Phytoplankton Dynamics of the Fresh, Tidal Potomac River, Maryland, for the Summers of 1979 to 1981

A Water-Quality Study of the Tidal Potomac River and Estuary

United States Geological Survey Water-Supply Paper 2234–C

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By Ronald R. H. Cohen

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FOREWORD

Tidal rivers and estuaries are very important features of the Coastal Zone because of their immense biological productivity and their proximity to centers of commerce and population. Most of the shellfish and much of the local finfish consumed by man are harvested from estuaries and tidal rivers. Many of the world's largest shipping ports are located within estuaries. Many estuaries originate as river valleys drowned by rising sea level and are geologically ephemeral features, destined eventually to fill with sediments. Nutrients, heavy metals, and organic chemicals are often associated with the sediments trapped in estuaries. Part of the trapped nutrients may be recycled to the water column, exacerbating nutrient-enrichment problems caused by local sewage treatment plants, and promoting undesirable algae growth. The metals and organics may be concentrated in the food chain, further upsetting the ecology and threatening the shell and finfish harvests. Our knowledge of the processes governing these phenomena is limited and the measurements needed to improve our understanding are scarce.

In response to an increasing awareness of the importance and delicate ecological balance of tidal rivers and estuaries, the U.S. Geological Survey began a 5-year interdisciplinary study of the tidal Potomac River and Estuary in October of 1977. The study encompassed elements of both the Water Resources Division's ongoing Research and River Quality Assessment Programs. The Division has been conducting research on various elements of the hydrologic cycle since 1894 and began intense investigation of estuarine processes in San Francisco Bay in 1968. The River Quality Assessment program began in 1973 at the suggestion of the Advisory Committee on Water Data for Public Use which saw a special need to develop suitable information for river-basin planning and water-quality management. The Potomac assessment was the first to focus on a tidal river and estuary. In addition to conducting research into the processes governing water-quality conditions in tidal rivers and estuaries, the ultimate goals of the Potomac Estuary Study were to aid water-quality management decision-making for the Potomac, and to provide other groups with a rational and well-documented general approach for the study of tidal rivers and estuaries.

This interdisciplinary effort emphasized studies of the transport of the major nutrient species and of suspended sediment. The movement of these substances through five major reaches or control volumes of the tidal Potomac River and Estuary was determined during 1980 and 1981. This effort provided a framework on which to assemble a variety of investigations:

(1) The generation and deposition of sediments, nutrients, and trace metals from the Holocene to the present was determined by sampling surficial bottom sediments and analyzing their characteristics and distributions.

(2) Bottom-sediment geochemistry was studied and the effects of benthic exchange processes on water-column nutrient concentrations ascertained.

(3) Current-velocity and water-surface-elevation data were collected to calibrate and verify a series of one- and two-dimensional hydrodynamic flow and transport models.

(4) Measurements from typical urban and rural watersheds were extrapolated to provide estimates of the nonpoint sources of sediments, nutrients, and biochemical oxygen demand during 1980 and 1981.

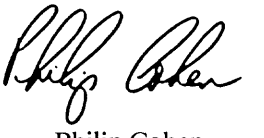
(5) Intensive summertime studies were conducted to determine the effects of local sewage-treatment-plant effluents on dissolved-oxygen levels in the tidal Potomac River.

(6) Species, numbers, and net productivity of phytoplankton were determined to evaluate their effect on nutrients and dissolved oxygen.

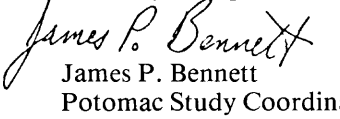
(7) Wetland studies were conducted to determine the present-day distribution and abundance of submersed aquatic vegetation, and to ascertain the important water-quality and sediment parameters influencing this distribution.

(8) Repetitive samples were collected to document the distribution and abundance of the macrobenthic infaunal species of the tidal river and estuary and to determine the effects of changes in environmental conditions on this distribution and abundance.

The reports in this Water-Supply Paper series document the technical aspects of the above investigations. The series also contains an overall introduction to the study, an integrated technical summary of the results, and an executive summary which links the results with aspects of concern to water-quality managers.



Philip Cohen
Chief Hydrologist



James P. Bennett
Potomac Study Coordinator

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By Ronald R. H. Cohen

Abstract

The distribution and abundance of phytoplankton in the fresh, tidal Potomac River, Md., was different during 1979–81 from that observed in the 1960's and 1970's. Concentrations of phytoplankton in the 1960's and 1970's reached maximum attainable levels that were limited only by self-shading. A sag in phytoplankton abundance, apparent during the summers of 1980 and 1981 between Rosier Bluff and Marshall Hall, appears to have been caused by the Asiatic clam, *Corbicula fluminea*. Reduced abundance of phytoplankton throughout the entire fresh, tidal river during the summers of 1980 and 1981 may have been due to grazing by *Corbicula*, high discharge, and perhaps phosphorus limitation in late August at and downstream of Hallowing Point. Phytoplankton growth rates and chlorophyll-to-cell ratios were highest at Hatton Point and Marshall Hall (the sag reach). A model was constructed that predicted phytoplankton growth rates by varying only chlorophyll *a* concentration and light penetration. Nutrient concentrations were not required to make the model fit the data.

Primary productivity was highest for the year during August 1980 and August 1981. Productivity-per-unit chlorophyll was highest at Hatton Point, where reduced concentrations of phytoplankton permitted the deepest light penetration in the fresh, tidal river.

