Phytoplankton Development Within Tidal Freshwater Regions of Two Virginia Rivers, U.S.A.

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ABSTRACT
Phytoplankton composition and the range of seasonal patterns of abundance are presented for the tidal freshwater regions in two Virginia rivers based on data accumulated monthly from 1986 through 1999. Diatoms dominated the flora during spring, summer, and fall, whereas, other taxonomic categories were more representative when the river flow rates decreased, allowing for a more stable water system and increased residency time within this tidal region during summer and early fall. This summer/fall period was associated with increased water temperatures, higher productivity rates and chlorophyll levels, increased total phytoplankton abundance and species diversity. The major components of the summer flora were autotrophic picoplankton, chlorophytes, and cyanobacteria. Mean, maximum, and minimum monthly abundance figures are given for the different phytoplankton categories, and total phytoplankton biomass and abundance, over this 13-year period. Although one station showed considerable influx of oligohaline water into its tidal freshwater region during sampling, no significant relationships were associated with phytoplankton biomass or productivity to these changing salinities.

Key words: Phytoplankton, Virginia, Rappahannock, Pamunkey, tidal freshwater

INTRODUCTION
Marshall and Burchardt, 1998, have described the tidal freshwater region as a unique component of a river system. It is daily influenced by tidal action, yet, the location of this region in a river will move upstream or downstream, depending upon daily or seasonal changes in the occurrence and duration of rainfall, or due to various hydrodynamic events that would influence tidal amplification and flow within the river. The tidal freshwater is defined as the region within a river possessing daily tidal movements bordered upstream by freshwater (<0.5 ppt) lacking a tidal response, and downstream by tidal waters of greater salinity. This is the tidal oligohaline region that is characterized by salinities 0.5 to 5.0 ppt. The algae entering the tidal fresh region upstream are dominated by chlorophytes, diatoms, and cyanobacteria in contrast to downstream flora (e.g. in oligohaline and mesohaline regions) where estuarine diatoms and dinoflagellates are the dominant taxa (Haertel et al., 1969; Forester, 1973; Jackson et al., 1987; Marshall and Alden, 1990). The tidal freshwater region may also contain a small percentage of estuarine species. These are introduced from sub-pycnocline waters advancing upstream during periods of low river discharge and when tidal
movement advances farther upstream into normally tidal freshwater regions (Marshall and Burchardt, 1998). Farrell, 1994 and Schmidt, 1994, have associated increased diatom abundance with increased river discharge common during spring months. Marshall and Burchardt, 1998, reported peak diatom development occurred in the tidal freshwater James River (Virginia) during periods of increased river discharge, with chlorophytes, cyanobacteria, autotrophic picoplankton, and euglenophytes having greater abundance during summer and periods of more stable water conditions. This study reports on the phytoplankton populations and water quality of tidal freshwater stations in the Pamunkey River and Rappahannock River, both located in southeast Virginia, U.S.A.

The Rappahannock River (ca. 34 km in length) is a major tributary of the Chesapeake Bay located in the eastern coastal plain of Virginia. The river flows southeasterly through predominantly forest, crop-land, and pasture before entering Chesapeake Bay. The Pamunkey River (ca. 96 km long), is also located in Virginia, just south of the Rappahannock River, flowing southeasterly through mostly forest and land used in agriculture, or for raising live stock. The river terminates at its confluence with the Mattaponi River, forming the York River that continues parallel to the Rappahannock River before entering the Chesapeake Bay. The climate in this region is moderate with an average annual temperature ca. 14°C and average rainfall ca. 106-116 cm.

Previous phytoplankton studies in the Pamunkey/York and Rappahannock rivers include those by Marshall and Alden, 1990; Marshall and Affronti, 1992; Marshall and Nesius, 1993; and Marshall and Burchardt, 2004. Their results identify the characteristic species composition and abundance in these rivers. Spring, summer, and fall productivity and abundance maxima were described in relation to dominant flora, with the autotrophic picoplankters being a major component and contributor to productivity during summer (Marshall and Nesius, 1993). Downstream studies in the York River section are mainly in the lower reach of the river where summer dinoflagellate blooms are common (Mackierman, 1968; Zubkoff et al., 1979). Relationships of phytoplankton distribution and stratification to tidal cycles in the York River are discussed by Haas et al., 1981 and Ducklow, 1982.

