance, composition, and distribution of phytoplankton (Smayda 1983; Schuchardt and Schirmer 1991). Light and nutrient availability are two of the primary factors that affect phytoplankton growth, and both play a major role in controlling large-scale patchiness of phytoplankton abundance in estuaries (Platt and Denman 1980).

The availability of light for the growth of phytoplankton is controlled by three primary factors: incident irradiance, attenuation of phytosynthetically active radiation (PAR), and mixing depth. In estuarine environments, riverine inputs of suspended solids and dissolved organic material have a direct impact on light attenuation and can result in light limitation of phytoplankton growth, as shown for the central Georgia embankment (Oertel and Dunstan 1981) and Mississippi delta plain (Madden et al. 1988). In estuaries subject to riverine inflows of organically stained waters, such as Charlotte Harbor in Florida, a significant color-dependent absorption of light has been shown to limit primary production (McPherson and Miller 1987).

Despite the relative abundance of nutrients in some riverine waters (Knox 1986; Madden et al. 1988; Jordan et al. 1991), the availability of nutrients, most frequently nitrogen, can limit phytoplankton growth in associated estuaries (Randall and Day 1987). Nitrogen to phosphorus and silica to phosphorus ratios are typically lower in marine waters than in riverine waters (Hecky and Kilham 1988). This conforms to the observation that phosphorous (P) often limits phytoplankton growth in freshwater and nitrogen (N) frequently limits growth in marine waters (Hecky and Kilham 1988; Tomasky and Valiela 1995). There are exceptions to this generality. For example, Smith (1984) observed that P, rather than N, limited the phytoplankton standing crops in some subtropical semi-enclosed estuaries. And some tropical freshwater lakes have been shown to be more N than P limited (Moss 1969; Hecky and Kilham 1988; Phlips et al. 1997).

The nutrient limiting status of an estuary or plume region is often reflective of the nutrient status of its associated terrestrial watershed. Excessive loading of P or N can induce limitation of the complementary nutrient (Ryther and Dunstan 1971). External inputs of P can be enhanced by anthropogenic activities. For example, Laws and Redalje

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(1979) reported N limitation in a subtropical embayment, Kaneohe Bay, Hawaii, where waste inputs increased P loading to the bay.

The focus of this study is the region of the Suwannee River and its plume, which up to the past decade has seen less land development and point source pollution than most other coastal regions in Florida (Bass and Cox 1988). Recent trends in land use within the Suwannee River drainage basin have resulted in elevated N concentrations in the groundwater (Jones and Upchurch 1996, 1997; Pitman et al. 1997). This increase is related to the porous karst topography of the Suwannee River watershed, which allows nitrates to leach into the aquifer (Kreitler and Browning 1983). These nitrates ultimately enter the Suwannee River via the hundreds of groundwater springs along its banks.

This study describes the spatial variability of the phytoplankton standing crops from the Suwannee River to the Gulf of Mexico during four flow regimes ranging from low flow to flooding conditions. We hypothesized that the nature of the interaction between relatively clear, nutrient-poor Gulf of Mexico waters (Eppley 1980; Randall and Day 1987) and highly colored, nutrient-rich Suwannee River water (Suwannee River Water Management District 1995a,b, 1996) would be correlated to spatial and temporal patterns of the abundance and structure of phytoplankton communities in the Suwannee River and coastal outflow regions. The results are discussed in relation to light and nutrient availability and other factors, which control phytoplankton populations, e.g., grazing pressures and hydraulic flushing rates.

Methods

Study Site Description

The Suwannee River is a blackwater river, which originates in the Okeefenokee Swamp in southeastern Georgia before winding southward 394 km to the Gulf of Mexico (Bass and Cox 1988). The Suwannee River, with its tributaries the Alapaha, Withlacoochee, and Santa Fe Rivers, drains 28,500 km^2 of southern Georgia and northcentral Florida (Wolfe and Wolfe 1985). Freshwater flow is augmented by substantial groundwater contributions of numerous springs along the riverbanks (Florida Department of Environmental Resources 1985) and consequently the Suwannee River has the second highest mean annual discharge of any river in Florida, at a rate of 301 m^3 s^{-1} (Palmer 1984).

Located at approximately 29°17.50′N and 83°10.00′W, the Suwannee River coastal area includes a delta region near the river mouth, which is characterized by a network of oyster reefs (Fig. 1). The river plume is thought to be generally well mixed due to its shallow nature, although it can become vertically stratified depending on tide, wind, and river discharge (Orlando et al. 1993).

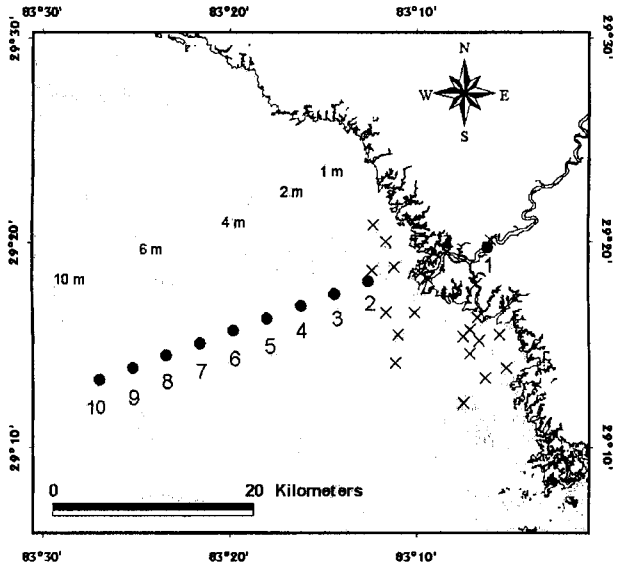

Fig. 1. The study area with nearshore stations identified with ×. Transect stations seaward of the river mouth are represented by ●.

Field Procedures

Water was collected at 10 stations along a northeast-southwest transect and an inshore matrix of 21 stations (Fig. 1). The transect stretched from the eastern-most station, 6.4 km upstream from the mouth of the river, to a station located approximately 31.5 km from the coast in the Gulf of Mexico. This sampling design was not intended to determine the river plume magnitude and direction but to establish the transition zone between coastal areas impacted by the Suwannee River and unimpacted Gulf waters. Stations were separated by approximately 3.7 km (two nautical miles) while inshore station locations were selected randomly from a grid pattern with no less than 1 km between stations.

Sampling dates were chosen based upon the flow of the river in 1996 and 1997, to examine the impact of the freshwater influence on coastal areas due to the river plume. In September 1996, a low flow period, the mean monthly discharge of the Suwannee River was 85 m^3 s^{-1}. The following month, October 1996, tropical storm Josephine increased the discharge to 225 m^3 s^{-1}. Sampling continued after the storm waters receded in November, when mean discharge was 135 m^3 s^{-1}. The spring flooding increased the discharge of the Suwannee River to 300 m^3 s^{-1} in February 1997 and peaked at 405 m^3 s^{-1} in March 1997. River flow

began to decrease in April 1997 with discharge rates dropping to 210 $m^3 s^{-1}$.

Conductivity (μmhos cm^{-1}), dissolved oxygen (mg l^{-1}), pH, salinity, and temperature (°C) were measured with a Hydrolab Surveyor II. Water samples were collected using a 3.0-m integrated sampler. Bottom samples were collected 0.5 m from the bottom using a 3-l Van Dorn bottle. For both depths, water was collected in triplicate then mixed. Subsamples were taken from each of the mixed surface and mixed bottom samples.