INTRODUCTION

Phytoplankton play a crucial role in riverine and estuarine ecosystems because they are the major source of energy for higher trophic levels and they are the source of energy that drives the nutrient cycles. Phytoplankton produce organic compounds from inorganic nutrients using light as an energy source. The organic material formed by the phytoplankton is called primary production, and primary production per unit time per volume of water, or under a unit surface area, is called primary productivity. Photosynthesis, the process by which phytoplankton synthesize organic material, consumes inorganic carbon and releases oxygen. Phytoplankton are the major source (other than the atmosphere) of dissolved oxygen in waters and become a dissolved-oxygen sink after death. They account for most of the nutrient fluxes from dissolved to particulate forms, and for much of the flux from particulate to dissolved forms due to their high biomass and turnover rates. With the rapid response time of algae to nutrient inputs, phytoplankton are key indicators of cultural and natural eutrophication. Phytoplankton biomass and growth rate vary with the seasons and are controlled by light, nutrients, discharge, temperature, and grazing. It is important to identify the ecosystem components that control growth rate and biomass. The sources of the differences in phytoplankton distribution in the fresh, tidal Potomac River between the 1960's and 1970's period and the 1979–81 period must be documented.

Purpose and Scope

The purpose of this study in general is to identify and quantify the effects of biotic (for instance, clams and zooplankton) and abiotic (light, nutrients, and discharge) components of the environment on phytoplankton growth rates and biomass in the fresh, tidal Potomac River. Specifically, the purpose of the report is (1) to assess and describe phytoplankton growth rates; (2) to characterize the effects of light, nutrients, discharge, and toxic substances on phytoplankton growth rates; (3) to assess the effects of invertebrates on phytoplankton; (4) to explain the differences in phytoplankton distribution and abundance between the period 1960 to the late 1970's and the period 1980–81; and (5) to differentiate between phytoplankton and nonphytoplankton respiration.

Data collection and field and laboratory experiments were required to elucidate important processes. The data and experiments in this report encompass the tidal, fresh Potomac River, Md., from the station at Chain Bridge (figs. 1*A* and *B*) to the cross section at Quantico, Va. The summers of 1980 and 1981 are emphasized, but data on phytoplankton biomass from August and September 1979 and primary productivity in all seasons from May 1980 to September 1981 also are included.

Measurements of chlorophyll *a*, numbers of phytoplankton cells, nitrogen species, and phosphorus were made and reported. Experiments were performed to examine nutrient limitation, mollusk and zooplankton grazing, effects of toxic substances, and phytoplankton growth rates.

The report includes data collected as part of the Potomac River Quality Assessment Program and published as U.S. Geological Survey open-file reports (Blanchard and Coupe, 1982; Blanchard and others, 1982).

Description and History of Area

The tidal Potomac River and estuary, Md., extends 187 km, from the fall line near Chain Bridge (upstream from Washington, D.C.) to the Chesapeake Bay (fig. 1*A*). The fresh, tidal river, approximately 62 km long, has a volume of 3.4×10^8 m^3 and receives drainage from both metropolitan Washington, D.C., and the nontidal Potomac River (fig. 1*B*). It has an average flow of 310 m^3 s^{-1} at Chain Bridge and receives approximately 1.4×10^{-6} m^3 of wastewater per day from municipal treatment facilities.

The maximum flow of record was 13,700 m^3 s^{-1} in 1936 and the minimum was 17 m^3 s^{-1} in 1966. The maximum flow during the 1979–81 study period was 2377 m^3 s^{-1} on September 7, 1979. The minimum flow was 24 m^3 s^{-1} on August 29, 1981.

Three major changes in wastewater treatment resulted in major changes in nutrient loading to the river. In 1959, secondary treatment added to the Blue Plains Sewage Treatment Plant (km 170) caused a 50-percent drop in carbon loading. Phosphorus removal began in 1974, and by 1978, phosphorus loads were reduced 70 percent compared to peak levels. Nitrification facilities at this plant began operation in September 1980.

The fresh, tidal Potomac River produced high concentrations of phytoplankton (100 to 300 μg L^{-1} chlorophyll *a*; 5 to 20×10^7 cells L^{-1}) during every July to September low-flow[1] period of the 1960's and 1970's (Jaworski and others, 1972; Clark and Roesch, 1978; Smith and Herndon, 1980). The zone of high phytoplankton biomass in the late summers of the 1960's and 1970's extended from river kilometer[2] 180 at Memorial Bridge,

[1]Less than 115 m^{-3} s^{-1}.

[2]Kilometers measured along the channel from Chesapeake Bay.

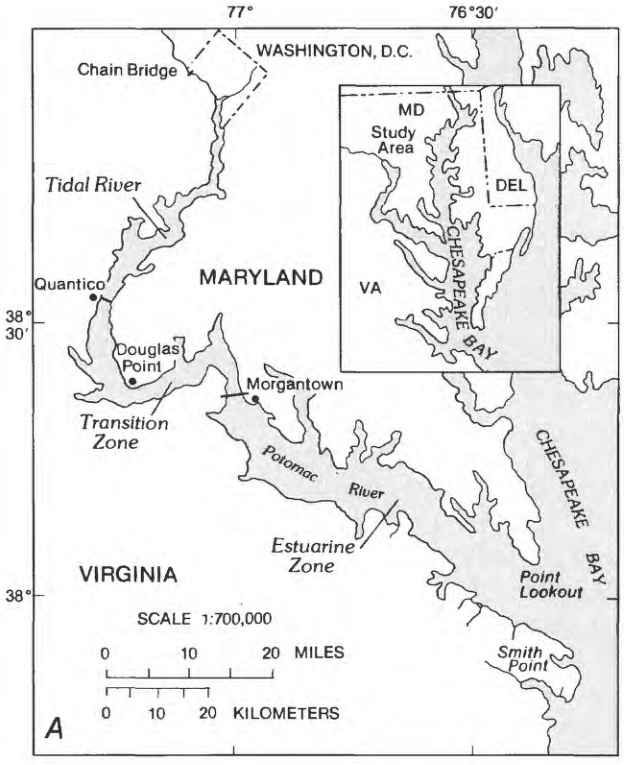

Figure 1A. The tidal Potomac River and Estuary, Md. Heavy lines at Chain Bridge and Quantico delineate the fresh, tidal river. The line at Morgantown indicates the beginning of the estuary.