The objectives of this study are to identify the seasonal developmental patterns of the phytoplankton composition within the tidal freshwater regions of two rivers. Using a long-term data base the annual biomass patterns are described to indicate the range of population fluctuation that may occur within these systems. Additional characteristics and environmental relationships between the phytoplankton community and several physical and chemical factors associated with these rivers are also presented.

METHODS

Monthly water samples were taken at the tidal freshwater stations in the Rappahannock River (TF3.3, 38° 01' 07'' N; 76° 54' 30'' W) and the Pamunkey River (TF4.2, 37° 34' 47'' N; 77° 01' 19'' W) from July 1986 through December 1999 (13.5 years) (Figure 1). The mean depths at these stations were ca.6.8 m and ca.8.9 m respectively (Figure 1). The mean depths at these stations were ca.6.8 m and ca.8.9 m respectively

Partial water samples were drawn off and fixed with Lugol’s solution. These samples were analyzed using a modified Utermöhl technique following a series of settling and siphoning steps over time to produce ca. 40 mL, concentrate of the original sample for subsequent microscopic analysis (Marshall and Alden, 1990). Identification and cell abundance for each sample were based on a minimum microscope cell count of 200, using a minimum of 10 random fields examined at 115X and 500X, plus including other species observed by scanning the entire counting chamber at 125X. An additional 24 samples from 1998-1999 at these stations were examined for further species identification.

The autotrophic picoplankton cells were identified using epifluorescence microscopy as described in Marshall, 1995. Also determined were 13C productivity rates, beginning in July 1989, using protocols described by Marshall and Nesius, 1993. Biomass was determined from cell volume measurements made for the different species and transferred to cell carbon according to Smayda, 1978. The Margalef Diversity Index was used regarding species diversity. River water discharge rates were provided by the U.S. Geological Survey from locations near station TF3.3 (38°19'20'' N, 76°54'30'' W), and station TF4.2 (37°46'03''N, 77°01'19'' W) in the Pamunkey River, Virginia.
FIGURE 2. Monthly mean discharge rates (1986-1999) for stations adjacent to stations TF3.3 in the Rappahannock River and TF4.2 in the Pamunkey River

Chesapeake Bay Monitoring Program. These included analysis of water taken on station for total nitrogen (TN), total phosphorus (TP), total suspended solids (TSS), and dissolved oxygen. Seasonal references are defined as winter including the months of December, January, and February, followed by the sequential 3-month periods for spring, summer, and fall. A Student T-test was used to determine distribution relationships of the phytoplankton and productivity to salinity differences noted during the sampling period at the Rappahannock River station TF3.3.

RESULTS

The drainage area above the two sampling stations is 4,133 km² and 1,739 km² for the Rappahannock and Pamunkey Rivers respectively, with the monthly discharge pattern similar at both sites. Peak water flow at these stations was from winter through early summer (December-June), with decreased flow in mid-summer that continued into early fall (July-September), after which flow increased, from mid-fall into the winter months (Figure 2). The summer minimum and winter-spring maximum of the mean monthly rates of flow differed at the two stations, ranging from 25.8 m³ sec⁻¹ (912 ft³ sec⁻¹) in July to 76.7 m³ sec⁻¹ (2,711 ft³ sec⁻¹) in March for the Rappahannock River, and from 12.4 m³ sec⁻¹ (438 ft³ sec⁻¹) in August to 52.7 m³ sec⁻¹ (1,863 ft³ sec⁻¹) in February for the Pamunkey River. The major annual influence to these seasonal flow patterns was the amount of rainfall within these two river watersheds. U.S. Geological Survey records of flow rates began in 1951 and are the basis for estimating average and extreme periods of monthly and annual mean flow. Those annual rates that were within the 25 to 75 percentile of this data set were considered average, or normal. If the annual rate falls below the 25 percentile it would be considered a “dry” year, whereas, flow rates above the 75 percentile would be classified as “wet” years. During this study the annual flow into these rivers varied greatly. There were 5 “wet” and 5 “dry” years, and 3 years where the flow may be considered “normal”, or “average”. As these differences in annual rainfall occur, they will have major influence on the horizontal range and dynamics associated with the tidal fresh and various downstream salinity regions of these rivers. Progressing into this study it became evident that salt-water intrusion frequently occurred at TF3.3 in the Rappahannock River. Over the 13 year period, Station TF3.3 had freshwater status (<0.5 ppt) 40.6% of the collection dates, whereas, during 59.4% of the dates the salinity was >0.5 ppt. Tidal freshwater status was associated with periods of increased rainfall and coincided with the spring diatom bloom (e.g. January-May). Periods when salinity intrusion into this area was most common occurred during the summer and fall months (June-October). In contrast, station TF4.2 in the Pamunkey River had freshwater status on 97.7% of the collection dates. Overall, more water flowed through the Rappahannock station, and at a faster rate, than at the Pamunkey station.