One-liter aliquots of subsampled water were used for chlorophyll *a* (chl *a*) determination and 125-ml aliquots were taken for determination of total phosphorus (TP), total nitrogen (TN), silica, nitrate/nitrite, ammonium, and soluble reactive phosphorus (SRP). Samples were held on ice and returned to the lab for processing. An additional 15 l were collected at stations 1, 2, and 10 for subsequent nutrient limitation bioassays.

Laboratory Procedures

Water color was determined from filtered station water (0.3-μm glass fiber filter). Samples were analyzed using platinum cobalt standards from protocols described in Standard Methods (APHA 1989) on a Hitachi U2000 dual beam spectrophotometer at 400 nm.

Inorganic nutrients ($NO_2^- + NO_3^-$, PO_4^+, and NH_4^+) were refrigerated upon returning to the lab and analyzed within 24 h of sampling. Concentrations were determined colorimetrically with a Technicon AutoAnalyzer (Murphy and Riley 1962; Armstrong et al. 1967; Strickland and Parsons 1972; Parsons et al. 1984) from filtered aliquots (Gelman A/E glass fiber filters). Silica (SiO_2) was determined from frozen whole water samples using manual colorimetric methods (APHA 1989). Acidified sample blanks (APHA 1989) eliminated interference from tannin stained water. TN and TP were determined from frozen whole water samples using the persulfate digestion method (APHA 1989) and analyzed with a Technicon AutoAnalyzer.

Chlorophyll *a* was estimated from samples (500 ml) filtered onto Gelman A/E glass fiber filters and then frozen. Filters were placed in test tubes with 8.0 ml of 95% ethanol and heated in a water bath for 5 min at 78°F (Sartory and Grobbelaar 1984). After passive extraction (24 h), the filters were removed and samples were centrifuged to exclude particulate debris. Chlorophyll *a* concentrations were determined with a Hitachi U2000 dual beam spectrophotometer. The concentrations were corrected for phaeophytin using the acidification method (APHA 1989).

Phytoplankton Analysis

Fluorescence microscopy was used to enumerate small celled cyanobacteria (Fahnenstiel and Carrick 1992). Subsamples of station water were filtered onto 0.2-μm pore Nucleopore filters and mounted between microscope slides and coverslips with immersion oil. These were counted immediately with a Nikon research microscope equipped with autofluorescence for phycobilins (green light 530–560 nm excitation and > 580 nm emission). Numerical abundance of cyanobacteria cells was determined by counting a minimum of five ocular micrometer grids at 1,000×. The number of grids counted was determined by cell density. Counts were completed upon reaching a minimum of 100 cells.

General phytoplankton composition was determined using the Utermohl method (Utermohl 1958). Lugols preserved water samples were settled in 19-mm diam cylindrical chambers. Phytoplankton cells were identified and counted at 400× and 100× with a Nikon phase contrast inverted microscope. At 400×, counts were completed upon reaching 100 cells of single dominant taxa, but a minimum of 30 ocular micrometer grids was counted. Large celled taxa (> 30 μm) were enumerated by a complete count of the settling chamber at 100×.

Cell biovolumes were estimated by assigning combinations of geometric shapes to fit the characteristics of individual taxa. Specific phytoplankton dimensions were measured for at least 30 randomly selected cells. Volumes were calculated for each cell, from which the mean cell volume was derived (Smayda 1978). With the mean cell volume, cell counts were transformed to biovolume. The total biovolume per sample was the sum of the estimated cell volumes for each species.

Light Extinction Coefficient

Light attenuation (K_d) (m^{-1}) or Lambert-Beer's Law, (Eq. 1), described the decrease in light penetration with depth:

$$K_d = \frac{\ln(I_o/I_z)}{z} \quad (1)$$

Incident irradiance, I_o, and light intensity, I_z, at depth z (m), were determined with Li-Cor Instruments Inc. (Lincoln, Nebraska) submersible quantum light probes (cosine corrected) which simultaneously recorded surface and downwelling light (μmol photons m^{-2} s^{-1}) of photosynthetically active radiation (PAR) with a data logger. Surface reflection, based upon the angle and declination of the sun, was subtracted from the surface values prior to calculation. Secchi disk (m) measurements

were used to determine K_d in September, (as light data were not recorded), using regression analysis ($y = 3.082x^{-0.8028}$, $r^2 = 0.815$) of secchi depth versus K_d from the other sampling periods.

Partial extinction coefficients caused by components of light attenuation (Kirk 1983; Verduin 1982) were estimated using conversion factors from the literature. Light attenuation by chl *a* containing phytoplankton, K_c, was estimated by multiplying chl *a* concentrations by 0.030 m^2 mg^{-1} (Wolfsy 1983) and light attenuation attributed to seawater, K_w, was set at 0.038 m^{-1} (Lorenzen 1972). Light attenuation due to colbalt, K_{ac}, was estimated by multiplying platinum color units by 0.015 pt^{-1} m^{-1} (McPherson and Miller 1987). Light attenuation due to tripton, i.e., non-algal suspended solids, K_s, was calculated as $K_s = K_d - (K_c + K_{ac} + K_w)$ (Kirk 1983).

The mean light available in the mixed layer, I_m, was estimated after Stefen et al. (1976):

$$I_m = \frac{I_0}{K_d Z_m}(1 - e^{-K_d Z_m}) \quad (2)$$

where Z_m is the depth of the mixed layer (m), and I_o is the mean daily surface PAR irradiance as estimated from the literature (Oswald and Gotaas 1957). The depth of maximum change in the halocline and/or thermocline from 3 yr of subsequent monthly sampling (1996–1999) was used to estimate Z_m due to diurnal variation (Bledsoe unpublished data). The level of I_m at the onset of light limitation has an estimated range of 0.9 to 4 mol photons m^{-2} d^{-1} (Geddes 1984; Phlips et al. 1995a).

The ratio of photic depth to mixing depth (Z_p:Z_m) was estimated as follows:

$$Z_p{:}Z_m = \frac{4.61/K_d}{Z_m} \quad (3)$$

where K_d is light attenuation (Eq. 1) and Z_m is mixing depth. Photic depths (Z_p) calculated from light attenuation were often deeper than the mean water depths. Net water column production decreases and approaches zero when Z_p:Z_m ratios is < 1.0 (Cloern 1987).

Nutrient Limitation Bioassays

Nutrient limitation status was determined using whole water collected from the river (station 1), a representative nearshore station (station 2), and an offshore station with minimal influence from the Suwannee River (station 10). In October, water from station 10 was not collected. The experimental design was based on that described by Aldridge et al. (1995). Assays were conducted under controlled laboratory conditions in 500-ml Erlenmeyer flasks with 300 ml of whole water collected from the field. Treatments (in triplicate) were: N addition (400 μg NO_3–N l^{-1}), P addition (40 μg PO_4–P l^{-1}), N + P addition (400 μg NO_3–N l^{-1} + 40 μg PO_4–P l^{-1}), N + P + Si (400 μg NO_3–N l^{-1}+ 40 μg PO_4–P l^{-1} + 400 μg Si l^{-1}), and N + P + Si + Trace elements (400 μg NO_3–N l^{-1} + 40 μg PO_4–P l^{-1} + 400 μg Si l^{-1}+ 4 μg Mn l^{-1} + 4 μg Fe l^{-1} + 4 μg Mo l^{-1}). Whole water samples without nutrient additions served as controls. Incubations were conducted in temperature-controlled water baths with bottom illumination. Incubation temperatures were set at ambient temperatures recorded on each sampling date. Light intensity was fixed at 120 μmol photons m^{-2} s^{-1}. Photoperiod was 12/12 (dark/light hours) from October through March and 10/14 (dark/light hours) in September. Subsamples were taken from each flask at 0, 24, 72, 96, and 120 h. Change in algal biomass was estimated by measuring net change of in vivo fluorescence (IVF) of chl *a* using a Turner Designs Model 10 fluorometer with a 1-cm path length.

