

Light availability and variations in phytoplankton standing crops in a nutrient-rich blackwater river

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Abstract

In this paper we examine the potential role of light limitation in the regulation of phytoplankton standing crop in Florida's largest river, the St. Johns. We hypothesized that spatial and temporal patterns in standing crops of phytoplankton are strongly affected by variations in light availability in the mixed layer, particularly as they relate to river basin morphology and changes in water color, which reach high levels in the St. Johns River. This hypothesis was examined within the context of four principal research objectives: (1) Determination of the spatial and temporal patterns of phytoplankton standing crops and key environmental parameters related to nutrient concentration and light extinction, (2) Estimation of spatial and temporal patterns of mean light availability in the mixed-layer, (3) Examination of the correlations between phytoplankton standing crops and light availability, and (4) Evaluation of the relative role of different limiting factors on the regulation of phytoplankton standing crop. The results of this study revealed a relationship between standing crops and light availability. Twelve sampling sites along a 130 km reach of the river were sampled and analyzed for phytoplankton abundance, water chemistry, and light attenuation over a three year period. Our empirical results, along with the outcome of our efforts to model light availability for planktonic production were consistent with our original hypothesis. Temporal variations in color were strongly correlated to variability in phytoplankton standing crops. Spatial trends in standing crop were most readily explained through the effects of changing basin morphology and flushing rates. The results are discussed in the context of the River Continuum Concept and variations on this theme specific to blackwater ecosystems.

The dark amber stain of blackwater ecosystems results in a unique underwater light environment (Kirk 1994). The preferential uptake of photosynthetically active radiation (PAR) in the critical blue-green region of the visible spectrum by dissolved organic humic and fulvic substances heightens the potential for light limitation of primary production. In aquatic environments subject to high levels of dissolved organic color a large proportion of incident PAR can be lost within the top few meters of the water column, resulting in severe restriction of the euphotic zone. In many aquatic ecosystems with high light transparency the structure, standing crops, and dynamics of phytoplankton populations are strongly correlated to the supply of nutrients, but in blackwater systems light availability can be a major limiting factor for primary production (Edwards and Meyer 1987; Lewis 1988).

A number of Florida's major rivers and lakes fall into the category of highly colored blackwater ecosystems (Clewell 1991). In some of these systems, like the St. Johns and Suwannee Rivers, the presence of high concentrations of bioavailable nutrients do not always lead to correspondingly

high phytoplankton standing crops and productivity. This apparent deficiency in primary production may be a result of light limitation of algal growth, as reported in a number of other blackwater rivers, including the Ogeechee River in the Southeastern United States (Edwards and Meyer 1987) and the Orinoco River in Brazil (Lewis 1988).

In this paper, we examine the potential role of light limitation in the regulation of phytoplankton standing crop in Florida's largest river, the St. Johns. Our study focused on the 130 km reach of the river from Lake George to the City of Jacksonville, below which the river is subject to significant tidal water exchange with the Atlantic Ocean and the biological community takes on distinct estuarine characteristics. We hypothesized that spatial and temporal patterns in standing crops of phytoplankton are strongly affected by variations in light availability in the mixed layer, particularly as they relate to river basin morphology and changes in water color. This hypothesis was examined within the context of four principal research objectives: (1) Determination of the spatial and temporal patterns of phytoplankton standing crops and key environmental parameters related to nutrient concentration and light extinction, (2) Estimation of spatial and temporal patterns of mean light availability in the mixed-layer, (3) Examination of the correlations between phytoplankton standing crops and light availability, and (4) Evaluation of the relative role of different limiting factors on the regulation of phytoplankton standing crop. The results of this study revealed a relationship between standing crops and light availability. These relationships are discussed within the context of the River Continuum Concept (Vannote et

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al. 1980; Minshall et al. 1985), and variations on this theme specific to blackwater ecosystems (Meyer 1990).

Methods

Site description—The St. Johns River is a major sixth order river, draining the northeastern portion of the State of Florida in the southeastern U.S. The St. Johns is physiographically unique in that its 24,424 km² drainage basin is wholly contained within the Atlantic Coastal plain, resulting in a river of extremely low fall, less than 7.6 meters over 512 km. Long term net mean discharge is estimated at 173 m³ s⁻¹ (Morris 1995). The St. Johns is also a morphologically unique river in that it is a series of interconnected lakes, and that within its estuarine portion, it narrows at its mouth, rather than opening continually wider to the sea. The lower St. Johns is defined as that portion of the river below the mouth of one of its largest tributaries, the Ocklawaha River, 161 km upstream (U.S. Geologic Survey Hydrologic Unit 03080103). The lower St. Johns is broad and lagoonal, with a surface area of 33,834 hectares and mean residence times of between 40 d in October to 95 d in May. The lower St. Johns can be subdivided into three salinity regimes: a fresh-tidal lacustrine zone, extending from river-km 173 through 61; an oligohaline lacustrine zone, from river-km 61 through 41; and a mesohaline zone from river-km 41 to the mouth of the river.

In this study, 12 sites (Fig. 1) were sampled on a monthly basis for three years. Sites were numbered according to the distance (km) from the rivers outlet into the Atlantic Ocean. Each site is also associated with a landmark designation—i.e., Sites, 40 Jacksonville; 58 Mandarin; 74 Popo Point; 81 Wright; 89 Picolota; 97 Racey Point; 113 Federal Point; 119 Rice Creek; 126 Palatka; 137 Dunns Creek; 144 Buffalo Bluff; 173 Lake George.

Field collections—Water samples were collected with an integrating tube which captured a vertical composite of the water column from the surface to a depth of 3 m, or to 0.1 m from the bottom in cases where total depth was less than 3 m. At each location, five individual integrating tube collections were composited in a sample churn, and samples drawn from the churn. Samples for select “dissolved” chemistry constituents were vacuum-filtered through a 0.45 μm millipore filter at the time of collection. Two liter aliquots of water were collected for chlorophyll *a* (Chl *a*) determination and epifluorescence microscopy. One liter aliquots were preserved with Lugols for light microscopy. All sample aliquots were held on ice and returned to the lab for processing.

Water chemistry analyses—Water samples were analysed for nitrate + nitrite nitrogen (EPA 353.2, colorimetric, cadmium reduction), ammonia + ammonium nitrogen (EPA 350.1, colorimetric, automated phenate), dissolved orthophosphate (EPA 365.1, colorimetric, automated ammonium molybdate/ascorbic acid), color (Standard Methods 2120 B, filtered, platinum-cobalt standards visual comparison), total suspended solids (Standard Methods 2540D), dissolved or-

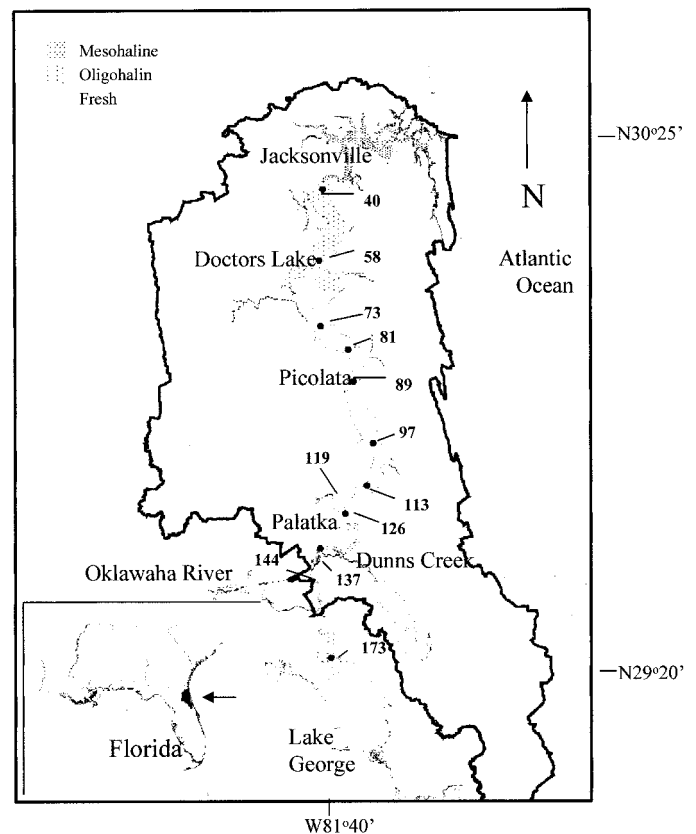


Fig. 1. Locations of sampling sites in the lower St. Johns River. Sampling sites are numbered according to the distance (km) from the mouth of the river.

ganic carbon (Standard Methods 5310) and chlorophyll (Standard Methods 10200 H, spectrophotometric acid).

