Virginia Journal of Science
Volume 43, Number 1A
Spring 1992

Spatial, Seasonal, and Interannual Patterns in the Phytoplankton Communities of a Tidal Freshwater Ecosystem

R. Christian Jones, Department of Biology
George Mason University, Fairfax, VA 22030
Claire Buchanan, Interstate Commission on the
Potomac River Basin, Rockville, MD
Victoria Andrle[1], Department of Biology
George Mason University, Fairfax, VA 22030

ABSTRACT

Phytoplankton were enumerated by species on samples collected on a biweekly to monthly basis over 6 years from 11-13 sites in the tidal freshwater Potomac River. Cell densities were analyzed by analysis of variance examining spatial, seasonal, and interannual variability. Phytoplankton densities were higher in the two embayment areas than in the river mainstem. A nearly exponential increase in phytoplankton was observed from March through August with a rapid decline in September and October. This pattern differed significantly among years resulting in a significant month-year interaction. Differences among years was also significant with the two lowest years correlating with low residence times. Loss processes, particularly flushing, appeared to be generally more important than growth processes in explaining seasonal and interannual variation. Both growth and loss factors contributed to spatial variation. Diatoms were dominant in spring and various cyanobacterial species were most important in summer.

INTRODUCTION

The pelagic zones of tidal freshwater ecosystems provide phytoplankton with a habitat similar to that found in freshwater lakes, large rivers, and reservoirs. During periods of low freshwater inflow and long retention times, tidal freshwater systems may function as lakes with an added component of tidal movement of the water masses. During periods of high freshwater inflow, retention times may be short enough and associated factors such as turbidity high enough that large rivers may provide a better analogy. In some ways perhaps the best analogy is with reservoirs which have variable retention times depending on inflow rate and associated variations in turbidity and nutrient loading (Soballe and Kimmel, 1987).

Tidal freshwater habitats are common along the east coast of North America (Odum et al., 1984). Many of the larger rivers in this area discharge into drowned river valleys which provide a restricted basin in which to collect the freshwater inflow. Mixing with brackish water is restricted to a narrow front some distance seaward of the head of tide. The volume of water collected in the freshwater zone and the size of the resulting tidal freshwater habitat will vary depending on the balance between mixing at the seaward end and freshwater input at the landward

---

[1] Current address: 970 National Center, U.S. Geological Survey, Reston, VA 22092.

end of the basin. Clearly, the size and importance of the tidal freshwater portion of a given river system will vary with basin morphology as well as freshwater input with the latter resulting in significant seasonal variations. The volume of water comprising the tidal freshwater Potomac River varies by a factor of four seasonally from 200 x 10^6 m^3 in early fall to nearly 800 x 10^6 m^3 in late spring as a result of seasonal patterns in freshwater inflow (Lippson et al., 1979).

Phytoplankton communities in tidal freshwater should respond to factors such as light, temperature, nutrients, and hydrologic regime which show marked variation seasonally and may follow different seasonal patterns from one year to the next. In eutrophic freshwater systems previous studies indicate that seasonal maxima generally occur in spring and late summer-early fall (Marshall and Peters, 1989). Sommer et al. (1986) summarize research on the seasonal patterns in abundance in eutrophic lakes. Increased phytoplankton abundance in the spring is correlated with the onset of increased light and abundant nutrients. The decline in phytoplankton abundance in early summer is thought to be related to removal by zooplanktonic grazers and nutrient depletion. In highly eutrophic systems phytoplankton increase again in mid-summer upon relaxation of grazing stress. This summer rebound may not be found in systems where grazing pressure remains strong, summer flushing rates remain high, or nutrient concentrations are low. Eutrophic systems may be characterized in fall by either a distinct peak in abundance or a continuation of the high summer levels. The onset of winter brings low phytoplankton densities due to low light, low temperature, and possibly high flushing.

Interannual variations in climatic, edaphic, and biotic factors may result in substantial differences in seasonal abundance patterns among years. In a nine-year study of a shallow eutrophic lake, Bailey-Watts (1978) found decreasing trends in phytoplankton biomass associated with a decrease in nutrient loading and a shift to a *Daphnia*-dominated zooplankton community capable of more efficient grazing. Davis (1964) reported that spring and fall peaks in phytoplankton cell density increased in magnitude as nutrient loading increased in the early half of the 20th century in Lake Erie. By 1962 maximum values had shifted from spring to late summer-early fall. Variations in grazing intensity due to annual variations in herbivore populations or multiyear oscillations in higher trophic levels may also be important in regulating phytoplankton standing crop (Mills and Forney, 1988).

These same factors may result in marked variation spatially within the same system. Marked differences in bathymetry, flushing rates, mixing depths and nutrient loading can occur over rather small spatial scales. Cloern et al. (1983) noted that phytoplankton doubling time was almost 10 times longer in a deep river channel than in an adjacent embayment. Longitudinal gradients in primary production have been noted in a number of reservoirs related to light and nutrient availability (Kimmel et al., 1990).

Species composition of phytoplankton communities also shows seasonal, spatial and interannual variation. Numerous authors have noted the propensity of diatoms to dominate phytoplankton populations in spring, while greens and cyanobacteria are characteristic of summer populations (e.g., Welch, 1980). The affinity of diatoms for spring has been related to lower temperatures, high light levels, vigorous circulation, and abundant nutrients. In highly productive systems successional patterns during the summer growth period often lead to dominance by cyanobacteria (blue-green algae). Cyanobacteria have generally been associated with high temperatures, high pH (and low CO2), nitrogen limitation (Shapiro, 1973), favorable N:P ratios (Smith, 1983), and physically stable conditions (Paerl, 1988). In fall dominance shifts toward diatoms as temperature decreases and turbulence increases. Seasonal variations in grazing pressure and selectivity will also influence the outcome of competition among algal species (Reynolds et al., 1982; Bergquist et al., 1985).