A nutrient was considered limiting when the addition of that nutrient, or combination of nutrients, resulted in significantly greater growth than the control. When algal growth in the control increased relative to the initial control, it was concluded that surplus bioavailable nutrients were present at the time of sampling. Primary limitation was defined as the nutrient(s) limiting within the initial 24 h of the experiment. Any subsequent growth responses to a nutrient addition was defined as secondary limitation. The classification for the growth response was determined using Boolean logic (Aldridge 1995). Relationships between different variables and treatments were determined using ANOVA analysis.

Results

Salinities in the Suwannee River were less than 0.1‰ during all sampling periods while stations furthest offshore exhibited salinities near 35.0‰ for all sampling periods. Salinities among the other stations generally increased with distance from the mouth of the river and varied with tidal and wind conditions as well as riverine discharge (Fig. 2).

Color values were greatest within the river and decreased with distance from the Suwannee River outflow. After the heavy rains of tropical storm Josephine in October, river water color increased substantially and this water color extended some distance offshore. Water color tended to increased with flow rate of the river, but could not be specifically correlated with riverine discharge. For example, water color concentrations in the spring of 1997 were less than that observed after the tropical

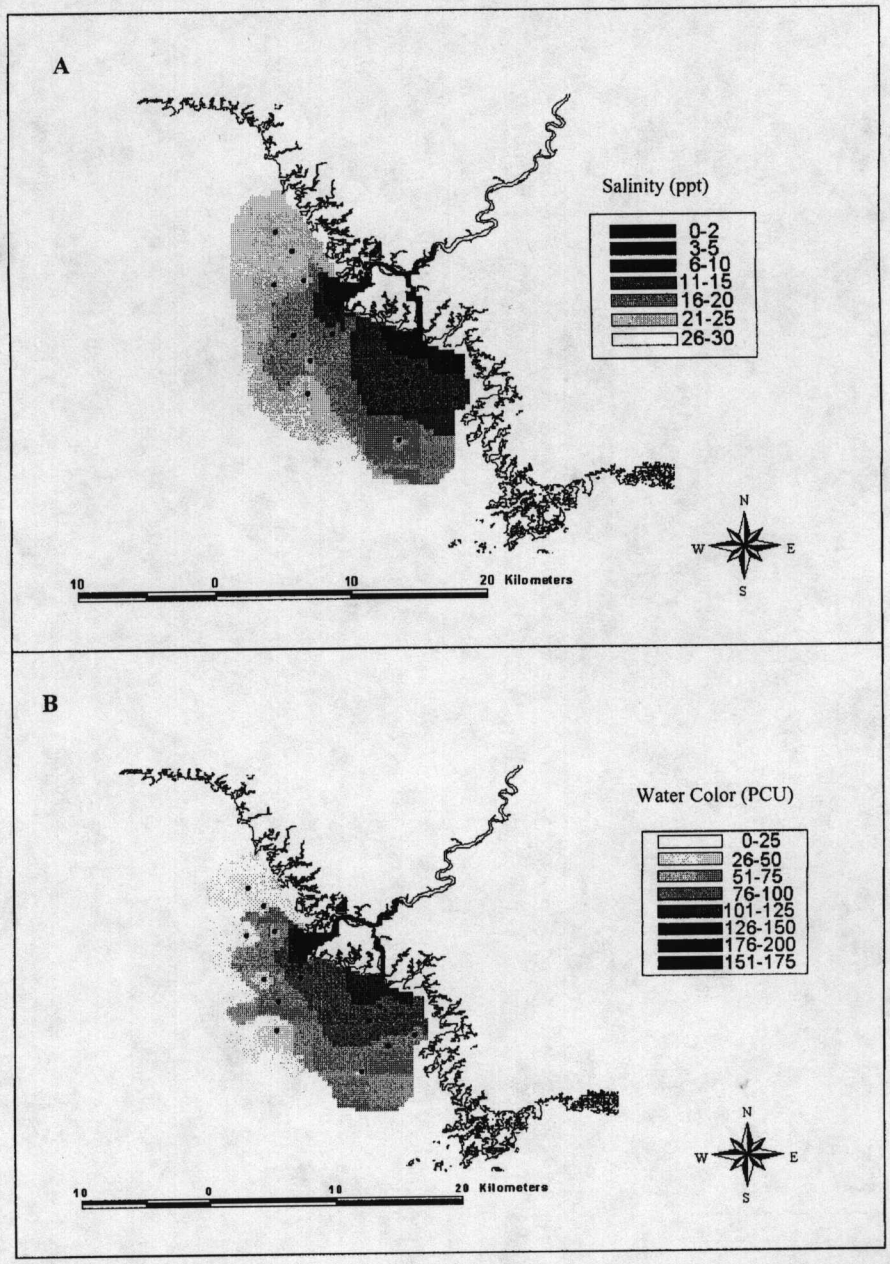

Fig. 2. Mean surface salinity (‰) (A) and mean surface water color (PCU) (B) for 1996–1997. The Suwannee River plume was estimated using salinity and water color during the time period of this study.

storm even though spring flooding nearly doubled the river discharge. Outside the mouth of the river, color concentrations tended to decrease and varied, like salinity, most probably due to shifts in tidal and wind conditions, as well as river flow.

Nitrate + nitrite concentrations were highest in the river during periods of lower discharge (i.e., September and November) and decreased rapidly with distance from the river mouth. Offshore (beyond 10 km), nitrate + nitrite concentrations were generally not analytically detectable (Table 1).

Spatial and temporal patterns of ammonium concentrations were similar to those observed for nitrate + nitrite. Ammonium was rarely analytically detectable at offshore stations, with the exception of March (Table 1).

Total nitrogen (TN) concentrations were highest in the river for all sampling dates. Levels of TN

TABLE 1. Nitrogen components (μg N l^{-1}) in surface (top value) and bottom water (bottom value) along the ten station transect for each sampling period.

	Station									
	1	2	3	4	5	6	7	8	9	10
September 1996										
Nitrate + nitrite	860	60	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	—	—	—	—	—	—	—	—	—	—
Ammonium	10	20	0.0	0.0	0.0	0.0	20	10	10	0.0
	—	—	—	—	—	—	—	—	—	—
Total nitrogen	920	190	190	250	190	210	150	220	150	260
	—	—	—	—	—	—	—	—	—	—
October 1996										
Nitrate + nitrite	650	190	130	0.0	0.0	30	0.0	0.0	0.0	30
	610	140	20	0.0	30	20	20	0.0	10	20
Ammonium	40	80	90	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	20	140	30	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total nitrogen	1,100	640	590	340	320	240	250	180	200	180
	1,120	640	440	330	290	230	220	170	220	150
November 1996										
Nitrate + nitrite	810	60	180	180	0.0	0.0	0.0	0.0	0.0	0.0
	730	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ammonium	40	320	20	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	30	40	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10
Total nitrogen	1,190	380	480	430	340	300	320	200	160	120
	1,200	280	690	210	220	290	120	90	90	70
March 1997										
Nitrate + nitrite	360	80	80	60	0.0	0.0	0.0	0.0	0.0	0.0
	330	50	10	10	0.0	0.0	0.0	0.0	0.0	0.0
Ammonium	50	40	20	20	10	20	10	10	30	10
	50	40	20	10	10	10	0.0	0.0	0.0	20
Total nitrogen	850	380	290	350	280	170	170	100	130	150
	840	250	260	190	170	140	160	100	120	100

decreased substantially outside the river mouth and declined steadily with distance from shore (Table 1).