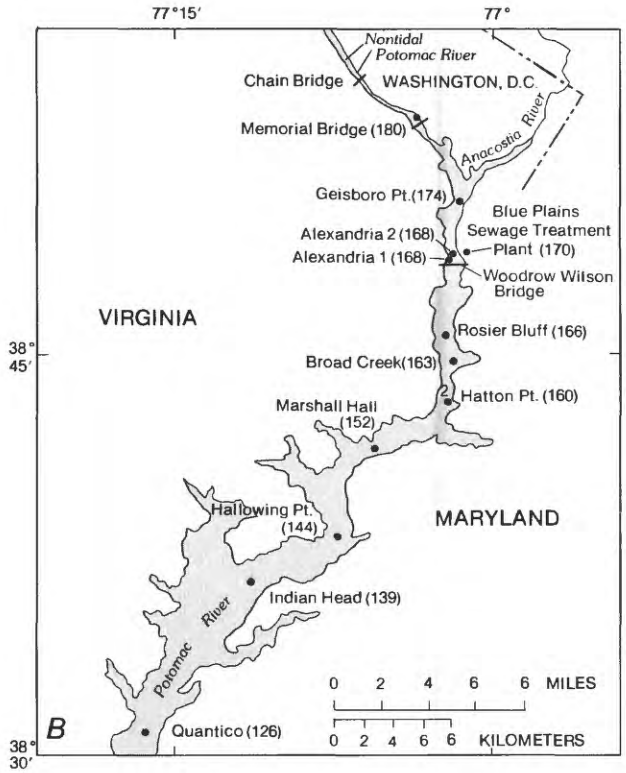

Figure 1B. The fresh, tidal Potomac River, Md. River kilometers from the mouth at Point Lookout are shown in parentheses.

Washington, D.C., to km 126 at Quantico, Va., the approximate, late-summer location of the brackish-freshwater interface (figs. 1*A* and 1*B*). The chlorophyll *a* concentrations and phytoplankton cell numbers typically increased from Memorial Bridge (km 180) to Indian Head, Md. (km 139), except for a few days after a peak discharge (Clark and Jaworski, 1972; Pheiffer, 1976).

No algae blooms were reported before 1920 (Lear and Smith, 1976). Water chestnuts invaded the Potomac River in the 1930's (U.S. Army Corps of Engineers, 1934) and were physically removed by the Corps of Engineers. The Eurasian water milfoil (*Myriophyllum spicatum*) population increased dramatically in the 1940's and 1950's and disappeared in the late 1950's. At that time, blue-green algae, dominated by *Anacystis* (also known as *Microcystis*) *cyanae* and *Anabaena*, formed dense mats in the tidal river. In 1977, the U.S. Environmental Protection Agency (EPA) reported the dominant bloom algae to be the blue-green *Anabaena* (Clark, 1980). A detailed history of Potomac River water quality is presented by Champ and others (1981).

In the summers of 1980 and 1981, cell abundance and chlorophyll *a* concentrations did not increase continuously from the Memorial Bridge to Indian Head segment as in previous years (Cohen and others, 1984). Phytoplankton abundance between Rosier Bluff, Md., and Hatton Point, Md., was 40 to 60 percent lower than that observed upstream of river km 168 and downstream of Hallowing Point, Va. This depression of phytoplankton abundance, or sag, (relative to upstream and downstream values) was observed in both summers. Phytoplankton abundance throughout the fresh, tidal Potomac River was less than that observed in the 1960's and 1970's.

METHODS

Measurement of Phytoplankton Biomass and Cell Numbers

Depth-integrated phytoplankton samples were collected from the water column on 24 longitudinal transects once and sometimes twice a day in July and August 1980, and 13 transects in July and August 1981. Samples were preserved with Lugol's iodine and acetic acid. Phytoplankton sampled in 1980 were counted at a magnification of 400 by K. E. Boulukos and V. A. Stoelzel by the Utermöhl method (Utermöhl, 1958; Lund and others, 1958)[3]. Between 60 and 120 cells were counted in each sample. On some rare occasions, when phytoplankton abundance was very low, fewer cells were counted. Phytoplankton sampled in July and August 1981 were counted by a technician at Wapora, Inc.[4] (a minimum of 100 cells per sample were counted). Five percent of the July and August 1981 samples were subsampled and counted by Boulukos and Stoelzel. The Wapora, Inc., counts were performed at a magnification of 280 and were consistently lower than those made by Boulukos and Stoelzel. Therefore, the absolute values of 1980 counts should not be compared to those of 1981. Correction factors were obtained using regression analysis to make the counts of Boulukos and Wapora comparable to those of Stoelzel (Cohen and others, 1984). Two double-blind tests for cell-count precision demonstrated that the standard deviation of four to five replicate counts was 10 percent of the mean (see Cohen and others, 1984).

Benthic sediment samples for chlorophyll *a* and phaeopigment analyses were taken with a gravity corer. All but 8 to 10 cm of water over the core was siphoned immediately after sampling. The 8- to 10-cm water column was retained until resuspended sediment settled and the core was then sampled. The core tubes were placed in the dark to avoid light-mediated degradation of algal pigments. The tip of a 30-cm^3 syringe was cut so that a uniform cylinder remained (2.1 cm diameter). Samples for chlorophyll *a* (also referred to as chlorophyll) and phaeopigment analyses were taken by plunging the modified syringe into the sediment and collecting 4 cm^3 of surface sediment. The sample was then immersed in acetone for chlorophyll and phaeopigment extraction (Strickland and Parsons, 1972). To disintegrate clumps of sediment, samples were agitated in the dark in a shaker several times during the extraction. Chlorophyll *a* and phaeophytin *a* (a degradation product of chlorophyll *a*) were determined on a Turner Designs fluorometer (Strickland and Parsons, 1972).