METHODS

Sampling was conducted at 11-13 stations monthly or semimonthly from March through November from 1984 through 1989 (Figure 1). Due to the well-mixed nature of the water column in all seasons, samples were integrated over the entire water depth. Depth-integrated samples were constructed using equal volumes of water collected by submersible bilge pump from near surface (0.3 m), mid-depth, and near bottom (0.3 m above bottom). At water depths less than 1.5 m only near surface and near bottom samples were used. Phytoplankton samples were preserved with acid Lugol's iodine to a final concentration of 1% and stored in brown glass bottles.

Phytoplankton enumeration by taxa was conducted using the inverted microscope-settling chamber method (Lund et al., 1958). At least 100 and normally several hundred cells were counted from each sample. Cells were identified to species where possible. References used for identification included Prescott (1962), Weber (1971), Van Landingham (1982), Butcher (1967), Anton and Duthie (1981), Whitford and Schumacher (1973), Smith (1950), and Huber-Pestalozz (1938, 1941, 1950).

Initial examination of the phytoplankton data indicated that stations could be grouped spatially into three regions: Gunston Cove (Stations 4, 5, 6, 7, 10, and 11), Potomac Mainstem (Stations 8, 9, 12, 14, 16, and 18), and Dogue Creek (Station 15). Samples were further classified by month and year for analysis of total phytoplankton density by ANOVA. The classification by month, year, and region resulted in some classes containing only one replicate while others had as many as 13 when there were two sampling dates in a month. For those with 2 or more replicates, mean and variance were calculated with both untransformed and log-transformed data. Log transformation was found to be necessary to stablilize the variance and total phytoplankton density was log-transformed for all statistical procedures. The pooled variance using all the log-transformed (Base 10) replicated samples was 0.105.

Patterns of numerical dominance in phytoplankton populations were analyzed by compiling a table of dominant algal taxa for each month of the year for each of the three regions of the study area. On each date average abundance was computed for each taxon for each region. When one taxon clearly dominated, it was used as the sole dominant. If other taxa were within 10% of the most numerous taxon, all were considered co-dominant. The dominant taxon for each unique combination of month, year, and region was given a value of 1. If several taxa were co-dominant, then the value was divided equally among them.

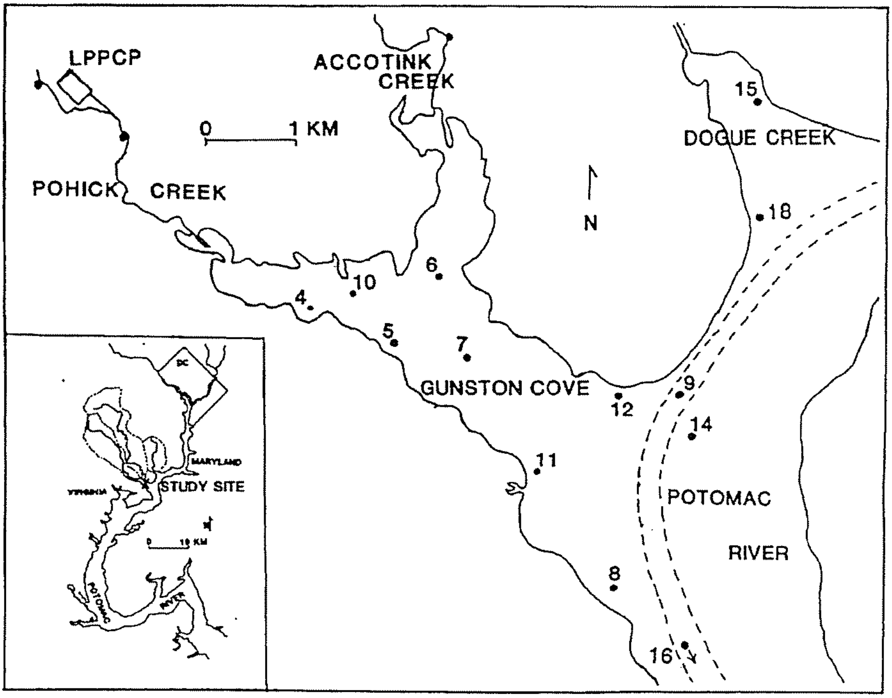

FIGURE 1. Study site showing sample locations.

RESULTS

A simple three-way analysis of variance model using the mean values for each combination of month, year, and region resulted in highly significant main effects ($P < 0.001$) for each of these factors. The model explained 78.5% of the data and the error mean square was very close to the variance determined from replicate determinations (Table 1). The grand mean over all combinations of year, month, and region was 53,580 cells/mL.

This model, which assumes no interaction between the three factors, can be examined by looking at mean values for each factor separately. A steady, exponential increase in average phytoplankton density with month was observed from March through August with a decline in September and October (Figure 2a). Phytoplankton densities were above the grand mean from June through September and below the grand mean during the spring and October. Cove stations averaged substantially above, the river substantially below and Dogue very close to the grand mean (Figure 2b). An examination of the effect of year showed that 1984 and 1989 had densities averaging below the grand mean while 1985-88 averaged above the grand mean (Figure 2c).

Although the model appeared to explain most of the variance in the data, it seemed unlikely that month, year, and region effects were so consistent that significant interactions would be totally absent. Examination of residuals from the

TABLE 1. Results of Three-way Analysis of Variance Model with Phytoplankton Density (cells/mL, log-transformed) as the response variable.