Total phosphorus and soluble reactive phosphorus (SRP) were highest in the river for all sampling dates and varied with riverine discharge (Table 2). Spatial patterns of TP concentration were similar to those observed for N components. SRP concentrations declined precipitously within the nearshore stations and were not detectable beyond 15 km.

Silica concentrations were highest in the Suwannee River for all sampling periods (Table 3). However, the values varied considerably among the stations for each sampling event.

Total light attenuation was generally greatest in the river (station 1) and tended to decline with distance from shore (Fig. 3). The highest light attenuation values were observed during periods of high riverine discharge. Light transparency was greatest at stations farthest from the river mouth for all dates sampled as indicated by low light attenuation values.

Light attenuation in the river was primarily caused by water color (K_{ac}) for all sampling periods (Fig. 3). Tripton (K_s) contributed notably to the light attenuation in the river during the March sampling period. In the shallow nearshore region (stations 2, 3, 4, and 5), tripton was a substantial component of light attenuation, but tripton levels gradually decreased with further distance from shore. Chlorophyll *a* had a relatively small contribution to light attenuation for each sampling period. Light attenuation outside the mouth of the Suwannee River was attributed to chl *a* (estimation of living phytoplankton in the water column), tripton (non-algal suspended solids), and water color (dissolved organic matter).

The depth at which surface radiation is reduced to 1%, the photic depth (Z_p), was shallowest in the river for each sampling date and deepest in the stations furthest from shore (Table 4). Within the mixed layer, mean light availability, I_m, was generally lowest in the river (station 1) and highest offshore (station 10) (Table 5). During periods of lower flow (September and November) photic depth was deeper than during periods of high flow (October and March). The ratio of Z_p to mixing depth, Z_m, was used to estimate light availability and followed the general trends of mean light availability. Ratios were lowest in the river (station 1) and in the nearshore area (stations 2, 3, and 4)

TABLE 2. Phosphorus components (μg P l^{-1}) in surface (top value) and bottom water (bottom value) along the ten station transect for each sampling period.

	Station									
	1	2	3	4	5	6	7	8	9	10
September 1996										
Soluble reactive phosphorus	50	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total phosphorus	70	10	0.0	0.0	50	0.0	0.0	0.0	0.0	0.0
October 1996										
Soluble reactive phosphorus	80	60	30	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	80	50	20	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total phosphorus	180	80	50	10	10	10	0.0	0.0	0.0	10
	190	80	270	120	10	0.0	0.0	0.0	0.0	0.0
November 1996										
Soluble reactive phosphorus	70	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	80	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total phosphorus	130	10	30	30	20	10	0.0	0.0	10	0.0
	130	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
March 1997										
Soluble reactive phosphorus	80	20	10	10	0.0	0.0	0.0	0.0	0.0	0.0
	80	20	10	0.0	10	0.0	0.0	0.0	0.0	0.0
Total phosphorus	90	20	10	10	0.0	0.0	0.0	0.0	0.0	0.0
	80	20	10	10	10	0.0	0.0	0.0	0.0	0.0

(Table 5), however, deeper areas (stations 5, 6, 7, 8, 9, and 10) had low ratios periodically.

Bioassays showed phytoplankton growth in the river was not initially limited by nutrients (N, P, Si, or trace metals) in September, October, November, or March (Table 6 and 7).

In the nearshore region, phytoplankton growth was limited by N in the nearshore coastal samples. Substantial loss of detectable phytoplankton occurred near the third day of the experiment for each sampling period (Table 6 and 7).

Both N and P were limiting to phytoplankton growth in the offshore region of the transect during the September, November, and March experimental bioassays. Significant phytoplankton growth was observed in samples spiked with N + P but not in those spiked with either nutrient. Nutrient additions were not performed in October for the Gulf of Mexico (Table 6 and 7).

Chlorophyll *a* concentrations in the river were consistently low (< 1 μg l^{-1}) during all sampling periods (Fig. 4). Chlorophyll *a* concentrations were also low at the most offshore stations (9 and 10). A chlorophyll maximum was observed between the river and offshore sites during all four sampling dates.

Total phytoplankton biovolumes observed in September were greatest at stations 2, 3, and 4 (Fig. 4). The river station was biovolumetrically dominated by cryptophytes and spherical green algae 2–3 μm in diameter (Table 8). All other stations were biovolumetrically dominated by large diatoms (*Rhizosolenia stolterfothii*) (> 96% of the total biovolume).

In October the total phytoplankton biovolume peaked at stations 3, 4, and 5 (Fig. 4). The dominant phytoplankton by volume in the Suwannee River (station 1) during this period was *Melosira* sp. and *Cryptomonas* sp. Other stations were primarily dominated by diatoms (*R. stolterfothii*) on a biovolume basis, except station 2, when large *Cryptomonas* sp. were volumetrically important (Table 8).

TABLE 3. Silica (mg Si l^{-1}) in surface (top value) and bottom water (bottom value) along the ten station transect for each sampling period.

	Station									
	1	2	3	4	5	6	7	8	9	10
September 1996	6.0	1.5	1.8	2.8	2.2	0.76	0.66	0.24	0.55	0.83
	—	—	—	—	—	—	—	—	—	—
October 1996	10.9	5.5	4.8	1.8	0.98	1.4	0.94	1.7	7.1	1.3
	11.0	3.1	2.2	1.5	1.3	0.0	0.0	0.0	3.4	0.0
November 1996	9.8	2.2	3.4	5.5	2.2	1.9	1.5	0.0	5.2	1.7
	9.4	3.6	1.7	1.1	6.7	0.91	0.0	0.10	3.1	1.1
March 1997	6.9	1.4	1.4	2.4	1.1	0.69	2.2	0.74	0.39	0.64
	7.5	1.3	0.78	0.77	0.74	0.42	0.67	0.38	0.36	4.3