Determination of phytoplankton standing crops—Phytoplankton standing crops were determined in two ways: Chl *a* concentration (see above for method) and cellular biovolume. Small-celled cyanobacteria were enumerated with fluorescence microscopy using live filtered samples. Subsamples of station water were filtered onto 0.2 μm pore Nuclepore filters and mounted between microscope slides and cover slips with immersion oil. These were stored at -20°C and counted within 24 h to minimize fading of fluorescence. Samples were counted with a Nikon research microscope equipped with autofluorescence for phycobilins (green light 530–560 nm excitation and >580 nm emission). Numerical abundances of cyanobacteria cells were 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. Samples were concentrated by settling Lugols preserved samples. For counting of cells, concentrated samples were settled in cylindrical counting chambers. Phytoplankton cells were identified and counted at 400× and 100× with a Nikon phase contrast inverted microscope using

methods described by Cichra et al. (1995). Phytoplankton biovolume was estimated by converting numerical cell abundances to biovolume using the closest geometric shape conversion method (Smayda 1979; Cichra et al. 1995).

Estimation of mean light availability in the water column—Light measurements used to develop the basic relationships between mean mixing depth and mean light availability in the water column, I_M , were made at three stations (see Fig. 1: Sites 58, 81, and 97) monthly from August 1994 through August 1996. The light data were collected as part of a different project and thus the sample dates do not coincide with the phytoplankton data. PAR, as downward flux in the air and downward flux in the water column, was measured as $\mu\text{moles quanta m}^{-2} \text{ s}^{-1}$ using Li-Cor Instruments cosine-corrected quantum sensors at fixed depth intervals of 0.5 m to a depth of 3 m. Compensation for the effects of wave action on depth was made by integrating the PAR measurements over a 30–60 s interval. A vertical diffuse attenuation coefficient for PAR, K_d (m^{-1}), was calculated as:

$$K_d = [(\ln(I_n - (I_n r)) - \ln(I_0))/Z][\cos(\arcsin(\sin \theta_a/1.33))]$$

where \ln = natural log, I_0 = downward irradiance ($\mu\text{moles quanta m}^{-2} \text{ s}^{-1}$) in air at the water surface, r = fraction of incident irradiance reflected off the water surface, Z = depth interval in m closest to the depth of 10% light transmission (typically 1.0 m in the SJR), I_z = downward irradiance at depth Z , θ_a = zenith angle of incidence of solar irradiance in air where $\theta_a = 0^\circ$ when the angle of incidence is perpendicular to the water surface, $\arcsin((\sin \theta_a)/1.33)$ = zenith angle of incidence in water (θ_w) resulting from refraction at the air/water interface and 1.33 is the average optical density of water.

A mean water column irradiance (I_M), defined as the daily irradiance in moles PAR quanta $\text{m}^{-2} \text{ d}^{-1}$ to which a random cell circulating through the mixed layer of the water column would be exposed, was modeled as:

$$I_M = (I_{0/\text{day}}/K_d Z_m (1 - \exp(-K_d Z_m)))$$

where Z_m = the mixing depth which, for the sake of this analysis, was assumed to equal mean depth for a given river section, $I_{0/\text{day}}$ = the PAR irradiance flux at the water surface in moles quanta $\text{m}^{-2} \text{ d}^{-1}$ (Stefan et al. 1976). The assumption of mixing depth being equal to mean depth was considered valid given the shallow depth range of the river (i.e., 3–5 m) and the long wind fetch typical of most of the river reaches included in the study (i.e., >1 km). This conclusion was supported by the general lack of vertical stratification in dissolved oxygen and temperature observed during the course of our study. I_0 data were obtained from a monitoring station located near the river approximately midway between Lake George to the south and the city of Jacksonville. Mean depth for each river section was obtained from hypsographic curves supplied by the St. Johns River Water Management District.

In an effort to relate the light attenuation model to the broader range of study sites included the phytoplankton standing crop analyses, estimates of light extinction coefficients were generated from information on dissolved color, suspended solids and chlorophyll concentrations. Partial ex-

inction coefficients K_d (i.e., $K_{\text{color}} + K_{\text{chl}} + K_{\text{water}}$) were derived by multiplying color, non-algal suspended solids (i.e., tripton, total suspended solids minus dry weight equivalence of phytoplankton biovolume determined microscopically, derived by multiplying biovolume by 0.42, as described in Mullin et al. 1966) and chlorophyll values by conversion values $0.014 (\text{Pt-Co units})^{-1} \text{ m}^{-1}$ (McPherson and Miller 1987), $0.04 (\text{g tripton})^{-1} \text{ Lm}^{-1}$ (Phlips et al. 1995a, Phlips pers. comm.) and $0.016 (\text{mg Chl})^{-1} \text{ m}^2$ (Reynolds 1984), respectively. The contribution of water to extinction was assumed to be constant at 0.0384 m^{-1} (Lorenzen 1972). Estimated K_d values were used in combination with the light availability models described above to generate mean I_M values for representative sampling sites and seasons.

Statistical methods—SAS statistical program for personal computers (SAS Institute) was used to carry out general linear models procedures and Pearson Correlation procedures. A significance level of $P < 0.05$, was used to compare mean values.

Results

Spatial and temporal patterns of phytoplankton standing crop—The overall spatial pattern of phytoplankton abundance in the lower St. Johns River from the fall of 1993 to the fall of 1996 (Fig. 2) was a decline of standing crop (i.e., cellular biovolume) from the primary source of inflow at Lake George (Site 173) to the beginning of the strongly saline impacted reach of the river near the City of Jacksonville (Site 40). Between Lake George and Jacksonville mean standing crops of phytoplankton frequently leveled off or went up between Palatka (Site 126) and Picolata (Site 89). Downstream of Picolata phytoplankton standing crops declined.

The greatest short-term variation (i.e., intraseasonal) in phytoplankton standing crop occurred in the spring and summer seasons (Fig. 2), which were also the seasons of highest abundance of phytoplankton in all three years of this study. Conversely, standing crops were least variable during the winter, when phytoplankton abundances were at their intra-annual minimum. Phytoplankton standing crops exhibited pronounced interannual variation (Figure 2). Standing crops were generally higher in the first and third years of this project than in the second year, within any given season. Interannual differences were smallest downstream of Picolata (Site 89), where phytoplankton standing crops were consistently lower than the remainder of the sampling reach.

Relationship between Chl a and cellular biovolume—The two measures of phytoplankton standing crops included in this study were cellular biovolume and Chl *a* concentration. Cellular biovolume was chosen as the primary indicator of standing crop because it is a more direct measure of biomass. However, an examination of Chl *a* concentration is warranted due to its widespread use in the literature. A comparison of cellular biovolumes and Chl *a* concentrations at four representative sampling sites within the study reach serves to illustrate the similarities and differences in how these two variables portray spatial and temporal patterns of phyto-

plankton standing crop (Fig. 3). The general picture of seasonal variation in standing crop derived from the two variables was the same. However, interannual changes in phytoplankton standing crop were differently represented by cellular biovolume and Chl *a* concentrations. In terms of cellular biovolume there was a distinct drop in phytoplankton standing crop in the second year of the project. In contrast, Chl *a* concentrations were as high, or higher, in the second year. The disparities between interannual patterns of cellular biovolume and Chl *a* concentration reflect changes in the Chl *a* content of phytoplankton over the study period (Table 1).

Spatial differences in the Chl *a* content of phytoplankton were also observed over the study reach. Chl *a* content of phytoplankton in the most downstream segment of the study reach was higher than in other regions of the river (Table 1). As a result of spatial variation in the Chl *a* content of phytoplankton, Chl *a* concentrations downstream of Picolata (Site 89) tended to overestimate cellular biovolume by comparison to more upstream parts of the river.