Tests for Effects of Toxic Substances

Phytoplankton samples were collected and incubated in natural water to test for possible effects of toxic substances and to examine growth rates. Water-column phytoplankton samples were collected with a depth-integrating sampler, filtered through 65-μm mesh to remove zooplankton and placed in 100-mL, clear, Plexiglas chambers, as described by McFeters and Stuart

[3]V.A. Stoelzel counted 80 percent of the samples analyzed in the U.S. Geological Survey laboratory and K. E. Boulukos counted 20 percent. The calibration counts by Stoelzel were used as a standard against which counts by Boulukos and Wapora were compared.

[4]The use of firm and brand names in this report is for identification purposes only and does not constitute endorsement by the U.S. Geological Survey.

(1972). The samples were contained in the chambers by placing a 142-mm diameter, 1.0-μm-pore size, Nuclepore filter on each side of the chambers. The chambers were submersed 7 cm below the water surface in 115-L, open-top, plastic cans filled with unfiltered water from either river km 163 (the sag region) or km 138, downstream from sag. The water in which the chambers were to be incubated was collected by compositing depth- and time-intergrated samples taken at a station approximately every 2 hours, from 0900 hours to dusk. The samples were incubated under natural solar radiation for 4 days. At the conclusion of the incubation period, water samples were withdrawn by syringe from the chambers and subsampled for cell counts, chlorophyll *a*, and phaeopigment measurements.

Measurement of Primary Productivity

A detailed description of the methods for determining primary productivity can be found in Cohen and Pollock (1983). A light- and dark-bottle oxygen method for determining phytoplankton productivity similar to that described by Greeson and others (1977) was used. Depth-integrated samples for productivity analyses were collected with an open, weighted, 4-L polyethylene bottle fitted with a vent tube. The bottle was filled as it was lowered and raised in the water column at a uniform rate. Samples were composited until a 20-L polyethylene carboy was filled. At the Quantico station, two verticals were depth integrated and composited. The samples were collected during the evening (between 1700 and 2100 hours) and incubated overnight and throughout the next day, for a total of approximately 24 hours. If degassing became apparent, the incubations were terminated about midday. The first two productivity determinations (May 1980) were performed dawn to dusk.

Short-term (4 hours or less) incubations minimize "bottle effects" (Berman and Eppley, 1974). Therefore, dawn to dusk incubations, and 4-hour and 2-hour incubations centered at midday have been recommended (Vollenweider, 1965). However, nutrients for nutrient-limitation bioassays must be added during the evening to demonstrate any significant stimulation during the next day (Stross, 1980). Lean and Pick (1981) state that uptake of phosphorus is light dependent only when samples first are incubated in the dark for long periods. They also report that bioassays cannot be interpreted if incubations are short. Enrichments in 4- to 12-hour incubations induce no response (Gerhart and Likens, 1975).

Long-term incubations (24 hours or more) give reliable results if algae populations remain healthy (Lean and Pick, 1981). Very long-term incubations (several days or more) may result in unhealthy algae (Kalff, 1971; Lean and Pick, 1981). Thus, our incubations, begun the evening before a day of sunshine, fulfilled the requirements for reliable bioassay results.

The calculation of depth-integrated primary productivity is described in Cohen and Pollock (1983). Growth rates in terms of carbon biomass were estimated from measurements of primary productivity. Initial biomass of carbon, B_0 (in micrograms per liter), was estimated as 30 times the chlorophyll *a* concentration (in micrograms per liter) (Parsons and others, 1977; Antia and others, 1963) because particulate carbon, determined by subtracting dissolved carbon from total carbon, often yielded results that were less than zero (Blanchard and others, 1982). Although carbon-to-chlorophyll ratios may range from 25 to 79 over several days (Antia and others, 1963), and even change several hundred percent over a day (Hunter and Laws, 1981), Strickland (1960) recommends a typical value of 30. The molecular ratio of CO_2 assimilated to O_2 evolved was assumed to be 1.0 (Parsons and others, 1977; Kelly and others, 1983). New carbon biomass, B, was calculated by adding net primary productivity (as carbon) to initial biomass. Thus, growth rate could be estimated by

$$(ln\ (\frac{B}{B_0}))/T = K_G \quad , \tag{1}$$

where

B = new carbon biomass, mg L^{-1};
B_0 = initial carbon biomass, mg L^{-1};
T = time, in days;
K_G = specific growth rate, day $^{-1}$;

and

$$K_G = (ln\ ((B_0 + NPP)/B_0))T \ , \tag{2}$$

where

NPP = net primary productivity in mg carbon L^{-1} day^{-1}.

Sampling stations for productivity analysis or productivity experiments are listed below (with the depth used to calculate depth-integrated productivity) and shown in figure 1*B*. Productivity analysis was done once at Marshall Hall and Douglas Point and then those stations were dropped from the routine analysis.

Station number	Station name	River distance, from Chesapeake Bay, in kilometers	Average depth, in meters
01652590	Potomac River at Alexandria, Va. (referred to as Alexandria 1)	168.0	2.2
384736077013300	Potomac River across from Alexandria, Va. near Maryland shoreline (referred to as Alexandria 2)	170.3	2.8
384318077020300	Potomac River at Hatton Point, Md.	160.0	3.9
384136077054600	Potomac River at Marshall Hall (Mount Vernon), Va.	152.0	3.7
383818077072800	Potomac River at Hallowing Point, Va.	144.0	5.6
01658710	Potomac River at Quantico, Va.	125.6	5.8
382640077159900	Potomac River at Douglas Point, Md.	116.7	3.8

Measurement of Phytoplankton Growth Rates

Growth rates were calculated from productivity data and from other laboratory and field experiments. Depth-integrated phytoplankton samples were collected at Alexandria, Va., Hatton Point, Md., or Hallowing Point, Va., and returned to the laboratory. Subsamples were enriched with $NaNO_3$, KH_2PO_4, and NH_4Cl to yield concentrations above ambient in mg L^{-1} of 0, 0.1, 0.25, 0.5, and 1.0 of NO_3; 0, 0.02, 0.05, 0.08, and 0.12 of PO_4; and 0, 0.05, 0.08, 0.1, and 0.2 of NH_4. Samples were incubated for 4 to 7 days in a light- and temperature-controlled growth chamber at ambient temperatures and a 10-hour light/14-hour dark cycle. Growth rates were calculated with equation 1, with B and B_0 in terms of either chlorophyll *a* concentration or nephelometric turbidity.