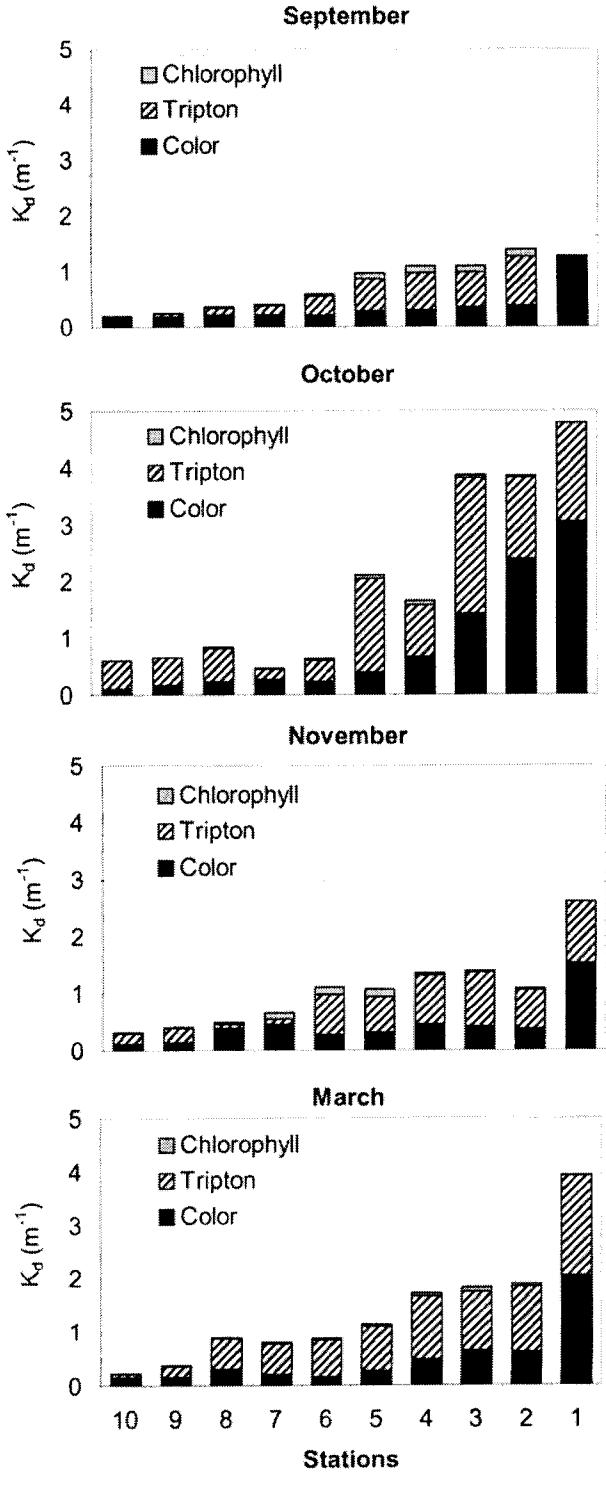

Fig. 3. Light extinction coeficients (K_d) and partial coefficients, K_c (chlorophyll containing particles), K_{ac} (apparent color), and K_s (tripton) for each sampling event.

The biovolume peak shifted farther offshore in November, with total phytoplankton biovolume highest at stations 5, 6, and 7 (Fig. 4). Riverine phytoplankton was composed primarily of small centric diatoms (Table 8). All other stations were again dominated biovolumetrically by centric diatoms (*R. stolterfothii*), which represented nearly 80% of the total algal biovolume.

In March, total phytoplankton distribution was bi-modal with peaks centered at stations 3 and 9 (Fig. 4). In the Suwannee River, green algae (2–3 μm) and *Cryptomonas* sp. were dominant biovolumetrically during the March sampling period. Outside the river mouth (station 2), dinoflagellates (*Ceratium hircus*) were the dominant species by volume. Large centric diatoms (*Pseudosolenia calcar-avis*) dominated nearshore stations (3, 4, 5, and 6). These diatoms represented between 35–72% of the total algal biovolume. Dinoflagellates (*Gymnodinium breve*) composed the greatest percent of biomass at offshore stations (7, 8, 9, and 10), representing nearly 37–92% of the total phytoplankton biovolume (Table 8).

Blue-green algae (1–2 μm) and green algae (2–4 μm) represented 86–97% of the total phytoplankton density for all stations at every sampling period.

The results of the correspondence analysis for September indicate similar composition in phytoplankton for all stations with the exception of the river (station 1). *Eutreptia* sp. and *Asterionella japonica* were found primarily within the river station, while *R. stolterfothii* and *Guinardia flaccida* dominated the composition of the other stations.

In October, stations 1 and 2 differed from the other stations along the transect. The phytoplankton community within the river (station 1), included *Ankistrodesmus convolutus, Euglena* sp., and a species of *Spirulina. Terpinsoe* sp., *Thalassiosira* sp. and *Synedra* sp. were found primarily at station 2. The offshore stations during this sampling period were similar in phytoplankton composition (*R. stolterfothii* and *G. flaccida*).

The November results indicated similar species composition within all stations with the exception of the river (station 1) which supported populations of *A. convolutus, Melosira* sp., *Spirulina* sp., and *Terpinsoe americana. R. stolterfothii* and *Pyrophacus horologium* distinguished the other stations along the transect.

In March, *A. convolutus, Scenedesmus quadricata,* and *Euglena* sp. were found only in the river (station 1). Stations 2, 3, and 4, however, supported large populations of *P. calcar-avis, Skeletonema costatum,* and *Gymnodinium splendens.* Large populations of *G. breve, Torodinium teredo,* and *Hermisium* sp. characterized the offshore stations (7, 8, 9, and

TABLE 4. Mean depth (m, SD in parenthesis), photic depth (Z_p) (m), and mixing depth (Z_m) (m, mixing range in parenthesis) for each station during four sampling events.

		September 1996		October 1996		November 1996		March 1997	
Station	Mean Depth	Z_p	Z_m	Z_p	Z_m	Z_p	Z_m	Z_p	Z_m
1	6.2	3.6	6.1	1.0	6.1	1.7	5.6	1.2	6.6
	(0.79)		(0.53)		(0.53)		(0.18)		(1.8)
2	3.1	3.3	1.5	1.2	1.3	4.1	1.3	2.4	1.6
	(0.41)		(0.0)		(0.34)		(0.18)		(1.8)
3	3.9	4.1	2.0	1.2	3.1	3.2	1.8	2.5	2.0
	(0.39)		(0.0)		(1.6)		(0.35)		(0.0)
4	4.2	4.1	1.8	2.7	3.3	3.3	4.0	2.6	2.2
	(0.33)		(0.35)		(1.1)		(0.44)		(0.35)
5	4.6	4.6	3.0	2.2	3.6	4.2	4.3	4.0	2.8
	(0.93)		(1.4)		(0.78)		(0.71)		(0.3)
6	6.2	7.3	4.0	6.8	4.1	4.0	6.0	5.2	5.0
	(0.99)		(0.0)		(0.078)		(1.1)		(0.0)
7	8.6	10.5	6.5	9.1	5.9	6.7	8.5	5.6	5.8
	(0.86)		(3.5)		(1.2)		(0.71)		(0.72)
8	10.1	11.5	10.0	5.3	7.8	8.7	10.0	5.1	8.2
	(0.51)		(0.0)		(2.5)		(0.71)		(3.5)
9	10.4	16.5	10.4	6.6	10.3	10.5	10.3	11.4	9.0
	(0.84)		(0.14)		(0.035)		(1.8)		(4.6)
10	12.2	19.2	12.0	7.1	12.0	13.5	12.0	17.4	10.3
	(0.43)		(0.0)		(0.0)		(0.71)		(4.6)

10). The phytoplankton communities of station 5 and 6 were structured similarly to both the nearshore and the offshore region.

Discussion

The results of our study of the Suwannee River and plume revealed a spatially restricted region of elevated phytoplankton standing crop in the nearshore region outside of the Suwannee River outflow. The exact location of the region could not be correlated to the level of freshwater discharge from the river (e.g., positioned further offshore during periods of higher riverine discharge). To explain this pattern of phytoplankton distribution, we examined the hypothesis that spatial and temporal gradients of nutrient and light availability in the Suwannee River and coastal region control the abundance, distribution, and composition of phytoplankton.

In the Suwannee River, high organic color concentrations make light availability a potentially important consideration in phytoplankton production. To examine the potential for light limitation we used two established measures of light sufficiency; the first was that used by Cloern (1987) and Phlips et al. (1995b). The ratio of euphotic depth and mixing depth (Z_p:Z_m) was used to define the potential for light limitation of phytoplankton production in two estuaries, San Francisco Bay and Florida Bay. As the ratio drops below 1.5, net water

TABLE 5. Ratio of photic depth (Z_p) to mixing depth (Z_m, top value) and mean irradiance (I_m, mol photons m^{-2} d^{-1}, bottom value) for 10 sites in the Suwannee River and plume region for each sampling period. Bold type indicates values are within the range of potential light limitation as defined in the text.