Both stations had similar surface water temperature patterns reaching highs of ca. 28 °C in July, with lowest mean monthly temperatures occurring in February at TF3.3 (3.6 °C) and in January at TF4.2 (4.8 °C). The dissolved oxygen concentrations were inversely related to the water temperature with lowest values during summer and highest in winter. The mean monthly range was from 6.5 in July to 12.2 mg L⁻¹ at TF3.3 in February, and 4.7 in August to 11.8 mg L⁻¹ in February at TF4.2. Monthly periods of peak total suspended solids (TSS) varied, with greatest loads during periods of high flow in spring (Figure 3). At station TF3.3, TSS were consistently higher than at TF4.2, ranging from 20.6 mg L⁻¹ in late summer (August) to 51.2 mg L⁻¹, in late winter (February). The TSS at station TF4.2 ranged from mean monthly values of 13.5 (Sept.) to 18.9 mg L⁻¹ (Dec.), showing a rather stable pattern throughout the seasons. The TSS increased gradually from summer into fall, reaching highest concentrations from early winter through spring. Maximum records of 140 and 168 mg L⁻¹ at TF3.3 occurred in January and May respectively. Mean monthly Secchi readings ranged from 0.31 m (February-April) to 0.64 m (September) at TF3.3, and from 0.51 m (January) to 0.82 m (September) at TF4.2. The annual monthly means for TF3.3 and TF4.2 were 0.45 m and 0.70 m respectively. These results indicated an association between increased water flow to higher TSS concentrations and reduced Secchi readings at TF3.3, in contrast to the reverse relationships during periods of reduced flow during summer. However, this relationship was less clear at TF4.2, where a lower and more consistent presence of TSS was recorded. More suspended solids were carried in the Rappahannock River, with the mean and range of Secchi readings less than in the Pamunkey River.

There were differences in the total nitrogen (TN) patterns at the two stations (Figure 3). At TF3.3, peak levels (monthly means) occurred in early spring (1.32 mg L⁻¹, March), decreasing into the summer and fall months to a low of 0.73 mg L⁻¹ (August) to increase through late fall and winter to the spring highs. Maximum levels occurred from mid-winter through mid-spring. The mean range at TF4.2 owed less variability, increasing from 0.69 mg L⁻¹ (November) to 0.88 mg L⁻¹ (June), resulting in the mean total nitrogen being higher at TF3.3 than at TF4.2. The mean monthly total phosphorus (TP) at TF3.3 ranged between 0.06 and 0.12 mg L⁻¹ throughout the seasons, showing a decrease from late spring into summer, before rising again in winter (Figure 3). At TF4.2, the monthly means ranged from 0.06 mg L⁻¹ in the fall (October), to a spring (March) high of 0.12 mg L⁻¹. Maximum TP occurred during winter-spring at TF3.3 and in summer at TF4.2 (Figure 3). Both stations had peaks that occurred in early spring, mid-summer, and fall, with the highest mean monthly means at TF3.3. The mean
the past ranges recorded for these categories. Variability also occurred over this time