In field experiments, growth rates were calculated from data collected while following a parcel of water in a Lagrangian sense and by incubating cells in Plexiglas growth chambers. The parcel was identified by following drogues. Cell counts following a parcel were averaged over 24 hours, and growth rates were calculated with equation 1, where B_0 was the mean count on day 1 and B was the mean count on day 2. In the Plexiglas growth chambers, the cell count on day 1 was B_0 and on day 5 was B.

Measurement, Filtering Rates, and Identification of Benthic Invertebrates

Data on *Corbicula fluminea* populations in the tidal Potomac River from 1977 through 1980 were obtained during fall, spring, and summer surveys of the benthic fauna. Sampling methods are described in Dresler and Cory (1980). In 1981, an intensive sampling program for *Corbicula* was begun. At 1.5- to 3-km intervals along the Potomac River from km 144 to km 176, marker buoys were deployed at 90-meter intervals from one bank to the other. At each marker, 0.093 m^2 of bottom sediment was taken with an orange-peel grab sampler. Samples were sieved through a 1.5-mm-mesh screen. Clams were returned to the laboratory for counting, and for size and wet-weight determination. Samples of *Unionid* clams were obtained along with the *Corbicula*.

Clams were weighed (wet weight with shell) and segregated into four size classes to study pumping and filtering rates of *Corbicula*. Each weight class was placed in a separate 2-L beaker and each beaker was filled with Potomac River water from the Alexandria station. Two additional beakers contained only river water and served as controls. The six beakers were stirred at 15 revolutions per minute with a six-gang stirrer. The mixing rate obtained was sufficient to suspend fine particulates but was not vigorous enough to disturb clam pseudofeces. Temperatures remained at 26.5° C (±1°) for the duration of the experiment. Nephelometric turbidity was measured every 15 to 20 minutes for 2 hours. Chlorophyll *a*, determined fluorometrically (Strickland and Parsons, 1972), was measured initially and at hourly intervals for the duration of the experiment. Upon completion of the experiment the water was drained and replaced by unfiltered, fresh river water, and the experiment was repeated. As clams remove suspended material from water and the concentration of suspended material decreases, the rate of reduction of concentration becomes proportional to concentration. Therefore, the following equations, derived by Jørgensen (1943) and used by Prokopovich for *Corbicula* (Prokopovich, 1969), account for the reduction of suspended material when studying clearance rates in closed systems:

$$ln \frac{S}{S_0} = - \frac{N \cdot a \cdot t}{V} \qquad (3)$$

where

S = turbidity at time t, nephelometric turbidity units (NTU);
S_0 = initial turbidity, NTU;
N = number of clams;
a = filtration rate dV/dt, mL H^{-1};
t = time, H;
V = volume, mL.

The equation was modified to subtract settling rates observed in control samples. There were no clams ($N=0$) or filtration in the controls. There was, however, settling of sediment. The clearance rate due to settling (a^1) can be determined by the equation

$$a^1 = (ln \frac{S}{S_0}) \cdot (\frac{V}{t}) \quad (4)$$

such that

$((a \times N) - a^1)/N$ = filtration rate (F) per individual. Filtration rates are given as mL per gram (wet weight with shell) per hour.

Measurement and Identification of Zooplankton

Zooplankton samples were collected from Memorial Bridge (km 180) to Quantico (km 126) at deep (channel) and shallow stations bank to bank along the Potomac River. Water samples were collected at selected depths using a depth-calibrated plastic hose fitted with a collecting funnel constructed from a clear plastic Imhoff cone. A centrifugal pump was used to pump 20 L of water through a ring net to concentrate the zooplankton. The samples were collected in a 30-μm net to ensure retention of rotifers. Zooplankton samples were preserved with a formalin-sucrose solution (Haney, 1973).

Vertical distribution of zooplankton was studied at the Quantico, Hallowing Point, Alexandria, and Memorial Bridge, Va., stations. The sampling hose was lowered from the surface to a depth of 2 m while the water was pumped into a bottle. The next 2-m-segment sample was pumped into another bottle. The process was repeated until the entire water column was sampled. At all other stations, surface-to-bottom, depth-integrated samples were collected. Zooplankton samples were microscopically counted at 40× magnification. Identifications were done by Buchanan and Schloss (1983) at 100× or higher magnification using the taxonomic keys of Ward and Whipple (1959).

Chemical Analyses

Dissolved inorganic nitrogen, total dissolved phosphorus, and particulate organic carbon analyses were performed at the Atlanta, Ga., Central Laboratory of the U.S. Geological Survey by standard procedures (Skougstad and others, 1979; American Public Health Association and others, 1975). Chlorophyll data for longitudinal transects were obtained from Blanchard and others (1982) and Blanchard and Coupe (1982).

RESULTS

Distribution Patterns of Phytoplankton

Two repeated patterns of phytoplankton distribution were reported by Clark and Jaworski (1972) and Smith and Herndon (1980) for July, August, and September low-flow periods of the 1960's and 1970's. The first, typified by September 1977 (Smith and Herndon, 1980) and July 1969 (Clark and Jaworski, 1972), demonstrated an increase of phytoplankton abundance (as chlorophyll *a*) from km 175 to km 140 (fig. 2). A similar pattern in chlorophyll *a* distribution may be inferred from data on three stations reported by Pheiffer (1976) for July and August 1969, 1970, and 1974.

The second pattern, typified by chlorophyll *a* data on August 5, 1968 (Clark and Jaworski, 1972), shows that phytoplankton biomass increased from Memorial Bridge (km 180) to Hatton Point (km 160) and gradually decreased downstream to Quantico (fig. 2). Similar patterns were reported for August 19–22, 1968, and September 1966 and 1967.