Station	September 1996	October 1996	November 1996	March 1997
1	**0.5**	**0.2**	**0.3**	**0.2**
	3.8	**1.3**	**2.0**	**1.7**
2	2.2	**0.8**	3.3	1.5
	12.5	7.8	16.3	13.7
3	2.0	**0.4**	1.9	1.2
	12.0	**3.1**	11.1	11.5
4	2.3	**0.8**	**0.8**	1.2
	13.2	6.8	5.4	11.3
5	1.5	**0.6**	**0.8**	1.4
	9.6	5.3	6.4	12.8
6	1.8	1.7	**0.7**	1.0
	11.1	13.2	4.4	9.7
7	1.6	1.5	**0.8**	1.0
	10.0	12.2	5.2	9.0
8	1.3	**0.7**	**0.9**	**0.6**
	7.5	5.7	5.7	5.9
9	1.6	**0.6**	1.0	1.3
	9.8	5.3	6.7	11.7
10	1.6	**0.6**	1.1	1.7
	9.9	5.2	7.2	14.9

TABLE 6. Results of the nutrient bioassay interpreted by phytoplankton doublings over the experimental incubation period. Treatments shown below include nitrogen additions (N) and the combination of nitrogen and phosphorus additions (N + P).

	Suwannee River		Suwannee River Plume		Gulf of Mexico	
	Control	N	Control	N	Control	N
September 1996	3.6	3.9	0.6	1.2	0.0	0.5
October 1996	1.4	2.0	0.4	2.1	—	—
November 1996	2.6	2.6	3.1	4.1	0.0	3.1
March 1997	2.2	2.2	0.7	1.5	0.2	3.2

TABLE 7. Results of nutrient bioassay for three selected regions of the Suwannee River and coastal region during each sampling period.

	1° Limitation	2° Limitation
September 1996		
Suwannee River	No limitation ($p < 0.001$)	Nitrogen ($p < 0.05$)
Suwannee River Plume	No limitation ($p < 0.001$)	Nitrogen ($p < 0.001$)
Gulf of Mexico	Nitrogen and Phosphorus ($p < 0.001$)	Nitrogen and Phosphorus ($p < 0.001$)
October 1996		
Suwannee River	No limitation ($p < 0.001$)	Nitrogen ($p < 0.05$)
Suwannee River Plume	No limitation ($p < 0.001$)	Nitrogen ($p < 0.001$)
November 1996		
Suwannee River	No limitation ($p < 0.001$)	No limitation ($p < 0.001$)
Suwannee River Plume	No limitation ($p < 0.001$)	Nitrogen ($p < 0.01$)
Gulf of Mexico	Nitrogen and Phosphorus ($p < 0.005$)	Nitrogen and Phosphorus ($p < 0.005$)
March 1997		
Suwannee River	No limitation ($p < 0.001$)	No limitation ($p < 0.001$)
Suwannee River Plume	No limitation ($p < 0.01$)	Nitrogen ($p < 0.05$)
Gulf of Mexico	Nitrogen and Phosphorus ($p < 0.02$)	Nitrogen and Phosphorus ($p < 0.02$)

column production decreases and approaches zero as Z_p:Z_m declines to 0.1 to 0.5 (i.e., critical range). Ratios of Z_p to Z_m observed in the Suwannee River were < 0.5 and within the critical range for light limitation for all sampling periods. Ratios increased seaward of the outflow but were periodically less than 1.0 but never fell within the critical range of light limitation.

Mean irradiance in the mixed layer (I_m) has also been used to establish light limitation in shallow polymictic lake ecosystems (Geddes 1984; Phlips et al. 1995a). The threshold level of I_m for the onset of light limitation has been estimated to be between 2 and 4 mol photons m^{-2} d^{-1} (Geddes 1984; Phlips et al. 1995b). Values for I_m in the Suwannee River and stations nearest the river mouth regularly fell within or below this threshold range. Values for the Suwannee River were within the estimated range of light limitation for all four sampling periods. The seaward extent of low I_m values was greater during high flow periods, most probably due to the elevated color levels in the plume reaching further out into the Gulf of Mexico. Stations further offshore were never within the critical range during this study.

Based on the two indices described above (i.e., Z_p:Z_m ratios and I_m) there is a clear potential for light limitation of phytoplankton production within the Suwannee River and to a lesser extent within the shallow nearshore region impacted by colored river water. In keeping with these observations, standing crops of phytoplankton in the Suwannee River were uniformly low throughout the sampling period, despite high levels of bioavailable nutrients. Light limitation resulting from elevated levels of dissolved organic material has been reported in other aquatic systems, such as the Rio Negro, Brazil (Furch and Otto 1987), St. Johns River, Florida (Phlips et al. 2000), and Charlotte Harbor, Florida (McPherson and Miller 1987). Color is the most important component of light attenuation in the Suwannee River contributing up to 95% of the total light attenuation. However, there are seasonal and long-term variations in color, which may impact the relative magnitude of light limitation in the river and nearshore regions. The character of river discharge influences the level of color on a seasonal basis. Within the lower Suwannee River, groundwater springs contribute relatively more to the river flow during the dry season or drought periods (Suwannee River Water Management District 1995a), thereby diluting color (Pitmann et al. 1997). The pattern of high and low discharge generally coincides with seasonal wet and dry periods in Florida, however, stochastic events, such as major tropical storms and broad climatic change

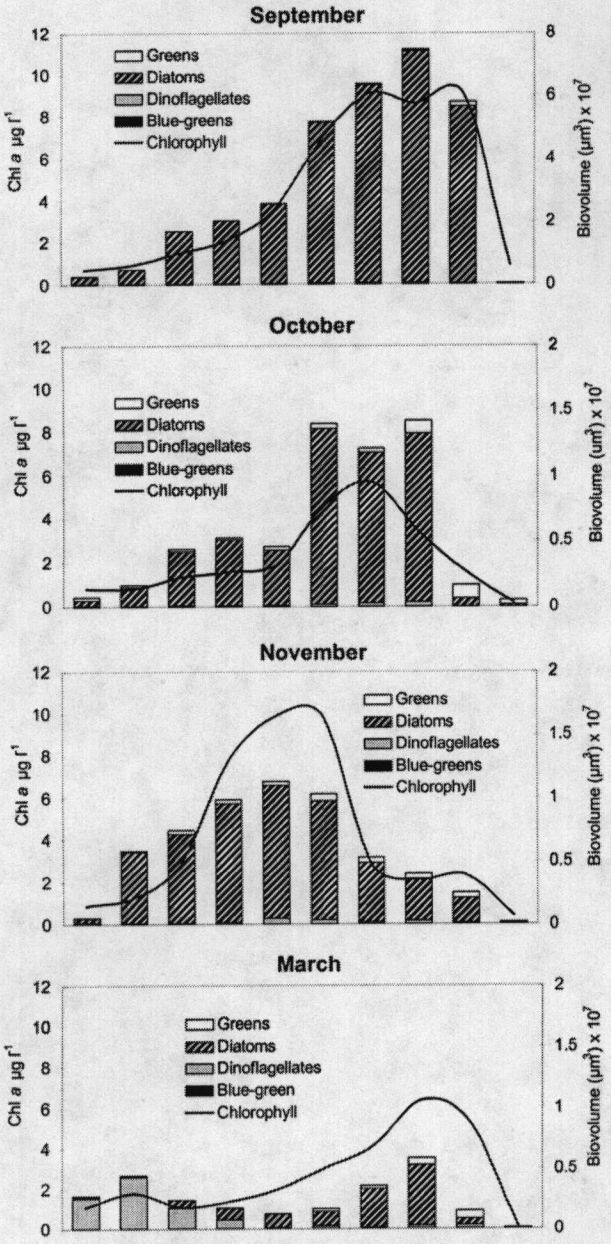

Fig. 4. Total phytoplankton biovolume ($\mu m^3 \times 10^7$) and surface chlorophyll *a* (phaeophytin corrected) concentrations ($\mu g\ l^{-1}$) for September, October, November 1996 and March 1997 along a transect, from the Suwannee River to the Gulf of Mexico.