Spatial and temporal patterns of water color, dissolved organic carbon and light availability—Dissolved water color was high (i.e., >50 Pt-Co units) at all sampling sites, throughout the study period (Fig. 3), as might be expected for a blackwater river. Spatial variation in color was minimal by comparison to temporal variation. Color and dissolved organic carbon concentrations were strongly correlated (i.e., Pearson Correlation Coefficient of 0.81, $P < 0.0001$, $n = 388$). The three years of the study showed distinctly different patterns in water color. Color remained comparatively low (i.e., <100 Pt-Co units) throughout the first year of the project, but increased dramatically in the first quarter (Fall 1994) of the second year of the project. Color remained very high (i.e., >200 Pt-Co units) from September 1994 through March 1995 throughout the study reach. In the third year of the project, very high levels of color returned during the fall of 1995, but showed an earlier decline than in the second year (Fig. 3). The high color values observed in our study suggest that color is a major component of light attenuation in the river. Color can shrink the euphotic zone to very shallow depths.

The diffuse vertical attenuation coefficient (K_d), determined for the three sites used in the light attenuation model relationships (58, 81, and 97), ranged from 2.16 to 6.53 m^{-1} with an average of 3.74 $m^{-1} \pm 0.10$ ($\pm SE$, $n = 74$). The temporal variance for K_d , assessed as the coefficient of variation (CV) for all stations between sample dates, was greater (CV = 23%) than spatial variance, mean CV for all dates between stations (CV = 8.5%). The temporal and spatial patterns of color and Chl *a* concentration observed in the phytoplankton study were comparable to the light attenuation study, where the highest light attenuation and color values were observed during the fall and winter months and the lowest attenuation and lowest color was observed during the spring and summer months. Color values were related to K_d , suggesting that color is the major component of light attenuation in the lower St. Johns River. A linear regression analysis with K_d as the dependent variable and color the independent variable explained 65% of the variance (Fig. 4). In

contrast, the regression of Chl *a* to K_d explained less than 10% of the variance (Fig. 4).

The daily surface irradiance (I_0), reported as the average moles of quanta $m^{-2} d^{-1}$ of PAR for each month ranged from 19.04 in December to 49.85 in May. The average daily surface light flux for a given month was considered to be relatively consistent for the reach of the river included in this study. The 62% difference between the minimum and maximum average daily irradiance is attributable to the seasonal variability in photoperiod and path length through the atmosphere between summer and winter months at the latitudes 29 to 30° N. The “winter” half of the year, between the spring and fall equinox, with incidence of lower light intensity and lower daily flux of surface irradiance were also the periods of greater color. The coincidental seasonality of color and surface irradiance forced a temporal function on the mean light availability in the mixed layer (I_M) where the compound effects of high color and lower daily surface irradiance in the “winter” greatly reduced the potential I_M in the winter.

Because of the low spatial variance for K_d and I_0 within sample dates, the spatial variance in I_M was primarily attributable to varying mixing depths (Z_m) along the river. The mean depths for all river sections ranged from 2.5 to 4.5. In terms of mean depth, the lower St. Johns River can be divided into four distinct reaches: (1) Lake George (river-km 173–202), with a mean depth of 2.5 m; (2) Lake George-Palatka (river-km 172–126), with a mean depth of 4.5; (3) Palatka-Picolata (river-km 126–89), with a mean depth of 2.6 m; and, (4) Picolata-Jacksonville (river-km 89–37), with a mean depth of 3.6 m. The relationship between mean mixing depth and I_M was mathematically derived for a range of K_d values (Fig. 5). Due to the large difference in the mean incident irradiance in the summer and winter, the two seasons were modeled separately.

During the winter, low I_0 and high K_d (resulting from high color values) combined to yield low I_M (i.e., <6 mol quanta $m^{-2} d^{-1}$) over the entire range of mean depths observed for river sections from Lake George to the City of Jacksonville, as exemplified by the I_M values for the four representative sampling sites along the river (Fig. 3). The winter of 1993/94 was an exception to this general pattern because of relatively low color levels. In summer, higher I_0 and lower color values resulted in increased estimates of I_M throughout the sampling reach (Fig. 3). At the mean depths encountered in Lake George and Palatka-Picolata reaches of the river, I_M values were frequently above the threshold range for light limitation suggested in the literature, i.e., 2–6 mole quanta $m^{-2} d^{-1}$ (Oliver 1981; Geddes 1984; Philips et al. 1995a). In contrast, estimates of summer levels of I_M for the Lake George-Palatka and Picolata-Jacksonville sampling reaches were more frequently within or below the 2–6 mole quanta $m^{-2} d^{-1}$ threshold range. It is important to keep in mind that I_M values for specific locations and times are impacted by temporal variations in color and to a lesser extent other components of light attenuation. For example, color values during the first year of this project were significantly lower than in the second and third years. Therefore, the potential for light limitation would be expected to be lower in the first year based on overall higher values for I_M (Fig. 3).

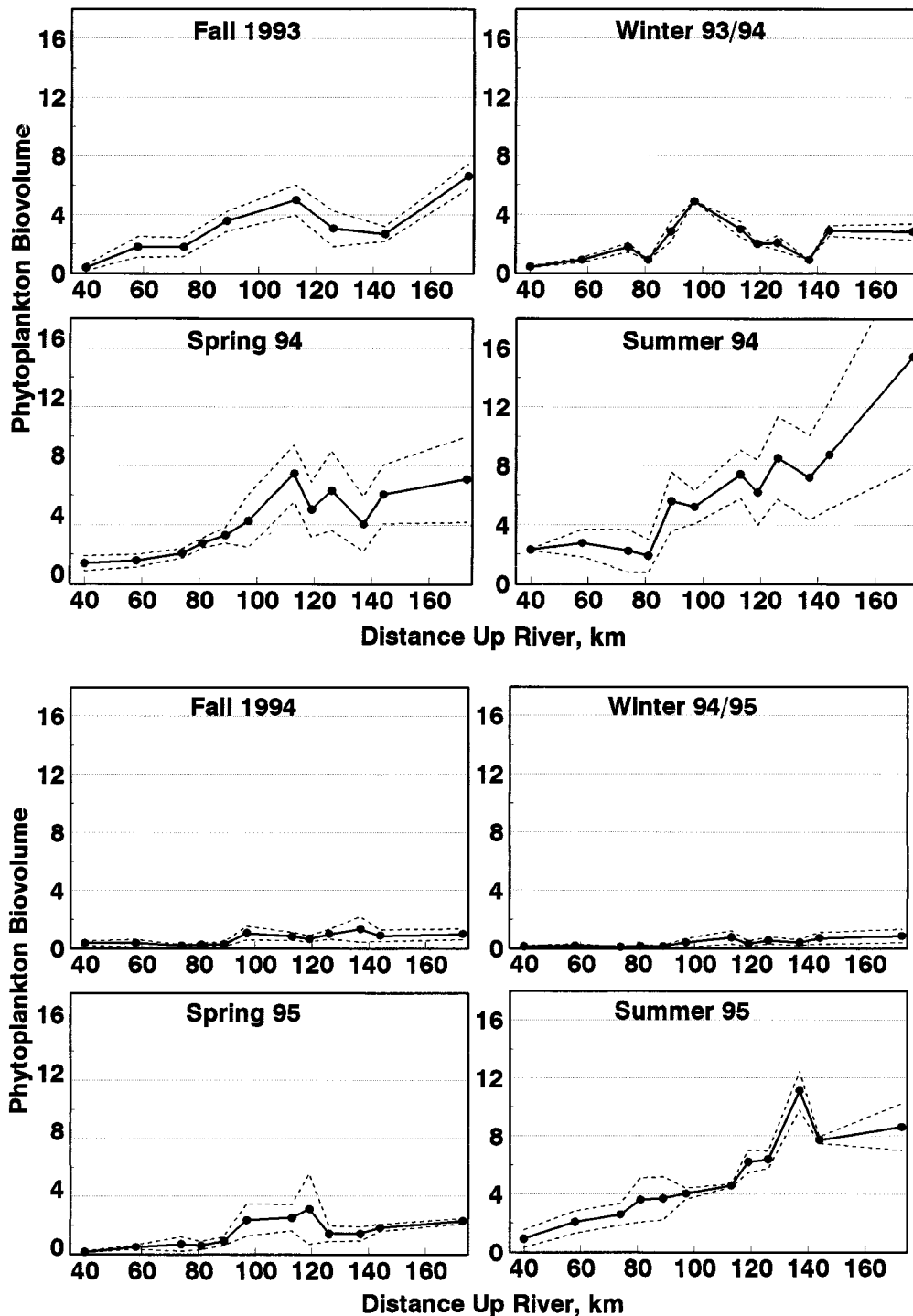


Fig. 2. Seasonal mean biovolume of phytoplankton ($\mu\text{m}^3 \text{ml}^{-1}$) over the three years of sampling in this project. Mean values for individual sampling sites are indicated by solid circles. Standard error for the means is designated by dashed lines.