All the data cited above demonstrate that, at low flow, phytoplankton abundance at Hatton Point was either higher than at upstream stations or that the station supported the highest phytoplankton abundance in the fresh, tidal Potomac River in the 1960's and 1970's. The pattern of phytoplankton abundance during the July and August 1980 low-flow period differed from those described above. The mean phytoplankton concentration observed in July and August 1980 between Rosier Bluff and Hatton Point (the mean discharge was 88 $m^3 s^{-1}$) had been reduced to levels 50 to 60 percent lower (55 to 65 percent by chlorophyll *a*) than levels observed upstream of km 168 (fig. 3). Mean cell abundances of the magnitude observed upstream of km 168 (Alexandria, Va.) were observed at Marshall Hall, leaving a 16-km river segment with phytoplankton concentrations lower than expected (based on comparisons to pre-1980 data). This sag pattern was observed on all nine upstream-downstream (longitudinal) transects from Memorial Bridge to Quantico in July and August 1980 (July 23, 30; August 4, 5, 6, 7, 8, 13, 20). The phytoplankton sag was

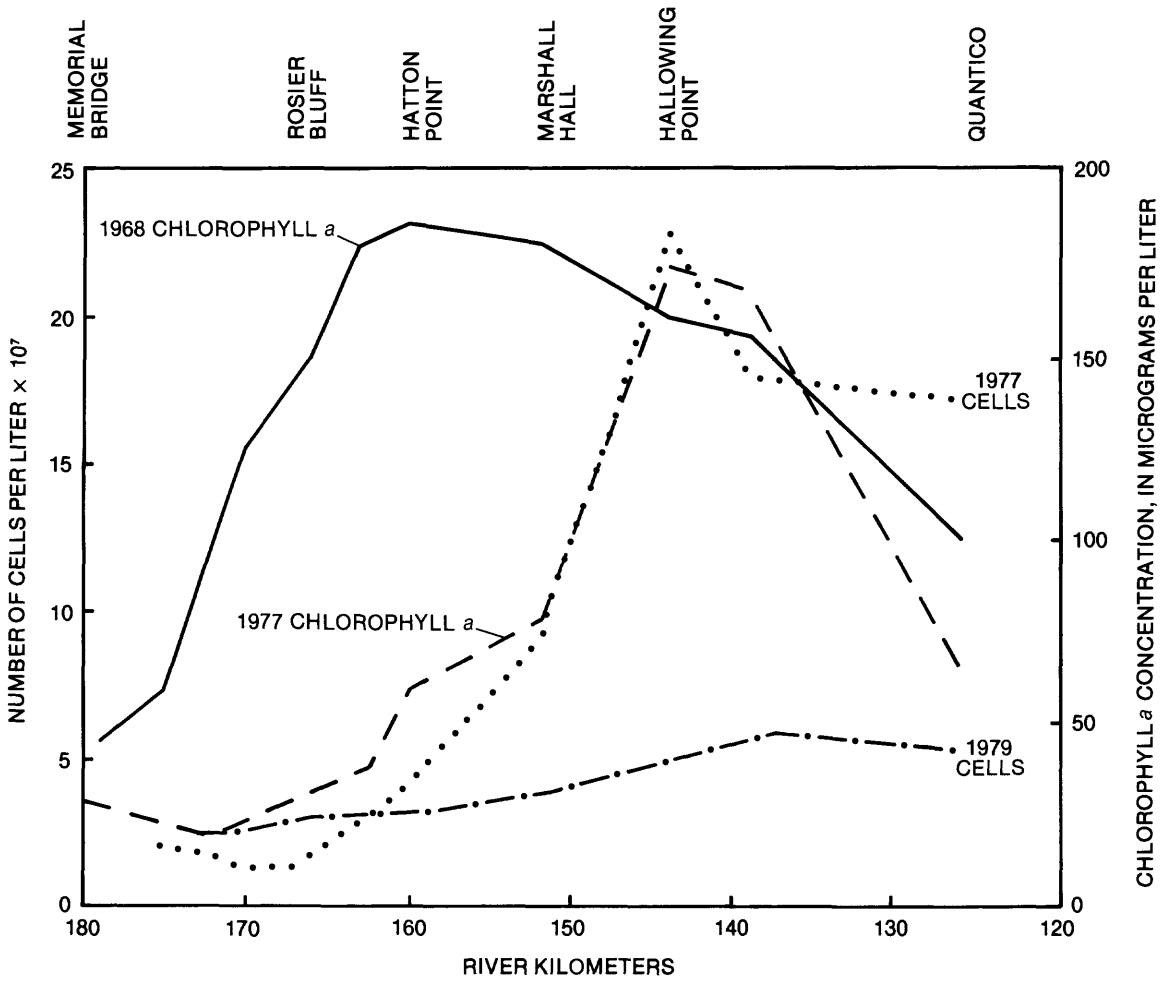

Figure 2. Variation of the mean concentration of phytoplankton, as measured by cell count and chlorophyll *a*, with location in the fresh, tidal Potomac River; 1968 data from Jaworski and others (1972); 1977 data from Smith and Herndon (1980).

prominent in July and August 1981 (mean discharge was 112 $m^3 s^{-1}$ for the July 8–28 transects and 91 $m^3 s^{-1}$ for the entire July–August period) based on mean cell numbers and chlorophyll *a* determined on five longitudinal transects (fig. 3). The 1981 sag extended farther downstream than in 1980, to Marshall Hall, resulting in a 24-km reach of river with depressed phytoplankton abundance. This pattern of phytoplankton distribution was observed on all July 1981 transects (fig. 4). Mean phytoplankton abundance at Marshall Hall in July 1981 was approximately 75 percent lower based on cell counts (40 percent lower based on chlorophyll *a*) than that above Woodrow Wilson Bridge (fig. 3). In August 1981, the sag was prominent with phytoplankton counts at Marshall Hall 20 to 30 percent lower (28 percent lower based on chlorophyll *a*) than those at Alexandria (fig. 3). The August 1981 cell counts are mean values of data from four longitudinal transects.