(e.g., drought periods and El Niño events), alter this general trend. After tropical storm Josephine in October 1996, discharge rates and water color concentrations increased substantially in the Suwannee River. The spring flooding event in March 1997, also increased riverine discharge, yet water color concentrations were lower than those following tropical storm Josephine.

During the four sampling events in our study color values in the river remained high enough to reduce light availability to limiting levels. It is possible that periods of exceptionally low flow, not encountered in our study, may yield higher standing crops of phytoplankton within the Suwannee River, as light becomes more available and retention times increase. This phenomenon has been observed in another highly colored river; St. Johns River, Florida (Phlips et al. 2000).

Outside the mouth of the Suwannee River, in the shallow coastal region, light attenuation is increasingly dependent on non-algal suspended solids (i.e., tripton), accounting for up to 76% of total light attenuation. Due to the very shallow depths encountered near the mouth of the river (i.e., 2 m), sediment resuspension may be a major contributor to tripton, as reported in other polymictic aquatic ecosystems in Florida and around the world, including Apalachicola Bay, USA (Myers and Iverson 1981), Fort Pierce Inlet, USA (Thompson et al. 1979), the Delaware Estuary, USA (Pennock and Sharp 1994), Florida Bay, USA (Phlips et al. 1995b), the Georgia Embankment, USA (Oertel and Dunstan 1981), The Great Ouse Estuary, England (Fichez et al. 1992), and the Gamtoos Estuary, South Africa (Schumann and Pearce 1997). Together, suspended sediments and water color contribute up to 98% of the total light attenuation in the shallow coastal region near the mouth of the Suwannee River. Despite the added influence of tripton on light attenuation in the nearshore region, overall light extinction within this region decreases, due to the rapid decline in water color. For this reason, light limitation of phytoplankton production in the surface waters outside the influence of the shallow, colored, and sometimes turbid waters of the inshore region is less likely, a conclusion supported by high Z_p:Z_m ratios and I_m values. These observations help to explain the presence of phytoplankton standing crop maxima just outside the influence of highly colored water.

Beyond spatial and temporal patterns of phytoplankton standing crop, species composition can also be viewed in terms of gradients of light and nutrient limitation. The Suwannee River can be characterized as a low light and high mixing environment. This type of environment can favor algae species with small cell-size, since greater surface to volume ratio can increase the ability to utilize low irradiance (Harris et al. 1983). The mean algal cell-size within the Suwannee River was significantly lower then the mean algal cell-size outside the mouth of the river. Small algal species found in the river included *Chlorella*-like green algae (2–4 µm), *Cryptomonad* sp., and small-celled diatoms. Spherical blue-green algae (1–2 µm) were numerically dominant in the river. Those found within the Su-

TABLE 8. Phytoplankton taxa representing over 1% of the total phytoplankton biovolume (μm^3) at ten individual sampling stations during four sampling periods.

Station	September 1996	October 1996	November 1996	March 1997
1	72% *Cryptomonas* sp.	24% *Melosira* sp.	31% centric diatoms	22% 2–4 μm
	15% green 2–4 μm	23% *Cryptomonas* sp.	22% *T. americana*	11% *Cryptomonas* sp.
	7% *R. stolterfothii*	14% *T. americana*	12% *Cryptomonas* sp.	
2	92% *R. stolterfothii*	30% *Cryptomonas* sp.	80% *R. stolterfothii*	17% *C. hircus*
	2% pennate diatom	25% *R. stolterfothii*	3% *Chlamymonas* sp.	14% *Cryptomonas* sp.
	2% *G. flaccida*	8% *Terpinsoe* sp.	3% *Cryptomonas* sp.	14% *P. calcar-avis*
3	97% *R. stolterfothii*	88% *R. stolterfothii*	87% *R. stolterfothii*	60% *P. calcar-avis*
	1% *Hermisium* sp.	3% *B. horologicals*	2% *P. horologicals*	16% *G. flaccida*
	1% *G. flaccida*	2% *Cryptomonas* sp.	2% *C. hircus*	4% *Coscinodiscus* sp.
4	96% *R. stolterfothii*	47% *R. stolterfothii*	92% *R. stolterfothii*	71% *P. calcar-avis*
	1% *G. flaccida*	1% *G. flaccida*	1% green 2–4 μm	16% *G. flaccida*
	1% *Glenodinium* sp.	1% *B. horologicals*	1% *P. horologicals*	3% *Coscinodiscus* sp.
5	97% *R. stolterfothii*	95% *R. stolterfothii*	92% *R. stolterfothii*	35% *P. calcar-avis*
	1% *G. flaccida*	2% *G. flaccida*	2% *P. horologicals*	25% *G. flaccida*
	1% *Glenodinium* sp.	1% *P. horologicals*	1% *B. malleus*	6% *Coscinodiscus* sp.
6	92% *R. stolterfothii*	88% *R. stolterfothii*	90% *R. stolterfothii*	50% *P. calcar-avis*
	4% *G. flaccida*	3% *B. malleus*	1% *Coscinodiscus* sp.	34% *G. flaccida*
		2% *D. cauldata*	1% *G. breve*	3% *L. danicus*
7	96% *R. stolterfothii*	95% *R. stolterfothii*	96% *R. stolterfothii*	37% *G. breve*
	2% *G. flaccida*	2% *G. flaccida*	1% *Cryptomonas* sp.	31% *G. flaccida*
		2% *G. breve*	1% *P. horologicals*	14% *P. calcar-avis*
8	98% *R. stolterfothii*	93% *R. stolterfothii*	96% *R. stolterfothii*	71% *G. breve*
	1% green 2–4 μm	3% *G. flaccida*	1% *Chlamymonas* sp.	15% *G. flaccida*
		1% *G. breve*	1% green 2–4 μm	4% *L. danicus*
9	94% *R. stolterfothii*	87% *R. stolterfothii*	97% *R. stolterfothii*	96% *G. breve*
	1% *P. calcar-avis*	5% *G. flaccida*	1% *C. tripos*	1% *G. flaccida*
	1% *Glenodinium* sp.	2% *G. breve*		
10	87% *R. stolterfothii*	67% *R. stolterfothii*	51% *R. stolterfothii*	91% *G. breve*
	5% *P. micans*	11% *Cryptomonas* sp.	25% *G. breve*	2% *Coscinodiscus* sp.
	1% *P. calcar-avis*		3% *Chaetoceros* sp.	2% green 2–4 μm

wannee River were morphologically similar to those found in the nearshore and offshore, but fluorescence microscopy revealed spatial differences in phycobilin composition. The spherical blue-green algae in the river primarily contained phycocyanin, while those outside the mouth of the river contained phycoerythrin. It is possible to hypothesize that these differences in pigments reflect the presence of at least two distinct species of spherical blue-green algae, one freshwater and one marine.

Outside the region of light limitation large-celled diatoms and dinoflagellates dominate plankton biomass, particularly the chain-forming centric diatom species *R. stolterfothii, G. flaccida, L. danicus, Coscinodiscus* sp., and *P. calcar-avis*. Chain formation has been suggested as a mechanism for reducing sinking rates (Smayda and Boeyn 1966; Reynolds 1984; Harris 1986). Additionally, high mixing energy in the near shore portion of the plume region (due to shallow depths, tides, and river outflow) help to maintain large-celled diatoms in suspension, thereby enhancing their exposure to light.

The Suwannee River discharges high concentrations of nutrients into the coastal region of west Florida. The availability of these nutrients for primary producers is evident from both the high concentrations of inorganic nitrogen and soluble reactive phosphorus, and the results of bioassays demonstrating the presence of surplus nutrients for algal growth. Outside the mouth of the river, chemical analyses, and bioassays both show a decline in bioavailable nutrients with distance offshore.