**Chlorophyll a** increased into summer from a winter low, with concentrations greater at TF3.3 than at TF4.2 (Figure 4). At TF3.3, the monthly mean ranged from 2.9 µg L\(^{-1}\) (January) to 13.9 µg L\(^{-1}\) (August). There was generally a late spring (May) development, a slight decrease in early summer, then highs from mid-summer through fall. At TF4.2, there was chlorophyll a increase during summer, with peaks in July and August (9.27, 8.37 µg L\(^{-1}\)), to a January low (2.09 µg L\(^{-1}\)). Also present were periods of maximum chlorophyll a concentrations from spring through fall at both stations. The mean productivity rates for both stations were lowest during mid-winter, then gradually increased to peaks during late spring, summer, and early fall, before declining into winter (Figure 5). The higher rates were consistently recorded at station TF3.3 and ranged from 12.2 mg cm\(^{-3}\) h\(^{-1}\) (Dec.) to 156.9 mg cm\(^{-3}\) h\(^{-1}\) (May). Increased productivity extended from April through August. At TF4.2, productivity ranged from 5.2 mg cm\(^{-3}\) h\(^{-1}\) (Dec.) to highs of 43.1 and 46.5 mg cm\(^{-3}\) h\(^{-1}\), for July and August respectively. This pattern was similar to seasonal chlorophyll a concentration differences between the two river stations with highest mean rates of productivity during the summer months. A total of 268 phytoplankton taxa were identified at these two stations (Marshall and Burchardt, 2004). There were 208 and 232 phytoplankton taxa represented at the Rappahannock River and Pamunkey stations respectively. Sixty one percent of the taxa were present at both stations, with the general composition of the dominant species similar. The major difference in composition was the estuarine taxa at the Rappahannock station during periods (summer/early fall) of increased salinity and upstream intrusion of tidal water from the oligohaline region. Collectively for both stations, there were 133 Bacillariophyceae, 63 Chlorophyceae, 31 Cyanobacteria (cyanoprokaryotes), 10 Dinophyceae, 11 Euglenophyceae, 6 Xanthophyceae, 5 Cryptophyceae, and 9 Chrysophyceae. The autotrophic picoplankton was identified as a separate and composite group from the above categories and consisted predominantly of single celled cyanobacteria. Figures 6 and 7 show the monthly maximum and minimum records, and means for the major phylogenetic categories. The two extremes indicated the past ranges recorded for these categories. Variability also occurred over this time period in taxon representation in each water sample analyzed with maximum representation of taxa per water sample in the summer months and least in winter (e.g. at TF3.3 these totals were 73 and 26 taxa, and at TF4.2, 52 and 22 taxa). The Margalef Diversity Index maxima during this period ranged from 2.3 (January) to 4.0 (July) at TF4.2, with the mean monthly range from 1.6 (March) to 2.4 (August). The diversity maxima at TF3.3 ranged from 2.3 (January) to 4.0 (July), with monthly means from 1.6 (March) to 3.4 (August). Diversity was lowest at both stations in late winter/early spring when flow in the rivers was greatest, increasing into summer during periods of reduced flow rates.

In presenting total phytoplankton abundance and total phytoplankton biomass at TF3.3 and TF4.2, 1986-1999, indicating mean (solid line), maximum (dotted line), and minimum (dot-dash line) records.

**FIGURE 3** Monthly concentrations for chlorophyll a, total phytoplankton abundance, and total phytoplankton biomass at TF3.3 and TF4.2, 1986-1999, indicating mean (solid line), maximum (dotted line), and minimum (dot-dash line) records.
There existed considerable fluctuation in the year-to-year patterns that were influenced by flow through the system and the initiation time for diatom development to occur. There were frequent salinity differences occurring in the tidal freshwater station (TF3.3) that might have contributed to the diatom community. The historic maxima during spring, summer, and fall that occurred at both stations were associated with the diatoms. At TF4.2, the biomass ranged from 91 to 818 x 10^6 µgcm^3 (December, April), with a maximum record of 4,902 x 10^6 µgcm^3 in July. Since there were frequent salinity differences occurring in the tidal freshwater station (TF3.3) in the Rappahannock River, student T-tests were run to determine the degree of phytoplankton/salinity relationships present. The results indicated there were no significant differences between total phytoplankton biomass (p = 0.236), diatom biomass (p = 0.116), cyanobacteria biomass (p = 0.399), or productivity (p = 0.823), to salinity values <0.5 and those >0.5 ppt. at this location.