Source of Variation	Sum of Squares	df	Mean Square	F	P
Year	8.130	5	1.626	16.328	<0.001
Region	7.458	2	3.729	37.445	<0.001
Month	31.413	7	4.488	45.062	<0.001
Error	12.847	129	0.100		

simple three-way ANOVA indicated a substantially greater deviation in some of the residuals than would be expected from a normal distribution. The ANOVA was recalculated adding each of the three two-way interactions in turn to the three main effects. Only the interaction between month and year resulted in a statistically significant F value ($P < 0.001$). In other words, the null hypothesis that the seasonal pattern of phytoplankton density is the same from year to year was rejected. The month-region and year-region interactions were not significant suggesting that patterns of seasonal and interyear variation are similar in all regions differing only in magnitude. The combination of the three main effects and the month-year interaction explained 90.7% of the variance in the data set (Table 2). The residual mean square from this ANOVA was even less than the variance between replicate observations. Examination of residuals from the model revealed no departures from normality.

The differences in seasonal patterns in phytoplankton densities among years are illustrated for cove stations in Figure 3. In most years there was a clear seasonal pattern in density with a steady increase from March through August and a decrease in September and October. However, in 1987 and 1989 major declines in phytoplankton density were observed in April and May, respectively. Note also that the decline in October was much stronger in 1989 than in other years. These and other differences in seasonal density patterns were responsible for the observed interaction of month with year. This figure also depicts the relationship between model predictions and observed values. Note that most observations are within about 0.2 log units of prediction.

Patterns in species numerical dominance were analyzed by month, region, and year. To illustrate overall seasonal patterns, dominance values were summed over region and year for each month (Figure 4). Diatoms were clearly the most frequent spring dominants. Of 36 observations in March and April, 30 were dominanted by diatoms. The two *Microcystis*-dominated samples were in 1984 and may have been the residue of a large summer 1983 bloom in the study area. By June, diatom dominance was usually waning and cyanobacterial genera were becoming more important. *Raphidiopsis* and *Microcystis* were most frequently dominant in summer with *Raphidiopsis* showing a tendency for early summer dominance and *Microcystis* for late summer dominance. *Merismopedia*, an important summer dominant, was clearly the most common fall dominant. *Chroococcus* and *Oscillatoria* exhibited haphazard seasonal dominance patterns.

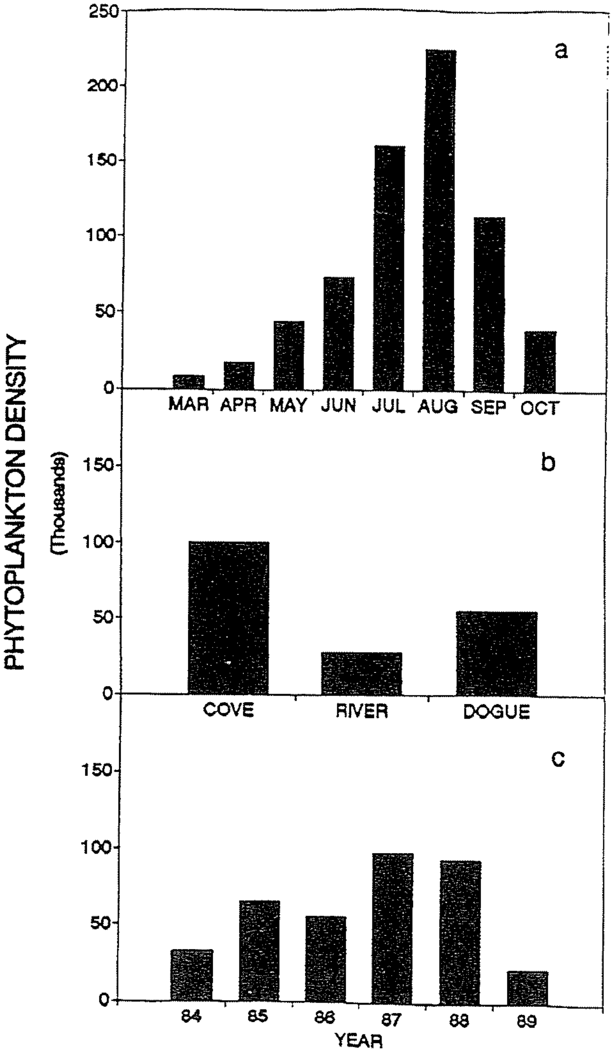

FIGURE 2. (a) Average phytoplankton density (cells/mL) by month. (b) Average phytoplankton density by region. (c) Average phytoplankton density by year.

TABLE 2. Results of Three-way Analysis of Variance Model including significant interactions with Phytoplankton Density (cells/mL, log-transformed) as the response variable.

Source of Variation	Sum of Squares	df	Mean Square	F	P
Year	8.130	5	1.626	16.328	<0.001
Region	7.458	2	3.729	37.445	<0.001
Month	31.413	7	4.488	45.062	<0.001
Year*Month	7.271	35	0.208	3.503	<0.001
Error	5.575	94	0.059		