Samples collected in the river during the fall dry season, e.g., before and after tropical storm Josephine, exhibited particularly high concentrations of inorganic nitrogen. Contrary to many other aquatic systems, in which increases in N concentrations result from surface water runoff to the watershed (Ryther and Dunstan 1971), increases in nitrate in the Suwannee River are more closely correlated to groundwater inflows, particularly during low flow periods (Suwannee River Water Management District 1995a,b, 1996). Many groundwater springs discharging into the Suwannee River have high concentrations of nitrate-N (up to 8.0 mg l^{-1}).

In addition to rising nitrate levels, P concentrations have been historically high in the Suwannee River (Suwannee River Water Management District 1995a). These high concentrations of bioavailable P are in part attributable to the natural deposits of phosphatic minerals (e.g., apatite) present in the Hawthorne Formation, which runs through the Su-

wannee River watershed (Crane 1986). The increase in P concentration during periods of elevated riverine discharge is most probably associated with surface runoff and erosional processes. Other sources may also contribute to the P concentration in the river such as industrial waste, sewage treatment plant discharges, surface draining from agricultural activities and phosphate mining activities in the upper Suwannee River basin (United States Environmental Protection Agency 1978; Ham and Hatzell 1996).

In contrast to the nutrient surplus in the river, nutrient limitation bioassays performed on the most offshore stations revealed strong nutrient limitation for all sampling dates. This is corroborated by the fact that, nitrate + nitrite, ammonium, and soluble reactive phosphorus were analytically undetectable at these stations. Phytoplankton growth was significantly greater in flasks treated with the addition of both N and P, compared to the control groups and groups with singular additions of N or P. These results indicate the presence of very low soluble N and P concentrations in the water column. It is probable that recycling of nutrients may be important for maintaining phytoplankton standing crops offshore. It has been suggested that one of the primary sources of N and P in such ecosystems is in the form of ammonium nitrogen and soluble reactive phosphorus released by zooplankton (Lehman 1980; Urabe 1993). It is also likely that the rate of external loading of nutrients to the nearshore environment is variable, depending on temporal changes in river outflow, longshore currents (Moller 1996), atmospheric deposition (Asman and Larsen 1996; Paerl and Whitall 1999), and sediment resuspension.

The variable, and frequently low, concentrations of soluble bioavailable N and P in the offshore areas not only impact the standing crop of phytoplankton but may also effect species composition. The large diatoms, like as *R. stolterfothii, P. calcaravis,* and *G. flaccida,* which dominate the plankton communities of this region may be well suited to this type of variable nutrient environment. Kilham and Kilham (1980) noted that large diatoms persist, if not flourish, under nutrient-poor oceanic conditions because of their ability to store nutrients and then use them for growth under nutrient-limited conditions. The storage of nutrients can occur as luxury uptake from the water column or as uptake within the sediment-water boundary layer. In the latter case large-celled diatoms may be considered meroplanktonic, i.e., during periods of low mixing energy they reside on the sediment surface and resuspend in to the surface water during periods of increased mixing energy. This phenomenon provides access to higher concentrations of bioavailable nutrients in the sediments and may be particularly important in shallow environments, which are subject to frequent resuspension events (Scheleske et al. 1997).

The low levels of bioavailable nutrients found in the offshore environment, combined with the light limiting conditions in the river leave a nearshore transitional zone where there is sufficient light and nutrients to sustain higher phytoplankton biovolumes. This region of high standing crops was observed during all our sampling periods.

While the focus of this study was the effects of light and nutrient availability on phytoplankton dynamics in the Suwannee River and nearshore region, there are clearly other factors, which need to be considered in the discussion of this subject. Grazing is a potentially important factor in temporal and spatial variations of phytoplankton communities. Owing to the high abundance of both benthic (i.e., macroinvertebrates) (Gaston et al. 1997) and pelagic grazers in this coastal region (Phlips and Cichra 1998; Bledsoe and Phlips unpublished data), predation pressures may be high. Grazing may influence both the abundance and structure of phytoplankton assemblages. The large-celled diatom species, which frequently dominate the phytoplankton community in the nearshore region, may be relatively resistant to grazing, helping to explain their dominance.

In addition to the more commonly acknowledged grazers, like copepods, the Suwannee River plume region is also characterized by periodically large populations of gelatinous organisms such as, doliolids, appendicularians, and salps (Bledsoe, Cichra, and Phlips unpublished data). These highly efficient organisms can filter large volumes of water thereby impacting both phytoplankton and zooplankton populations, directly and through trophic cascade effects (Harbison and Gilmer 1976). It also suggests that they may play a role in nutrient recycling, along with benthic filter-feeding macroinvertebrates, like oysters and clams, which are abundant in the northwest region of Florida's Big Bend.

Similarly, blooms of the dinoflagellate *Gymnodinium breve* observed in March may be in part related to differential grazing pressures. This red tide species is known to be highly toxic and poses a serious threat to the health of marine organisms and humans alike (Steidinger 1975). Resistance to grazing may result in large standing crops of these toxic species. In addition, the motility of dinoflagellates and their ability to grow heterotrophically provide them with a competitive advantage in the nutrient-limited offshore environment (Stoecker et al. 1997).

In addition to grazing, hydrodynamic flushing is

widely recognized as an important factor in the distribution of plankton in estuaries (Kennish 1986). In the Suwannee River, high flow rates can result in relatively short residence time (i.e., approximately 2 wk). Short residence time combined with light limitation maintain low phytoplankton standing crops in the river. Our nutrient bioassays indicated large increases in phytoplankton biomass after several days under conditions of surplus light and long retention periods. The bioassays revealed the potential for increased phytoplankton biomass under such conditions. Increases in residence time and clear groundwater spring inputs during the dry seasons could produce similar results.

Outside the mouth of the river, oyster reefs dominate the region and semi-enclose the plume during low tide. However, when the oyster reefs are flooded during high tide, tidal flushing may become a factor in the distribution of plankton populations. This effect is probably somewhat muted by the very shallow and broad extent of the continental shelf in this area of the Gulf of Mexico. Despite these hydrodynamic considerations, the consistency of the phytoplankton maxima near the river mouth indicates that water masses within the region have sufficient temporal integrity to allow for the development of high phytoplankton standing crops, at least under the limited range of hydrodynamic conditions encountered in this study.

Conclusions

The temporally consistent spatial patterns of phytoplankton standing crop in the Suwannee River and plume region observed in this study can be most easily explained in the terms of gradients in nutrient and light availability. Our results indicate discharge from the Suwannee River affect the large-scale distribution of phytoplankton standing crop in this coastal region. Planktonic algal biomass is restricted in the Suwannee River due to the combination of light limitation and elevated flushing rates. The impact of light limitation may also be reflected in the dominance of picoplanktonic blue-greens and greens, cryptophyta, and small diatoms in the river. Seaward of the river mouth, elevated light levels, combined with the high levels of bioavailable nutrients provided by the river, yield a region of elevated phytoplankton standing crop, which is dominated by large centric diatoms and occasionally dinoflagellates. Seaward of the influence of the Suwannee River plume, the diminishing abundance of phytoplankton biomass is most likely regulated by grazing and nutrient limitation.

Nutrient concentration and light availability, which regulate phytoplankton abundance and composition in the Suwannee River and its plume region, vary with changes in flow. Elevated light availability and nitrate concentrations in the river and plume region are typical of low flow conditions, while decreases in nitrate concentration and increases in humic acids, which reduce light penetration, characterize periods of riverine flooding both in the river and plume region. The existence of these relationships also highlight the potential importance that changes in nutrient loading and water use in riverine watersheds can have on plankton ecology of estuaries.

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