### Figure 5: Mean monthly carbon productivity rates for stations TF3.3 and TF4.2 from July 1989 to December 1999.

**1. Bacillariophyceae:**

The diatoms had mean monthly concentration peaks occurring during winter/spring, summer, and fall at both stations, with greater abundance recorded in the Rappahannock River (Figure 6). Diatoms represented the seasonally dominant flora at both stations. Mean monthly minimum and maximum concentrations were 3.2 to 11.4 x 10^6 cells L^{-1} (December, May) at TF3.3, and 1.0 to 3.5 x 10^6 cells L^{-1} (December, July) at TF4.2. The recorded minimum and maximum concentrations over this period were 0.5 and 53.1 x 10^6 cells L^{-1} at TF3.3 (October, January), and 0.007 to 28.2 x 10^6 cells L^{-1} at TF4.2 (October, April). The diatoms had a diverse assemblage of taxa that included the major producer of the spring diatom pulse, Skeletonema potamos, and an abundance of planktonic centrics and benthic pennates. Most common were Asterionella formosa, Aulacoseira granulata, A. granulata v. angustissima, A. distans, A. varians, Cyclotella meneghiniana, C. striata, Navicula cryptcephala, N. radiosa, Nitzschia acicularis, Surirella ovata, and a variety of other pennates and centrics <20 microns in size. This composition and dominant freshwater taxa were similar in both rivers. However, the summer/fall flora at TF3.3 contained ample representations of estuarine species, specifically Skeletonema costatum. The mean abundance for the diatoms was moderate within their maximum and minimum concentrations. However, there existed considerable fluctuation in the year-to-year patterns that were influenced by flow through the system and the initiation time for diatom development to occur. The maxima depicted here also illustrates the range of the potential growth for this community. The historic maxima during spring, summer, and fall that occurred at both stations greatly exceeded the mean concentrations.
2. Cyanobacteria:
At both stations, the predominant development of the cyanobacteria (cyanoprokaryotes) occurred from mid-summer into mid-fall, then decreased in late fall and winter (Figure 6). However, there were sporadic seasonal highs throughout the year with the mean monthly range from 1.2 to 22.2 x 10^6 cells L^-1 (April, July) at TF 3.3, and at TF4.2, from 0.2 to 6.3 x 10^6 cells L^-1 (December, July). Maxima at the two stations were 95.5 and 29.2 x 10^6 cells L^-1 respectively for TF3.3 and TF4.2, with both occurring in July. Several Clamensous taxa were common during winter and early spring. These included Oscillatoria limnetica, O. granulata, O. irrigua, O. pseudominima, Nodularia spumigena, L. litorea, and Lyngbya costata. Noted throughout the year was Dactylococcopsis rhipidioides. This species, plus D. rhipidioides v. falciiformis, O. granulata, O. angustissima, Microcystis aeruginosa, M. incerta, and Merismopedia marssonii were common representatives of the summer/early fall flora.

3. Chlorophyceae
The chlorophytes were among the most common taxa in the tidal freshwater region. They consisted of a diverse group of single cell, or small colonial forms in the Pamunkey (57 taxa) and Rappahannock Rivers (52 taxa). Seasonal maxima were greater at the Rappahannock River station, and developmental patterns also differed in the two rivers (Figure 6). At TF3.3, several seasonal peaks occurred in late spring, mid-summer, and early fall. The mean monthly range of cells varied from 0.5 to 2.7 x 10^6 cells L^-1 (April, July), with a maximum of 19.6 x 10^6 cells L^-1 in July. At TF4.2 lower concentrations prevailed, with the mean monthly abundance from 0.08 to 2.2 x 10^6 cells L^-1 (March, July), with a maximum of 11.0 x 10^6 cells L^-1 for September. At TF4.2 there was a single development during summer, rather than several peak periods.
present at TF3.3. Taxa most prevalent included a diverse group of Scenedesmus spp., Ankistrodesmus falcatus, A. falcatus v. fluviatile, Pediastrum duplex, plus several Crucigenia spp. and desmids. Scenedesmus quadricauda was recorded year round, but also common were S. bijuga, S. dimorphus, and S. acuminatus, with the filamentous Ulvophyta variabilis also abundant. The development of these taxa favored the less turbulent conditions in the rivers between the spring rains and the fall-winter period.

4. Dinophyceae:

Dinoflagellates were not abundant at these stations. Ten species common for this region were recorded and included the freshwater Peridinium cinctum, P. wisconsinense and Ceratium hirundinella, plus several other characteristic of the downstream estuarine waters, e.g. Heterocapsa rotundata, H. triqueta, and Prorocentrum minimum (Marshall and Affronti 1992). There were differences in their abundance, presence, and seasonal patterns at the two stations (Figure 7). TF3.3 contained the higher mean concentrations, exhibiting abundance peaks in spring, summer, and late fall, with lowest concentrations during the winter months when freshwater status was more common. The range was from 0.03 to 0.25 x 10^{6} cells L^{-1} (February, April), with a maximum abundance of 3.3 x 10^{6} cells L^{-1} for April. At TF4.2 the cell maxima occurred in early summer, with a maximum count of 1.5 x 10^{6} cells L^{-1} in June, and monthly ranges from 0.004 to 0.14 x 10^{6} cells L^{-1} (September, June), with late winter and mid-spring lows prevailing. These taxa were absent in numerous samples throughout the year and most common at TF3.3.