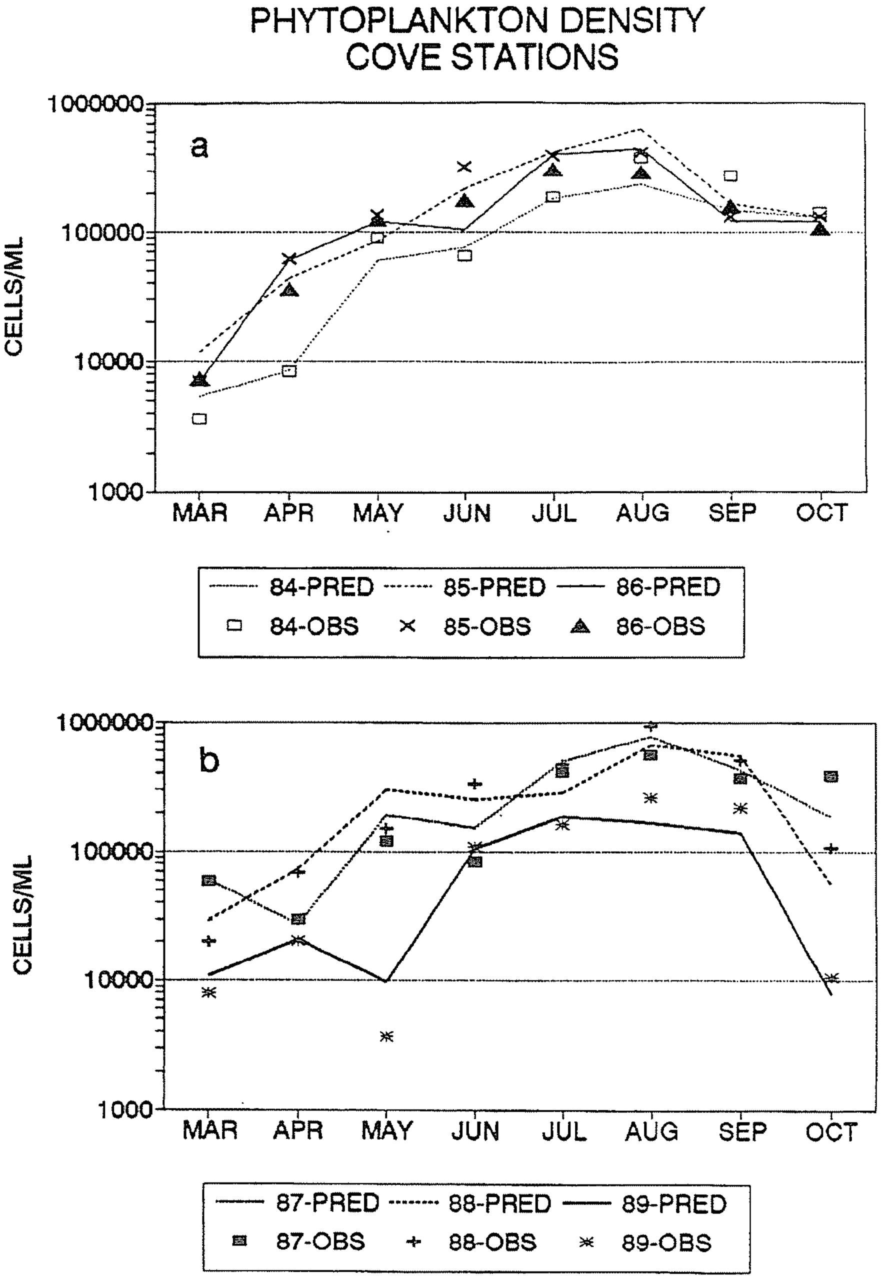

FIGURE 3. Phytoplankton density (cells/mL) at cove stations. Lines represent predictions of ANOVA model including Year-Month interactions. Symbols represent observed data. (a) 1984-86. (b) 1987-89.