Concentrations of inorganic nitrogen and phosphorus—Seasonal and interannual variation of dissolved inorganic nitrogen concentrations (i.e., DIN) followed a pattern similar to color, with peak values in the fall and winter and minimum values in the summer (Fig. 3). DIN concentrations were distinctly lower in the first year of the project than in

the subsequent two years, mimicking the pattern observed for color. DIN concentrations also varied on a spatial scale, exhibiting a distinct increase downstream of Picolata, Site 89. The spatial pattern was apparent all three years of the project.

Spatial and temporal patterns of variation in soluble re-

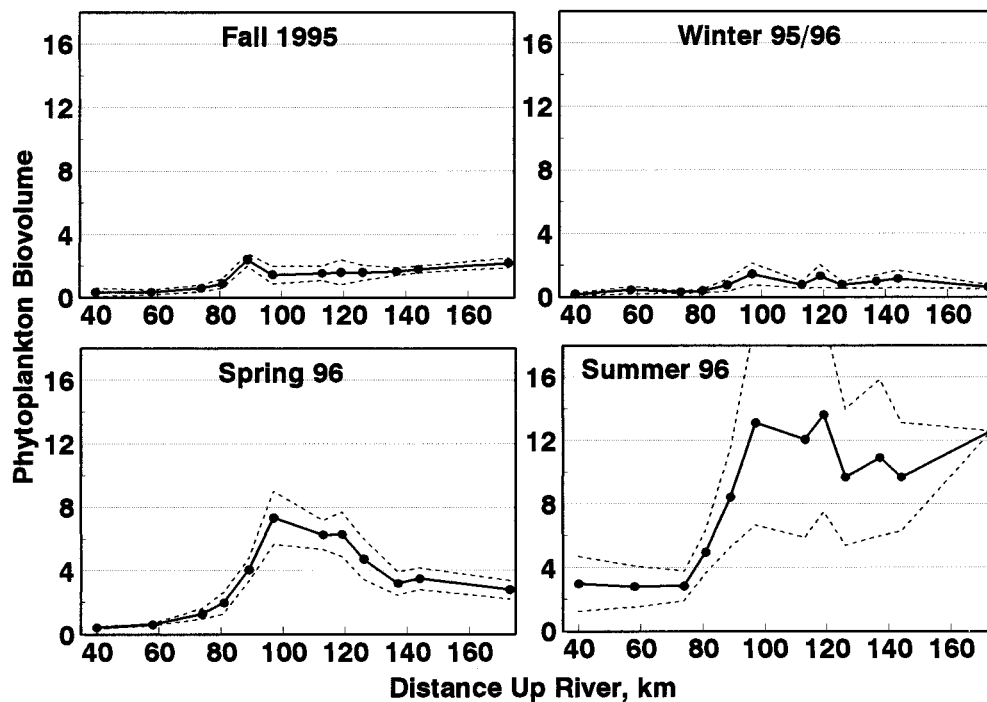


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active phosphorus (i.e., SRP) were similar to those observed for nitrate, with some noteworthy exceptions (Fig. 3). Although SRP concentrations were highest in the fall, summer, and early spring in much of the sampling reach, the opposite was true downstream of Picolata, Site 89. Upstream of Picolata, SRP concentrations were near levels of detection in the first year of the project, before increasing dramatically in the fall of the second year. Downstream of Picolata, SRP concentrations were high in the summer of the first year of sampling, even higher in the summer of the second year, before dropping in the third year.

Discussion

St. Johns River, the river continuum concept and blackwater ecosystems—There are several features of phytoplankton dynamics in the St. Johns River that do not conform to the general principles of the River Continuum Concept (i.e., RCC), as originally defined by Vannote et al. (1980). The RCC predicts increases in pelagic primary production and the photosynthesis/respiration ratio (i.e., P/R) with increasing river order. In the lower St. Johns River phytoplankton standing crops generally decline in the downstream direction, indicating that primary production is frequently outweighed by loss functions (e.g., respiration, sedimentation, senescence, grazing, washout). Along the same lines, the results of complimentary research on primary production in the St. Johns River indicates that P/R is often less than one in the lower reach of the river, particularly when color values are high (Aldridge et al. 1998). In this sense, the St. Johns River shares with other blackwater rivers high values for community respiration relative to primary production (Meyer and Edwards 1990).

Like many rivers located in watersheds containing extensive wetland habitat (Brinson 1976; Eckhardt and Moore 1990), the St. Johns River is high in dissolved organic carbon (i.e., mean dissolved organic content [DOC] concentration around 20 mg L^{-1}), a feature it shares with other blackwater rivers. Part of this pool of organic carbon is responsible for the high color values found in the St. Johns River, as indicated by the significant correlation between the two variables. DOC also represents a potential source of fixed-carbon for the growth of aquatic microorganisms, e.g., bacteria. Along this line of reasoning it is interesting to note that bacterial abundances in the St. Johns River increased markedly from the first to the second year of this study, along with a concomitant rise in DOC concentration (Phlips unpublished data). Other studies of blackwater rivers have noted that bacterial utilization of allochthonous DOC is inefficient compared to the use of autochthonous DOC and particulate organic carbon (Meyer 1990). The relative recalcitrance of DOC has been used to explain the long carbon turnover times and length of nutrient spiraling characteristic of blackwater ecosystems (Newbold et al. 1982; Meyer and Edwards 1990).

Beyond the broad-scale similarities between the St. Johns River and other blackwater rivers, the specific spatial and temporal patterns of phytoplankton standing crops are more appropriately discussed within the context of the unique physical, chemical, biological, geological, hydrodynamic, and meteorological characteristics of the river basin. The importance of defining the context within which to view the ecology of individual river ecosystems has been stressed by a number of researchers, in an effort to refine and broaden the applicability of the RCC (Minshall et al. 1985).