5. Cryptophyceae:

Although represented by a modest number (5) of species, this was a ubiquitous group throughout the year. There were seasonal fluctuations of development at both stations, with greater abundance at TF3.3 (Figure7). Mean monthly concentrations ranged from 0.7 to 1.8 x 10^{6} cells L^{-1}, and 0.3 to 1.2 x 10^{6} cells L^{-1} at TF3.3 and TF4.2 respectively. Maximum records for these two stations were 9.4 and 3.4 x 10^{6} cells L^{-1} in July and November for TF3.3 and TF4.2. The cryptophytes have been noted as a common background population to other flora within Virginia tributaries (Marshall and Alden 1990). The species recorded were Cryptomonas erosa, C. marsonni, C. ovata, C. reflexa, and Rhodomonas minutia. The major cryptomonad development was from early spring through mid-fall, and then decreased in early winter to a mid-winter low.

6. Autotrophic picoplankton:

Ubiquitous throughout the year, this category consisted of mainly isolated single cells, or in those small doublets of cells. Cells in this category were less than 2.0 microns in size and did not include species reported in the other categories. They consisted of mainly cyanobacteria and less abundant chlorophytes, with other eucaryotes occasionally present, but not dominant. Maximum concentrations occurred during the summer months (July-September), but these high numbers frequently extended into early fall and were similar to patterns described in these rivers and Chesapeake Bay (Marshall and Affronti, 1992; Marshall, 1995). The mean monthly ranges for TF3.3 were from 0.4 x 10^{6} cells L^{-1} (March, August), and for TF4.2 from 2.2 to 128.2 x 10^{6} cells L^{-1} (February, June), with maxima for these two stations at 870 and 537 x 10^{6} cells L^{-1} in summer and early fall. The patterns of development favored the less turbulent conditions in the rivers between the spring rains and the fall-winter period.
the lower temperatures of winter. At TF4.2, the greatest concentrations of chlorophyll were in summer, along with increased levels of both TN and TP. The mean TN:TP ratios increased during greater water flow within the rivers, when additional nitrogen input occurred, and followed by increased diatom development. The decreased flow of summer was associated with increased residency time, lower levels of TSS, deeper Secchi readings, increased picoplankton, increased productivity, greater species diversity, greater abundance of chlorophytes and dinoflagellates, plus higher chlorophyll concentrations. This was in contrast to the reverse status of these variables associated with the increased flow rates during the winter/spring months.

In contrasting the flora at these stations, the Pamunkey River contained a greater diversity of diatoms, cyanobacteria, chlorophytes, crytophytes, and euglenophytes. Of the 268 taxa identified at these two stations, 232 (86.6%) were recorded in the Pamunkey River, with 208 (77.6%) in the Rappahannock River, and there were 61.9% of the taxa common to both stations. Differences in composition were mainly noted in three algal categories (diatoms, dinoflagellates, chlorophytes), with additional eusturiine species recorded at TF3.3. There was greater phytoplankton abundance, productivity, and biomass in the Rappahannock TF3.3, which also contained higher TN and TP concentrations, with indications of less light availability than station TF4.2, as indicated by the more shallow Secchi depths recorded.

SUMMARY

The comparison of the tidal freshwater regions of the two closely located river systems indicated both differences and similarities in the abundance, diversity, and development of the phytoplankton populations. These differences, which include the ranges of seasonal and annual development among the various phytoplankton taxa, were a product of the unique combination of conditions in the two rivers (e.g. water quality, light and nutrient availability, seasonal flow rates). These cumulative factors, and others, influenced the floral composition and its seasonal abundance, plus determine the initiation and duration of development among the algal assemblages. These conditions were further influenced by the amount, timing, and duration of river water flow annually, when wet and dry years of water occur within these rivers. Yet, there were similarities in algal composition and dominant species within these rivers, and in their seasonal development transitions that extend beyond local conditions and are characteristic of broader developmental patterns typically associated with phytoplankton in temperate regions.

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LITERATURE CITED


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