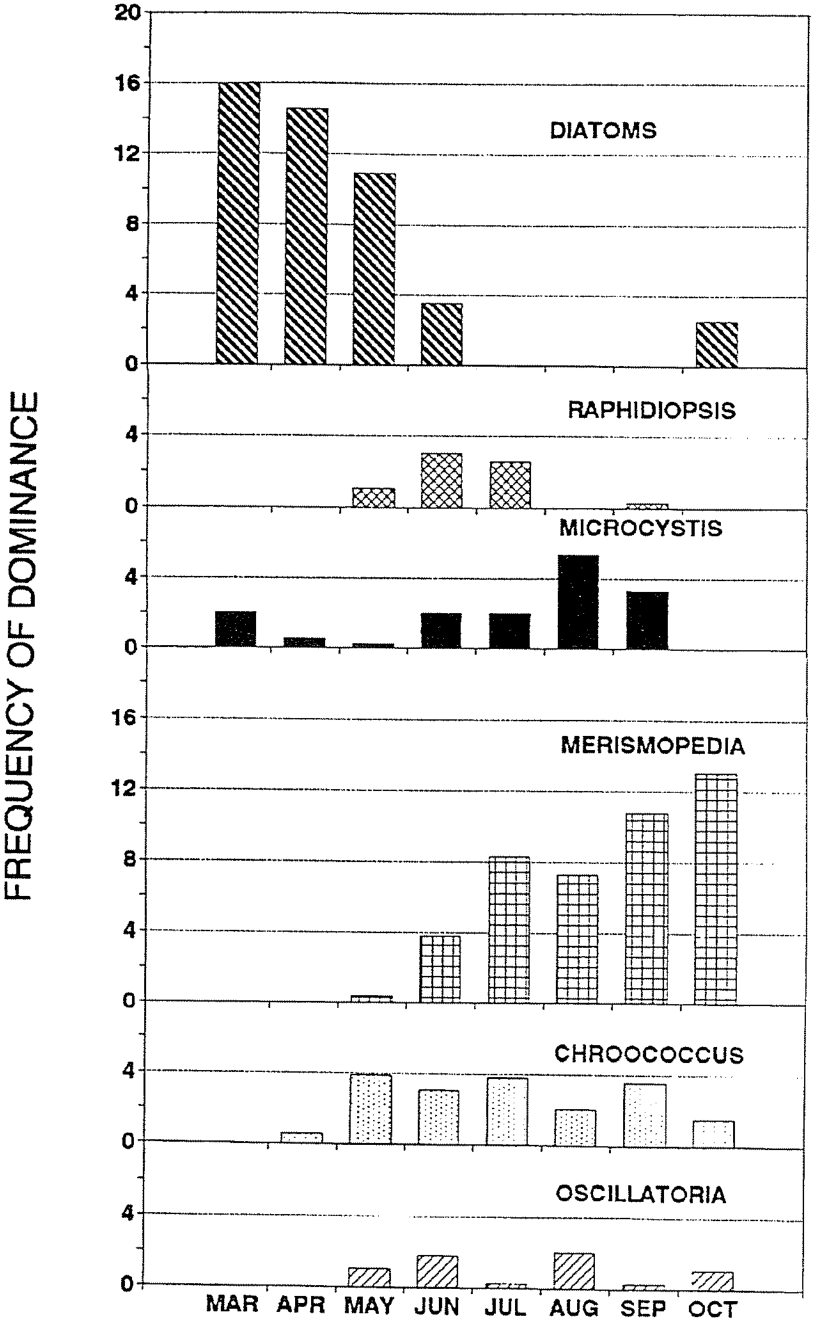

FIGURE 4. Frequency of numerical dominance (number of year-regions) of each taxa by month.

Regional patterns were assessed by summing dominance values over month and year (Figure 5). Diatoms were most frequently dominant at Dogue Creek and least frequently dominant in Gunston Cove. *Raphidiopsis* and *Oscillatoria* showed a pattern of greatest dominance in the Cove followed by substantial dominance in the river, but negligible dominance in Dogue. *Microcystis* was most frequently dominant in the cove, but was dominant in the river and Dogue on a few occasions. *Chroococcus* was more frequently dominant in the river than Dogue and the cove. *Merismopedia* was dominant in all study regions, but was most frequently dominant in Dogue. In fact, either diatoms or *Merismopedia* dominated almost all of the samples from Dogue. Dominance in the other two regions was more evenly distributed among the taxa.

Interannual trends were examined by summing dominance values over month and region (Figure 6). Diatoms showed the least variation in dominance frequency among years. *Merismopedia* displayed a tendency to increase dominance with year except for 1987. *Chroococcus* showed marked interannual variation in dominance with peak years in 1986 and 1987. *Oscillatoria* achieved appreciable dominance only in 1984, 1987, and 1988. *Raphidiopsis* was dominant only in the early years of the study. *Microcystis* was variable in dominance but was represented in all years except 1989. *Microcystis* exhibited major bloom outbreaks in the cove all years from 1985 through 1988. However, in most of these years the bloom was restricted to the cove and may have occurred for only one month. This was the case in 1986 and 1987. On the other hand, high dominance was found in 1984 when no large *Microcystis* bloom was observed. This was the result of *Microcystis* dominance during non-bloom periods. *Oscillatoria* appeared sporadically with major outbreaks in 1984, 1987 and 1988. In most years at least four taxa contributed to dominance. However, in 1989 virtually all samples were dominated by *Merismopedia* or diatoms.

Several taxa not found in Figures 4-6 were dominant on occasion. Green algae were dominant or co-dominant in April 1987 over the entire study area. *Coelosphaerium* was dominant or co-dominant in the cove in July of two years. Cryptophytes, *Phormidium*, and *Aphanizomenon* were dominant or co-dominant on at least one occasion.

DISCUSSION

The seasonal pattern of phytoplankton abundance observed in this study appears to contradict that reported for most eutrophic systems in that no late spring-early summer decline was noted. In fact phytoplankton densities generally sustained a nearly exponential increase from March through August. The lack of a decline during this period suggests that conditions for growth (light, temperature, nutrient availability) remain favorable and that loss factors (grazing, flushing, sedimentation) do not normally exceed growth.

Temperature certainly increases through the growth period, but solar radiation reaches a maximum in late June and by August is much reduced. Nutrient availability remains high with total phosphorus averaging 50-150 μg/L and total nitrogen 1.5-7.5 mg/L (Jones and Kelso, 1990). Crustacean zooplankton, the major planktonic grazers, reach maximum levels in late May and early June during the time of increasing phytoplankton densities. Thus, their feeding does not appear to