Growth Rates of Phytoplankton

Phytoplankton growth rates determined from field data were similar to those observed in the laboratory. Growth rate, as the amount of net carbon fixed per unit existing phytoplankton carbon, calculated from primary productivity data (table 1) is an overestimate (McAllister and others, 1964). According to McAllister and others (1964), the rate of particulate carbon production retained as cell biomass is only 60 to 70 percent of net primary productivity. Therefore, mean growth rates for the 1980 low-flow period (July through September) that were calculated from productivity data were multiplied by 0.6; the mean growth rates for each station (table 2) were 0.16, 0.22, 0.23, and 0.01 day^{-1} for Alexandria, Virginia channel (to be referred to as Alexandria 1); Alexandria, Maryland channel (to be referred to as Alexandria 2);

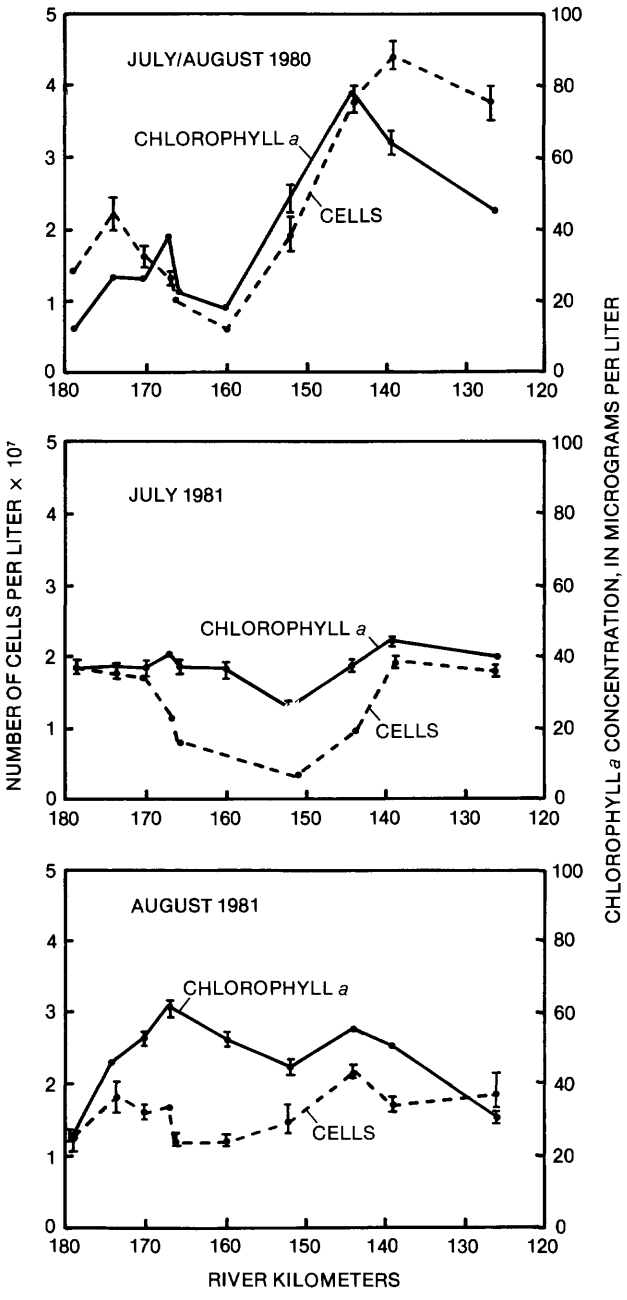

Figure 3. Variation of the mean concentration of phytoplankton, as cell count and chlorophyll *a* concentration with location in the fresh, tidal Potomac River July 23, to August 20, 1980, July 1981, and August 1981: chlorophyll *a*, solid lines; cell counts, dashed lines. Vertical bars are standard error of the mean.

Hatton Point; and Hallowing Point, respectively (table 2). The mean growth rate for all stations, based on productivity, was 0.16 day^{-1} in July through September 1980. The mean growth rates during July through August 1981 were 0.22, 0.09, 0.16, and 0.03 day^{-1} for the same four stations, respectively (table 2).

Samples from Alexandria 1, Hatton Point, and Hallowing Point were collected on June 30, 1981, and grown in the laboratory from July 1–6, 1981. Samples were collected at Alexandria 1 on August 25, 1981, and grown in the laboratory from August 26 to September 3, 1981. Growth rates determined by chlorophyll *a* measurements were higher than those determined by measuring nephelometric turbidity. The nephelometric growth rates ranged from 0.01 day^{-1} to 0.22 day^{-1}. Growth rate based on chlorophyll *a* ranged from 0.09 to 0.30 day^{-1}. The mean growth rate for all stations and all tests was 0.14 day^{-1} (S.D.= 0.08), similar to the summer 1981 mean growth rate of 0.13 day^{-1} based on productivity. It is interesting to note that, as with the growth rate determined by primary productivity, Hatton Point had the highest maximum growth rate (0.22 day^{-1}), followed by Alexandria 1 (0.19 day^{-1}) and Hallowing Point (0.05 day^{-1}) (table 2).

Growth rate was determined from the field data gathered during the phytoplankton-chamber experiments (fig. 5). Growth rate in water taken near Hatton Point in August 1981 was 0.14 day^{-1} (table 2). Water from the Hallowing Point area supports a growth rate of 0.03 day^{-1} (table 2). The growth-chamber rates closely match those determined for Hatton Point and Hallowing Point using productivity and laboratory analyses.