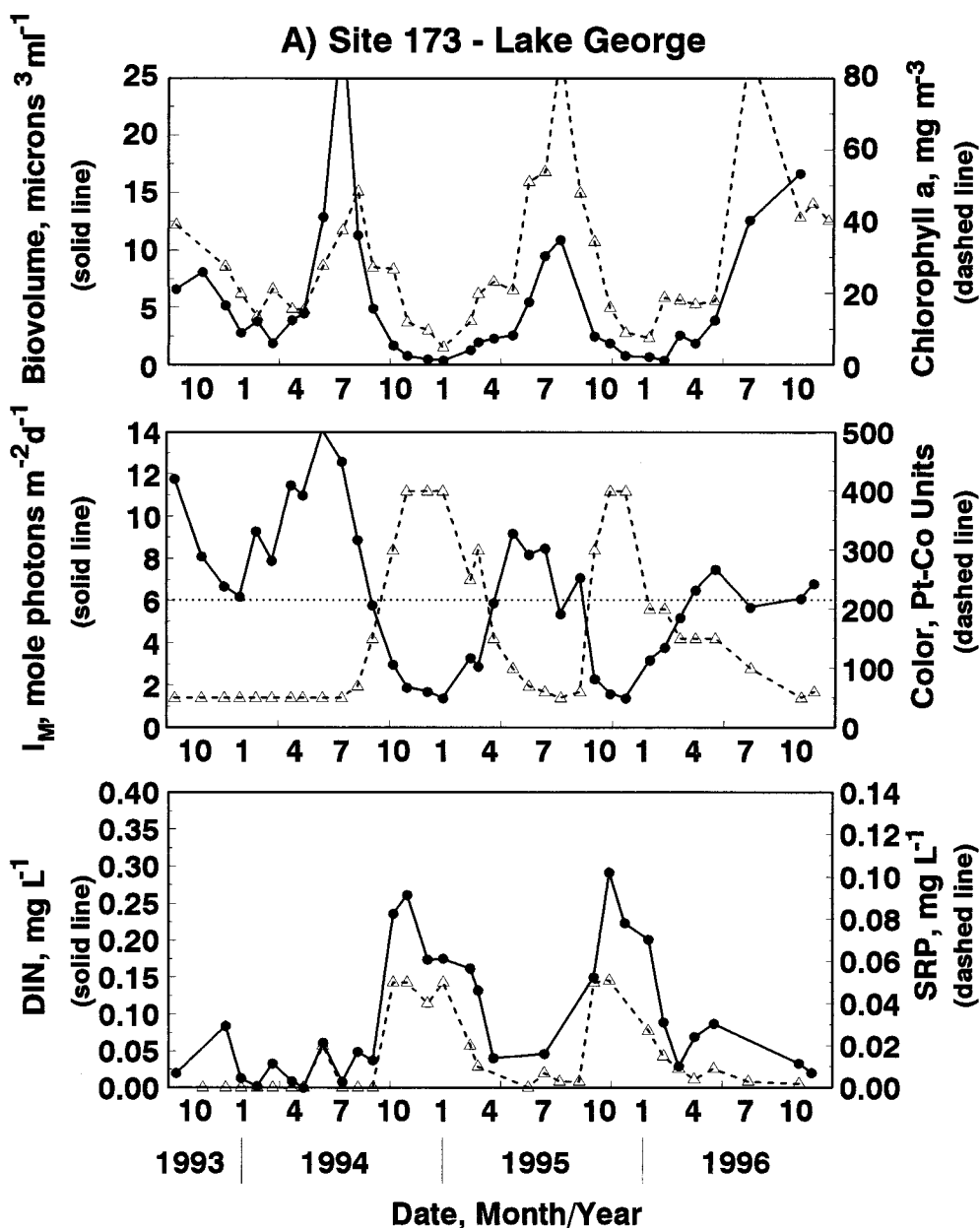


Fig. 3. Temporal variation in phytoplankton biovolume (top, solid line), Chl *a* concentration (top, dashed line), mean light availability in the mixed layer (I_M , middle, solid line), color (middle, dashed line), dissolved inorganic nitrogen (DIN includes ammonium, nitrate, and nitrite, bottom, solid line), and soluble reactive phosphorus (SRP, bottom, dashed line) at four sampling sites representative of the major regions of the lower St. Johns River: i.e., (A) Site 173 in Lake George, (B) Site 144 (Buffalo Bluff) in the Lake George-Palatka reach, (C) Site 113 (Federal Point) in the Palatka-Picolata reach, and (D) Site 58 (Mandarin) in the Picolata-Jacksonville reach. Horizontal dotted lines in the figures (middle) represent the I_M range for the threshold of light limitation.

Light as a limiting factor for phytoplankton standing crops—In an effort to identify the factors responsible for spatial and temporal patterns of phytoplankton standing crops in the lower St. Johns River our working hypothesis was that variations in light availability play a major role. This hypothesis is supported by several aspects of our results. Our models of mean light availability in the mixed layer (I_M), show that spatial patterns in I_M are strongly influ-

enced by differences in mixing depth (Fig. 5), since color (i.e., the major component of light attenuation) is spatially uniform in the lower St. Johns River, at any point in time. Conversely, temporal patterns of I_M are closely tied to seasonal and interannual variations in color and to a lesser extent seasonal changes in incident irradiance.

From the standpoint of spatial trends in phytoplankton standing crops, the lower St. Johns River can be divided into

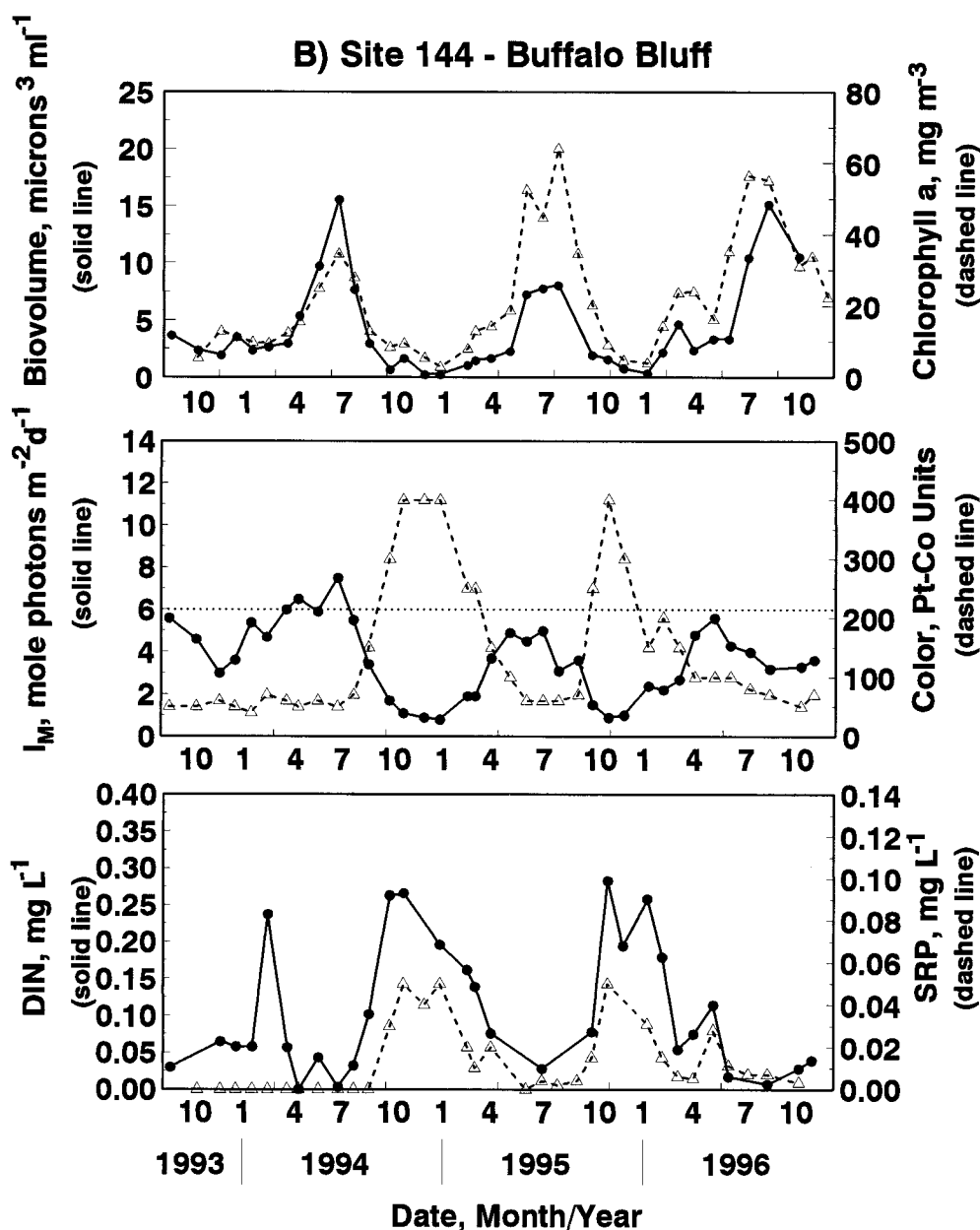


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four distinct regions—i.e., (1) Lake George, (2) Lake George (Site 173) to Palatka (Site 126), (3) Palatka to Picolata (Site 89), and (4) Picolata to the City of Jacksonville (Site 37). At the point of its emergence from Lake George the St. Johns River is already a higher order system characterized by high levels of color (i.e., 50–500 Pt-Co units). The eutrophic character and correspondingly high phytoplankton abundances found in Lake George are manifested in the high phytoplankton standing crops in the river at this point (i.e., Chl *a* levels regularly in excess of 50 mg m⁻³). Water inflow from Lake George makes up approximately 50% of the maximum volume of the lower St. Johns River, making it the largest single contributor of water. Downstream of Lake George the river is comparatively narrow, deep and fast

moving, and the abundance of phytoplankton generally decline up to the inflow of Dunns Creek (Fig. 2). At Palatka the river broadens, becomes shallower and flow rates diminish by over half, reaching flow rates as low as 1 km day⁻¹ (St. Johns River Water Management District, pers. comm.). Along with the broadening of the river, the extent of shallow fringing habitat is expanded. The Palatka-Picolata reach of the river is frequently characterized by an increase in phytoplankton standing crops (Fig. 2). Downstream of Picolata, mean depth of the river increases and phytoplankton standing crops decline dramatically.