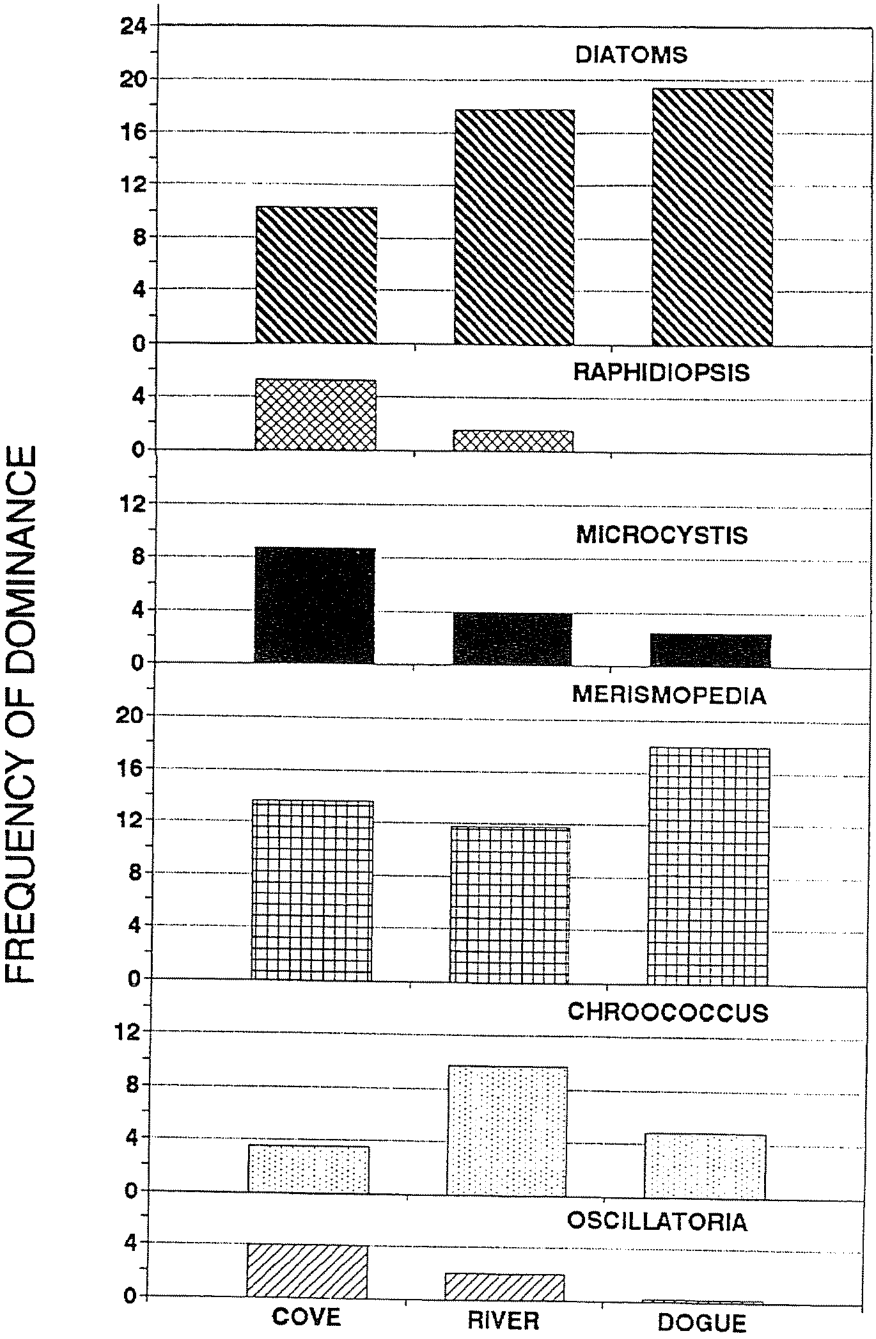

FIGURE 5. Frequency of numerical dominance (number of month-years) of each taxa by region.

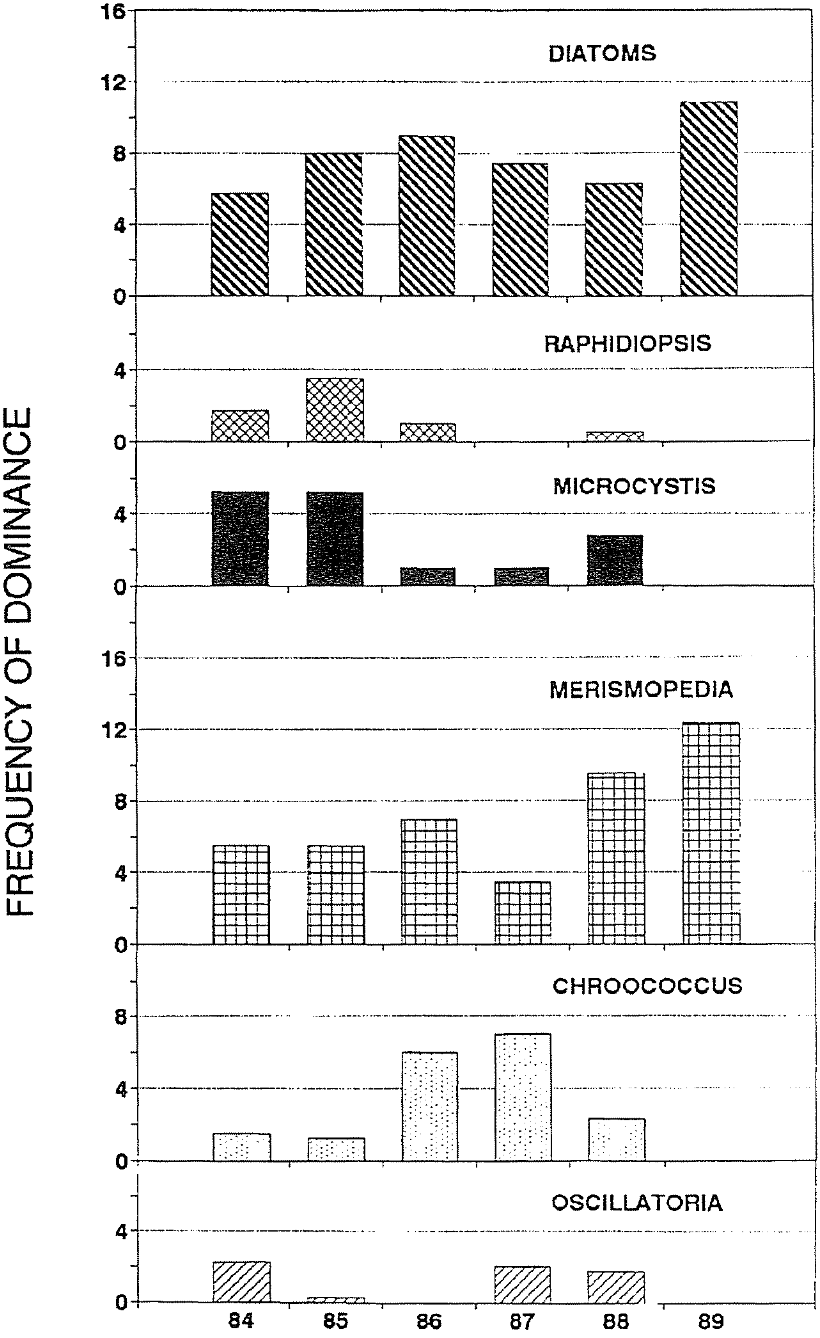

FIGURE 6. Frequency of numerical dominance (number of month-regions) of each taxa by year.

limit phytoplankton growth. Data are not available on seasonal sedimentation patterns. However, it is reasonable to suggest that these would be greatest during the lowest river flow periods of late summer which is also the time of highest standing crop.