One way of examining the potential affect of light limitation on phytoplankton standing crops in different regions of the lower St. Johns River is to compare the estimated I_M

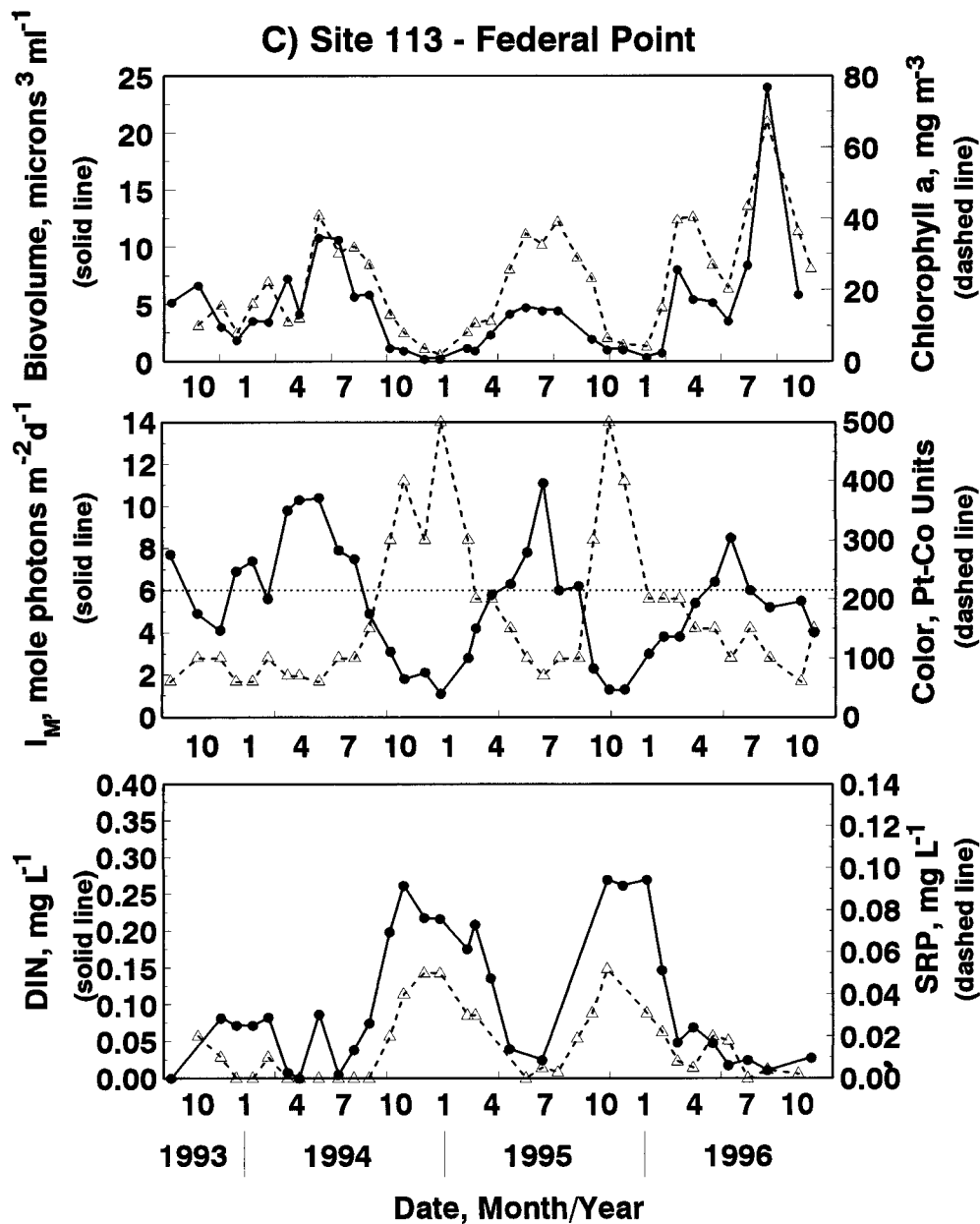


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values for different regions of the river with published estimates of critical I_M values (i.e., threshold I_M for light limitation) for other aquatic ecosystems. A threshold range of 2–6 moles quanta m⁻² d⁻¹ for light limitation of phytoplankton production and standing crops has been proposed for a number of freshwater ecosystems, including Lake Okeechobee in Florida (Phlips et al. 1995a), and Mt. Bold Reservoir (Oliver 1981), Lake Alexandrina and River Murray (Geddes 1984) in Australia. The threshold range for I_M provides a basis for discussion of spatial and temporal disparities in the degree of light limitation within the four regions of the river described above.

In contrast to the relatively high light availability in Lake George, I_M values for the Lake George-Palatka and Picolata-

Jacksonville reaches of the river are comparatively low, placing the plankton community within or below the threshold for light limitation, even during certain periods in the spring, summer, and fall (Fig. 3). This means that standing crops of phytoplankton in the latter reaches of the river have greater potential for light limitation than Lake George, as well as the Palatka-Picolata reach of the river. These model results match the observed decline of phytoplankton standing crops in the latter regions of the river.

From a temporal perspective, the St. Johns River is poised on the boundary between the subtropical and warm temperate climatic regimes of the Southeastern U.S. (Beaver and Crisman 1991). Seasonal patterns of phytoplankton abundance observed in this study more closely resemble the over-

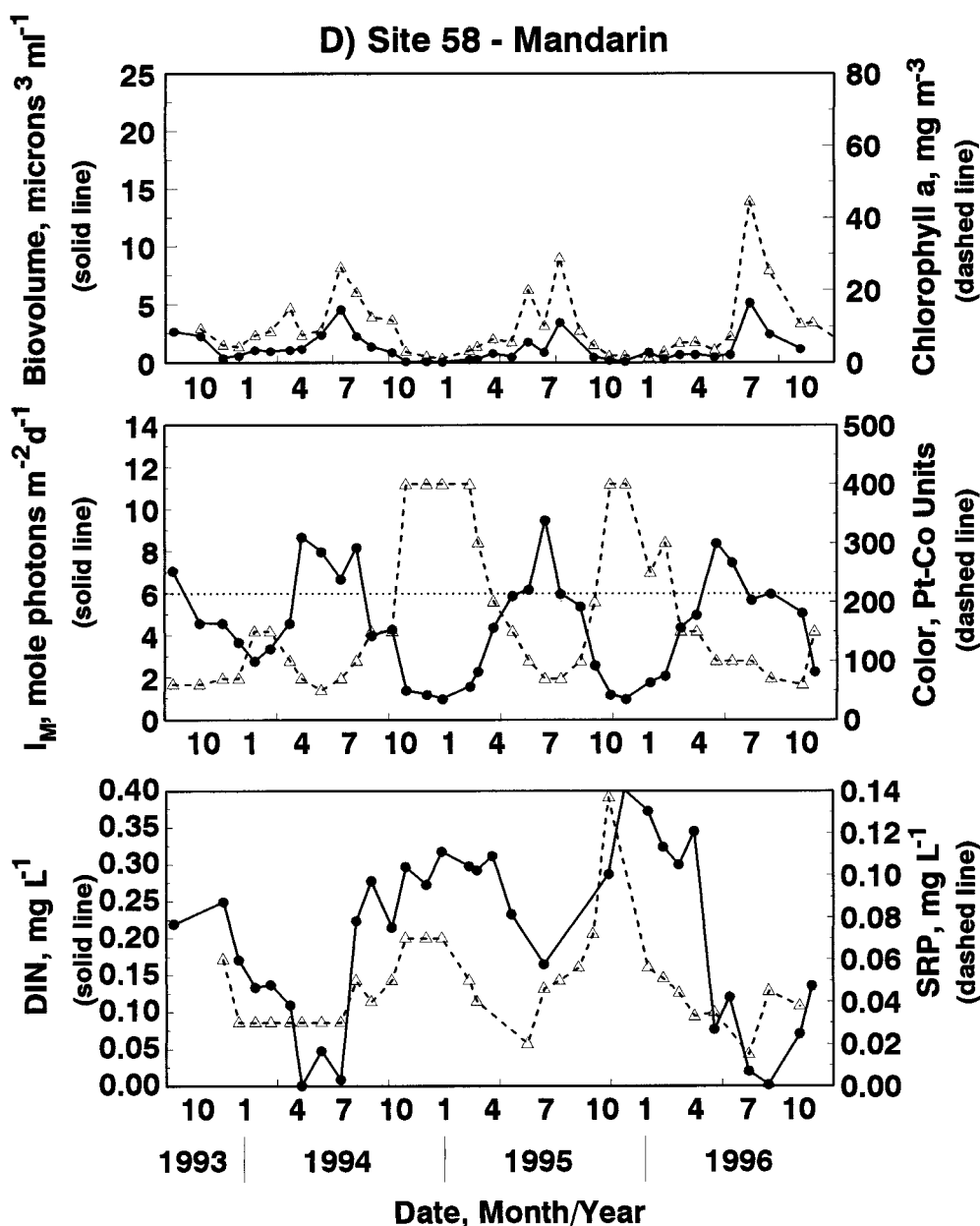


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all characteristics of temperate environments, namely, low phytoplankton standing crops in the winter, followed by elevated abundances in the spring and summer. It appears unlikely that the relatively modest seasonal variability in water temperature (i.e., which ranges from 15–20°C in the winter and 30°C in the summer) is the single major factor dictating seasonality of standing crop. The positive correlation between phytoplankton standing crop and light availability, i.e., I_M , suggests that light limitation plays an important role in controlling seasonal and interannual patterns of phytoplankton standing crops in the lower St. Johns River.

The two primary factors that control temporal changes in light availability in the lower St. Johns River are incident irradiance and color. In addition to the twofold difference

between incident solar irradiance in the summer and winter, winter is also the season of highest color, while summer is the season of lowest color. Between incident irradiance and color, the latter plays a more important role in both seasonal and interannual variation of I_M . This is illustrated by the fact that seasonal differences in incidence irradiance in the St. Johns River account for only a 2.5-fold change in I_M , but up to seven fold changes were observed between summer and winter in our study (i.e., at any given site). In keeping with the proposed role of light availability in controlling temporal patterns of phytoplankton abundance, standing crops were higher in the fall and winter of the first year than in the same seasons in subsequent years of the project. The low color values, and correspondingly high I_M values observed in the

Table 1. Spatial variation of mean chlorophyll *a*/phytoplankton biovolume ratio (pg mm^{-3}) between years and season. Four sites are shown; Jacksonville (Site 40), Federal Point (Site 113), Buffalo Bluff (Site 144) and Lake George (Site 173). Annual means are based on September–August monthly values. Seasonal means are based on monthly values for winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

	Site 40	Site 113	Site 144	Site 173
Year				
1993–94	8.6	3.9	3.6	4.0
1994–95	14.7	8.2	9.1	8.4
1995–96	12.5	7.6	7.1	9.8
Season				
Winter	15.2	7.8	6.3	10.0
Spring	11.3	5.3	6.1	5.1
Summer	9.7	5.6	5.6	5.3
Fall	11.2	7.8	8.0	8.7

first year reflect the low rainfall experienced in the St. Johns River watershed during this period of time.

The impact of color on light availability is heightened by the fact that both the quantity and quality of light are affected. The rapid extinction of light in the blue-green region of the visible light spectrum by organic stain represents a significant loss of photosynthetic potential based on differential elimination of major parts of the absorption maxima for photosynthetically active chlorophyll and carotenoid pigments (Kirk 1994). This fact may help to explain the observed importance of blue-green algae (i.e., cyanobacteria) in the St. Johns River (Cichra and Phlips unpubl. data), since these algae are characterized by the presence of photosynthetically active phycobiliprotein pigments that absorb light in the yellow-red region of the spectrum. Some species of blue-green algae are also distinguished by their ability to maintain an elevated position in the water column through regulation of buoyancy (Reynolds 1984), an ability that provides an advantage for these species in terms of light availability. Blooms of blue-green algae are a common feature of the lower St. Johns River (Cichra and Phlips unpub. data).

In addition to the apparent empirical relationships between light availability and phytoplankton standing crops in the St. Johns River, there is physiological evidence for light limitation of phytoplankton standing crop. The concentration of Chl *a* in phytoplankton cells is known to reflect their light history. Low light conditions can lead to significantly elevated concentrations of chlorophyll per unit cell biovolume (Kirk 1994; Phlips et al. 1995*b*; 1997). In this study, values for Chl *a*/phytoplankton biovolume ranged from 3 to 20. The ratios generally increased from the Palatka-Picolota reach to the Picolata-Jacksonville reach (Table 1) and were particularly high during periods of high water color (i.e., the second and third years of this study). The significant correlation between of pigment to biovolume ratios and I_M (Pearson Correlation Coefficient of -0.58 , $P < 0.0001$, $n = 151$) provide additional support for the importance of light limitation.

Other factors that may control phytoplankton standing crops—So far, we have focused attention on light availabil-

ity as a limiting factor for phytoplankton standing crops. However, there are clearly other factors that warrant consideration. Principal among these factors are nutrient availability, hydrodynamic characteristics (e.g., flushing rates) and grazing. In aquatic ecosystems where water residence time is sufficient to allow for the accumulation of significant phytoplankton biomass, like the St. Johns River, one of the factors most commonly used to explain both spatial and temporal patterns of phytoplankton abundance is nutrient availability. Many of the major tributaries entering the St. Johns River are nutrient-rich, which helps to explain the generally high concentrations of inorganic nitrogen and phosphorus in the river. The nutrients entering the lower St. Johns River through these tributaries are partially attributable to extensive agricultural activities in the watershed (Hendrickson and Konwinski 1998). Our observations confirm that bloom concentrations of algae occur regularly in the river, particularly during periods of low water color, during which light limitation is relaxed. Even in regions of the river where phytoplankton standing crops are typically low (i.e., Picolata-Jacksonville reach), bloom concentrations of algae appear episodically, most commonly in mid-summer (Phlips pers. comm.), when light availability is at a maximum. It remains to be seen what percentage of these blooms represent the autochthonous production and the inflows from algae laden regions like Lake George and Doctors Lake. As noted by Lewis (1988) in the Orinoco River of Brazil, the algal inocula contributed by tributaries can have a significant impact on the character of the phytoplankton community in the mainstem of a river.

To further examine the potential for nutrient limitation of phytoplankton standing crops in the St. Johns River it is useful to examine the relationship between bioavailable nutrient concentrations and phytoplankton standing crops. In general, there is an inverse relationship between the two, that can be seen in the empirical data (Fig. 3) and the results of correlation analyses (i.e., Pearson Correlation Coefficients: 1. Phytoplankton biovolume X DIN, -0.56 , $P < 0.0001$, $n = 348$; 2. Phytoplankton biovolume X SRP, -0.53 , $P < 0.0001$, $n = 386$). It is probable that these relationships reflect a draw-down of dissolved inorganic nitrogen and reactive phosphorus concentrations by phytoplankton standing crops. However, temporal and spatial variations in phytoplankton standing crops cannot be easily explained using nutrient availability as the principal limiting factor. From a temporal perspective, this is reflected in the observed inter-annual variations in phytoplankton standing crop and inorganic nutrients. During the low rainfall year of our sampling period (i.e., 1993/94) inorganic nitrogen and phosphorus concentrations were exceptionally low while phytoplankton standing crops were exceptionally high. One explanation for this relationship is the exceptionally high light availability observed during the 1993/94 period, a consequence of low water color. We hypothesize that the potential for nutrient limitation of phytoplankton production is elevated during periods of low color due to elevated primary production, as well as the reduced external loading that may be associated with reduced inflows. Another contributing factor may be reduced flushing rates associated with low rainfall periods. By contrast, the second and third years of our study were