One loss factor that does seem to be correlated with seasonal patterns of phytoplankton density is water residence time. Water residence time in Gunston Cove varies from 1-10 days in spring to 100-1000 days in late summer. Flushing also appears to be responsible for some of the major deviations from the simple seasonal model. A substantial drop in phytoplankton density in May 1989 was closely related to a dramatic decrease in water residence time to less than one day. Obvious departures from mean levels observed in April 1987 and October 1989 were also associated with a decline to less than 2 days in cove residence time. Thus, flushing may be a significant factor in both the normal seasonal pattern of phytoplankton density and in deviations from this pattern during certain years.

The clear effect of region on phytoplankton density may be related to both growth and loss factors. The shallower water column in the embayment areas of Dogue and Gunston provides a higher average light level for circulating phytoplankton leading to greater photosynthetic and growth potential than in the much deeper river mainstem. Nutrient concentrations are generally higher in Gunston than in the river (Jones and Kelso, 1990), but similar in Dogue and the river. This may help explain the intermediate position of Dogue Creek.

Regional variation in loss factors is more difficult to assess. Flushing of the Cove is probably dependent on local tributary inflow, whereas hydraulic inputs to the river mainstem are controlled by runoff from a much larger area upstream. This could result in a temporal difference in flushing rates between the two areas. Interestingly, the interaction of region with month was not significant indicating that temporal differences in flushing between regions, if present, were not of overriding signficance. Available data suggest that grazing losses in the study area are not excessive. Buchanan and Schloss (1983) estimated summer zooplankton clearance rates at generally less than 5% of river volume per day in the tidal freshwater Potomac mainstem. Futhermore, densities of crustacean zooplankton are generally greater in the embayments than in the river, the opposite of what would be expected if their grazing were responsible for regional differences in phytoplankton densities. It should be noted that cyanobacteria, the dominant phytoplankters during most of the year, are not efficiently grazed by most zooplankton (Fulton and Paerl, 1987). Another potentially important filter feeder, the bivalve *Corbicula fluminea*, is found in much higher concentrations in the river mainstem and may help explain the lower densities found there. Cohen et al. (1984) suggested that grazing by *Corbicula* in the Potomac river mainstem may be substantial enough to strongly depress phytoplankton populations. We have recently observed large populations of colonial rotifers on macrophytes lining the river channel which are capable of rapidly reducing phytoplankton populations in laboratory experiments (Jones, unpublished data).

The interannual variations observed seem to be related mostly to variations in loss factors. Freshwater inflow, both local to the cove and more broadly to the entire tidal Potomac, varied substantially among years. The two years with lowest average phytoplankton density had the highest frequency of high discharge days during the growing season. Potomac River flows exceeded 10,000 cfs on 15 days during the period June 15-August 31 in 1984 and on 36 days during a similar period in 1989. This level was exceeded no more than 4 days during the same period in any other study year. Likewise, discharges directly to the cove more frequently exceeded a daily average of 300 cfs (equivalent to a 2-day cove residence time) in 1984 and 1989 than in the intervening years.

The years 1984 and 1989 also differed from intervening years by the lack of a bloom of the cyanobacterium *Microcystis aeroginosa*. These blooms have been hypothesized to begin with prolonged periods of hot, calm weather which promotes the development of *Microcystis*. Blooms of this cyanobacterium are capable of attaining large numbers and raising pH to unusually high levels (Jones, 1991) presumably by CO_2 removal. At these pH levels phosphorus is released at high rates from the sediments (Kircher 1990; Oehrlein, 1990) fueling unusually high phytoplankton densities approaching or exceeding 1×10^6 cells/mL. The difference would probably have been greater if biomass had been examined since *Microcystis* has somewhat larger cells than the dominant cyanobacteria in non-bloom years.

The seasonal pattern of species dominance is similar to that observed in eutrophic freshwaters with diatoms dominant in spring and cyanobacteria in summer and fall. These patterns also correlate well with environmental conditions said to favor these two groups. High turbulence in spring allows diatoms to avoid the problems of sedimentation during this period when temperature and light levels favor their growth. Cyanobacterial dominance in the summer may be aided by high pH's (up to 11.0) and temperatures.

It should be noted that dominance in this paper was calculated based on cell density basis. Preliminary calculations of biovolume indicate that cyanobacteria are less important to phytoplankton biomass than cell count data would indicate and that in some cases other groups such as cryptophytes and green algae are actually dominant in biovolume at times of cyanobacterial dominance in cell density. Work is currently underway to calculate species abundance by biovolume which may resolve this uncertainty.

ACKNOWLEDGEMENTS

This data was collected as part of the Gunston Cove Study funded by the County of Fairfax, Virginia and thanks is due to Elaine Schaeffer and Jimmie Jenkins for their support. Thanks are also due to my co-PI Don Kelso and the students who have helped with field collections through the years. Jim Coles was instrumental in phytoplankton database management in the later years of this data set. This paper was initiated while the senior author was on study leave at Trout Lake Station of the Center for Limnology at the University of Wisconsin-Madison. We wish to thank reviewers Hans Paerl, Kevin Sellner, and Tim Kratz for their useful suggestions.

LITERATURE CITED

Bailey-Watts, A.E. 1978. A nine-year study of the phytoplankton of the eutrophic and non-stratifying Loch Leven (Kinroll, Scotland). J. Ecol. 66: 741-771.

Bergquist, A.M., S.R. Carpenter, and J.C. Latino. 1985. Shifts in phytoplankton size structure and community composition during grazing by constrasting zooplankton assemblages. Limnol. Oceanogr. 30: 1037-1045.