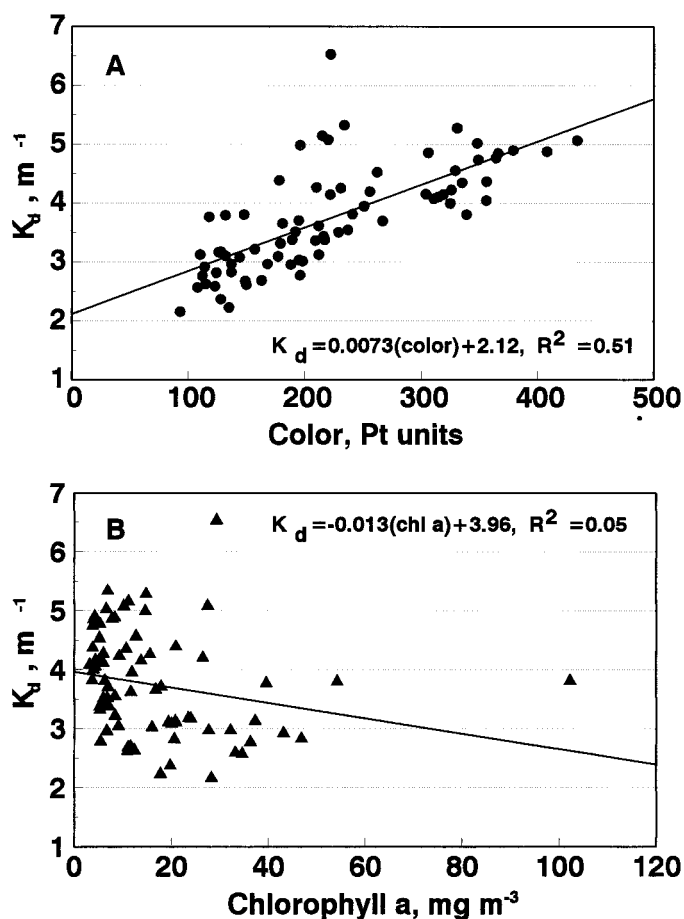


Fig. 4. Linear regression relationships between color (Pt units) and light extinction coefficient, K_d (m^{-1}), (upper figure), and Chl *a* concentration ($\mu g\ L^{-1}$) and K_d (m^{-1}) (lower figure).

characterized by higher inorganic nutrient concentrations and lower phytoplankton standing crops. Although, flushing rates during the latter two years were undoubtedly somewhat higher than in 1993/94 we hypothesize that residence times within the study reach were still long enough to allow for higher than observed standing crops, if it were not for light limitation caused by high color levels in the river.

From a spatial perspective, the disjunction between nutrient availability and phytoplankton standing crop in the St. Johns River can be seen in the lowest part of our sampling reach, Picolata-Jacksonville (Fig. 3). This part of the lower St. Johns River generally exhibits a dramatic decline in phytoplankton abundance. By contrast, concentrations of inorganic nitrogen and reactive phosphorus increase sharply within the same reach of the river. This inverse relationship between inorganic nutrients and phytoplankton abundance indicates the presence of other limiting factors for phytoplankton standing crop, light availability being a strong candidate. Alternatively, it may be argued that tidally-driven saltwater intrusion up the St. Johns River may dilute phytoplankton standing crops and cause osmotic stress for freshwater taxa. However, saline intrusion up the St. Johns River does not appear to extend far enough (i.e., normally less than 60 km) to account for the magnitude and location of the

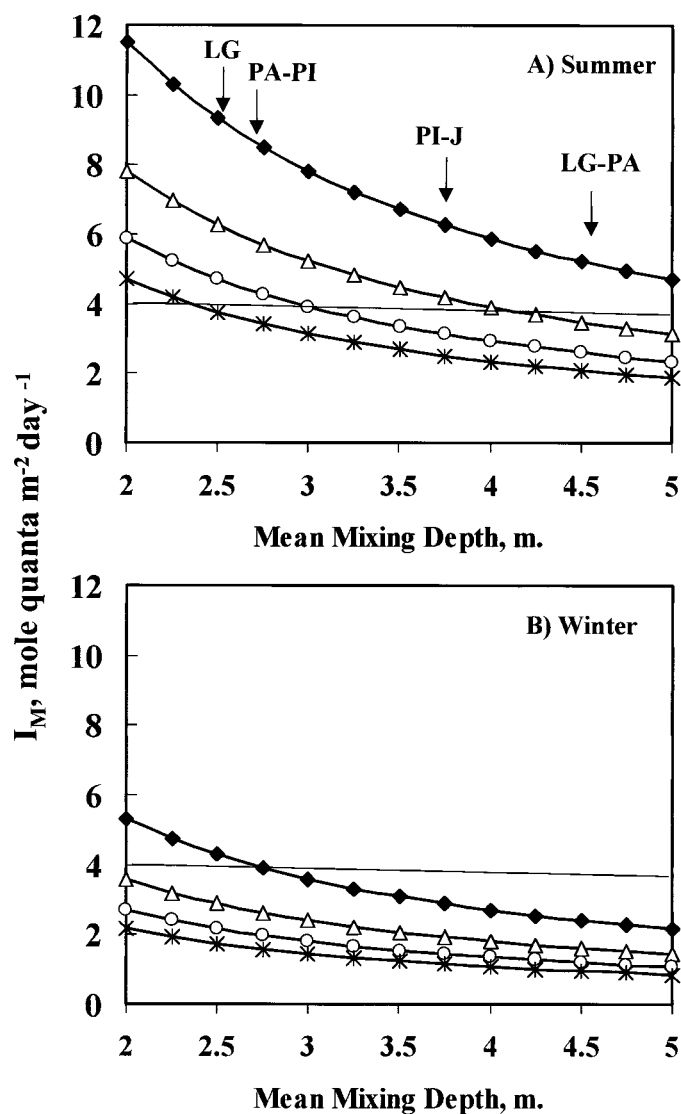


Fig. 5. Modeled relationship between mean mixing depth and I_M (i.e., mean daily light availability in the mixed layer). Model relationships for K_d (m^{-1}) values of 2–5 are shown in the figure for summer (A, upper figure) and winter (B, lower figure) seasons. The mean mixing depths for the four distinct reaches of the river included in this study are indicated by arrows. LG, Lake George; LG-PA, Lake George-Palatka reach; PA-PI, Palatka-Picolata reach; and PI-J, Picolata-Jacksonville reach.

general decline of phytoplankton standing crop and increase in inorganic nutrient concentrations downstream of Picolata (Site 89).

Another consideration in the discussion of spatial patterns in phytoplankton standing crops in the St. Johns River is the relative contribution of tributary inflows to flushing. Water inflows from less productive tributaries can result in dilution of standing crops. For example, the Oklawaha River, that flows into the St. Johns River within the Lake George-Palatka reach, contributes significantly to the volume of the river (i.e., 10–20%, depending on the degree of surface water runoff) and is characterized by low standing crops of phytoplankton (i.e., mean Chl *a* $< 10\ mg\ m^{-3}$). These inflows

undoubtedly contribute to the observed declines in phytoplankton standing crop along the lower St. Johns, but the magnitude of the declines appear to be too large to be explained by dilution alone (i.e., reaching more than 50% in the Lake George-Palatka reach and over 90% by the Picolata- Jacksonville reach), pointing again to a possible role for spatial patterns of light availability.

To this point, the emphasis of our discussion has been on physical and chemical factors that may control phytoplankton abundance in the St. Johns River, but mechanisms of top-down control can not be ignored. Spatial and temporal variations in grazing pressure may be involved in the regulation of phytoplankton standing crop. The freshwater reaches of the St. Johns River are dominated by small-celled zooplankton, principally rotifers (Cichra and Phlips unpub. data). The abundance of rotifers generally mimics the abundance of phytoplankton. However, major increases in rotifer abundance do not appear to coincide with concomitant declines in phytoplankton standing crops, rather the two appear to increase and decrease in consort. This pattern indicates that top-down mechanisms of phytoplankton loss may not be strong enough to account for the observed patterns of phytoplankton abundance. However, these strictly empirical observations are not by themselves sufficient to disregard the potential role of grazing in phytoplankton dynamics in the lower St. Johns River.

Conclusions

Blackwater rivers exhibit a number of important ecological characteristics not shared by other river types. The uniqueness of these ecosystems is in many ways related to the presence of high levels of humic and fulvic substances, that are the major contributors to color in blackwater ecosystems like the St. Johns River. A considerable body of literature exists on the impact of dissolved organic compounds on carbon cycling and heterotrophic metabolism in blackwater rivers. In this study, we examined a less well-described aspect of blackwater ecosystems, namely the impact of color on light availability for phytoplankton production. Our results indicate that temporal variations in light availability in the lower St. Johns River are strongly linked to changes in color and to a lesser degree incident light levels. These temporal changes in light availability are in turn correlated to temporal patterns of phytoplankton standing crops. Similarly, spatial patterns of river basin morphology, specifically mean depth, affect spatial patterns of light availability along the river, which in turn are correlated to spatial patterns of phytoplankton standing crops. Introduction of the concept of light limitation to the broader discussion of the factors that can control phytoplankton production, like nutrient availability and water flushing rates, help to explain why the high concentrations of bioavailable nutrients and long residence times found in the St. Johns River do not always support high phytoplankton standing crops. It is clear that light availability is an important component of an overall understanding of the ecological structure and function of the St. Johns River and potentially other blackwater systems.

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