Buchanan, C. and J.A. Schloss. 1983. Spatial distributions and hypothetical grazing pressures of zooplankton in the tidal, freshwater Potomac River. J. Freshwater Ecol. 2: 117-128.

Butcher, R.W. 1967. An Introductory Account of the Smaller Algae of the British Coastal Waters. Part IV. Cryptophyceae. London: Her Majesty's Stationery Office.

Campbell, P.H. 1973. Studies on Brackish Water Phytoplankton. Sea Grant Publication UNC-SG-73-07.

Cloern, J.E., A.E. Alpine, B.E. Cole, R.L.J. Wong, J.F. Arthur, and M.D. Ball. 1983. River discharge controls phytoplankton dynamics in the northern San Francisco Bay estuary. Estuar. Coast. Shelf Sci. 16: 415-429.

Cohen, R.R.H., P.V. Dresler, E.J.P. Phillips and R.L. Cory. 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. Limnol. Oceanogr. 29: 170-180.

Davis, C.C. 1964. Evidence for the eutrophication of Lake Erie from phytoplankton records. Limnol. Oceanogr. 9: 275-283.

Fulton, R.S., and H.W. Paerl. 1987. Effects of colonial morphology on zooplankton utilization of algal resources during blue-green algal (*Microcystis aeruginosa*) blooms. Limnol. Oceanogr. 32: 634-644.

Huber-Pestalozz, G. 1938. Das Phytoplankton des Susswassers. Band XVI. Teil 1. Die Binnengewasser. Schweizerbart'sche Verlagsbuchhandlung.

Huber-Pestalozz, G. 1941. Das Phytoplankton des Susswassers. Band XVI. Teil 2. Die Binnengewasser. Schweizerbart'sche Verlagsbuchhandlung.

Huber-Pestalozz, G. 1950. Das Phytoplankton des Susswassers. Band XVI. Teil 3. Die Binnengewasser. Schweizerbart'sche Verlagsbuchhandlung.

Jones, R.C. and D.P. Kelso. 1990. An ecological study of Gunston Cove: 1989-90. Final Report submitted to Fairfax County, Virginia. 280 pp.

Jones, R.C. 1991. Spatial and temporal patterns in a cyanobacterial phytoplankton bloom in the tidal freshwater Potomac River, U.S.A. Verh. Internat. Verein. Limnol. 24: 1698-1702.

Kimmel, B.L., O.T. Lind, and L.J. Paulson. 1990. Reservoir primary production. Pages 133-194 in Thornton, K.W., B.L. Kimmel, and F.E. Payne. (eds.) Reservoir Limnology: Ecological Perspectives. Wiley-Interscience. 246 pp.

Kircher, S.R. 1990. The effect of pH on the release of phosphorus from the sediments of Gunston Cove, Virginia. M.S. Thesis. George Mason University, Fairfax, VA. 49 pp.

Lippson, A.J., M.S. Haire, A.F. Holland, F. Jacobs, J. Jensen,, R.L. Moran-Johnson, T.T. Polgar, and W.A. Richkus. 1979. Environmental Atlas of the Potomac Estuary. Johns Hopkins University Press. 280 pp.

Lund, J.W.G., C. Kipling, and E.D. LeCren. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11: 143-170.

Marshall, C.T. and R.H. Peters. 1989. General patterns in the seasonal development of chlorophyll a for temperate lakes. Limnol. Oceanogr. 34: 856-867.

Mills, E.L. and J.L. Forney. 1988. Trophic dynamics and development of freshwater pelagic food webs. Pages 11-330 in: Complex Interactions in Lake Communities. S.R. Carpenter (ed). Springer-Verlag. 283 pp.

Odum, W.E., T.J. Smith, J.K. Hoover, and C.C. McIvor. 1984. The Ecology of Tidal Freshwater Marshes of the United States East Coast: A Community Profile. U.S. Fish and Wildlife Service. FWS/OBS-83/17.

Oehrlein, W.L. 1990. Sediment phophorus available to phytoplankton as a function of pH in Pohick Bay, Virginia. M.S. Thesis. George Mason University, Fairfax, Virginia. 43 pp.

Pearl, H. W. 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. Limnol. Oceanogr. 33:823-847.

Prescott, G.W. 1962. Algae of the Western Great Lakes Area. Brown.

Reynolds, C.S., J.M. Thompson, A.J.D. Ferguson, and S.W. Wiseman. 1982. Loss processes in the population dynamics of phytoplankton maintained in closed systems. J. Plankton Res. 4: 61-600.

Shapiro, J. 1973. Blue-green algae: why they become dominant. Science 179: 382-384.

Smith, G.M. 1950. The Freshwater Algae of the United States. McGraw-Hill Book Co. 719 pp.

Smith, V.H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221: 669-671.

Soballe, D.M. and B.L. Kimmel. 1987. A large-scale comparison of factors influencing phytoplankton abundance in river, lakes, and impoundments. Ecology 68: 1943-1954.

Sommer, U., Z.M. Gliwicz, W. Lampert, and A. Duncan. 1986. The PEG-model of seasonal succession of planktonic events in Freshwaters. Arch. Hydrobiol. 106: 433-471.

VanLandingham, S.L. 1982. Guide to the Identification, Environmental Requirements and Pollution Tolerance of Freshwater Blue-green Algae (Cyanophyta). US Environmental Protection Agency 600/3-82-073. PB83-163006. 340 pp.

Weber, C.I. 1971. A Guide to the Common Diatoms at Water Pollution Surveillance System Stations. US Environmental Protection Agency, Cincinnati, Ohio, USA.

Whitford, L.A. and G.J. Schumacher. 1973. A Manual of Freshwater Algae. Sparks Press, Raleigh, N.C.