Mean growth rate also was calculated from cell-count data taken while following a parcel of water beginning at Memorial Bridge. The mean cell count on August 11, 1981 (number of samples, n=19), was 1.25×10^7 (S.D.$=0.04\times10^7$) cells L^{-1} and 1.59×10^7 (S.D.$=0.33\times10^7$, n=27) cells L^{-1} on August 12. The number of

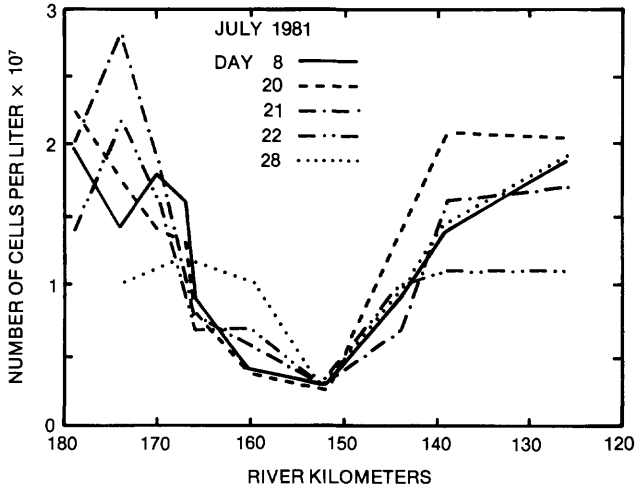

Figure 4. The distribution of phytoplankton abundance, as number of cells per liter, at five transects in July 1981.

Table 1. Growth rates of phytoplankton

[ALVA is Alexandria, Virginia channel; ALMD is Alexandria, Maryland channel; HAT is Hatton Point; HAL is Hallowing Point. Units are day^{-1}. Value should be multiplied by 0.6 to yield carbon-production growth rates. A dash line in table indicates that no data are available]

Date	ALVA	ALMD	HAT	HAL
May 22, 1980	0.55	0.25	—	—
June 24, 1980	0.20	-0.05	—	—
July 24, 1980	0.35	0.10	0.15	-0.08
July 30, 1980	0.69	0.71	0.46	0.05
August 5, 1980	0.79	0.41	0.66	0.05
August 8, 1980	0.86	0.52	0.72	0.14
August 14, 1980	0.56	0.57	0.68	0.19
August 21, 1980	-1.77	-0.07	-0.26	-0.01
August 26, 1980	0.47	0.84	0.67	-0.02
September 4, 1980	0.39	0.32	0.69	0.09
September 16, 1980	0.07	-0.12	-0.23	-0.22
November 19, 1980	0.56	—	0.36	0.06
December 17, 1980	0.92	0.00	-1.62	-0.37
February 5, 1981	0.04	0.18	0.04	-0.38
March 2, 1981	0.26	0.10	-1.46	-2.01
April 16, 1981	- .31	-0.27	-0.23	-0.27
May 20, 1981	- .08	-0.04	—	-0.26
July 1, 1981	- .24	0.03	-0.02	—
July 9, 1981	0.69	0.48	0.46	0.21
July 21, 1981	0.42	0.01	0.23	-0.03
August 4, 1981	0.27	—	—	—
August 19, 1981	0.13	0.08	0.13	-0.04
August 26, 1981	0.29	—	—	—

cells on August 12 was significantly higher than on August 11 ($\alpha = 0.05$, degrees of freedom, df = 44). The calculated growth rate was 0.24 (table 2). There was no difference between phytoplankton counts during a similar study on August 3–5, 1981, near Hallowing Point ($\alpha = 0.05$, df = 50). The mean light intensity was 291 langleys day^{-1} on August 11–12, 1981, and 431 langleys day^{-1} on August 3–5, 1981 (D. Shultz, written commun.).

Effect of Light on Phytoplankton Productivity and Growth

Solar insolation, combined with effects of water-column temperature (itself controlled by solar insolation), regulates primary productivity and growth. Gross primary productivity (GPP) in the Potomac River responded to the seasonal availability of light. Gross primary productivity at all stations was highest during July and August 1980 and 1981 and lowest during the winters of those years (fig. 6; Cohen and Pollock, 1983). The results are typical of east coast rivers and estuaries such as the Chesapeake Bay Estuary (Flemer, 1970), the Hudson River (Sirois and Frederick, 1978), and Peconic Bay (Bruno and others, 1980). Mean gross productivity, July through August 1980, was highest in the Maryland channel of the Alexandria cross section (Alexandria 2), followed by productivity at Hallowing Point, Hatton Point, and Alexandria 1. In June to August 1981, the highest mean productivity was observed at Alexandria 2, then Alexandria 1, Hatton Point, and Hallowing Point.

Water-column productivity per unit of depth-integrated chlorophyll (the assimilation number) was nearly identical for Hatton Point, Alexandria 1, and Alexandria 2 stations and was 75 percent lower at Hallowing Point for the summers of 1980 and 1981 (table 3). The results can be demonstrated more clearly in figure 7. In graphs of gross primary productivity versus depth-integrated chlorophyll *a*, the data show two slopes (fig. 7). All but two of the points higher than 250 mg chlorophyll *a* m^{-2} are from Hallowing Point.

It is important to note that GPP per unit chlorophyll *a* was different for the four stations. The difference is related to the biomass of phytoplankton and the depth of the euphotic zone. The total solar radiation in the water column that is available to phytoplankton decreases as

Table 2. Growth rates determined from field and laboratory experiments

[Alexandria 1 is near Alexandria, Va., in the channel. Alexandria 2 is across the river from Alexandria, Va., near the Maryland shore. Units are $^{-1}$. A dash line in table indicates that no data are available.]

	Station									
	Alexandria 1		Alexandria 2		Hatton Point		Hallowing Point		Mean for all stations	
Methods	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
Field Experiments										
Estimates from productivity analysis	0.16	0.22	0.22	0.09	0.23	0.16	0.01	0.03	0.16	0.13
Following a parcel	—	0.24	—	—	—	—	—	0.00	—	—
Phytoplankton chamber experiments	—	—	—	—	—	0.14	—	0.03	—	—
Laboratory	—	0.19	—	—	—	0.22	—	0.05	—	0.14

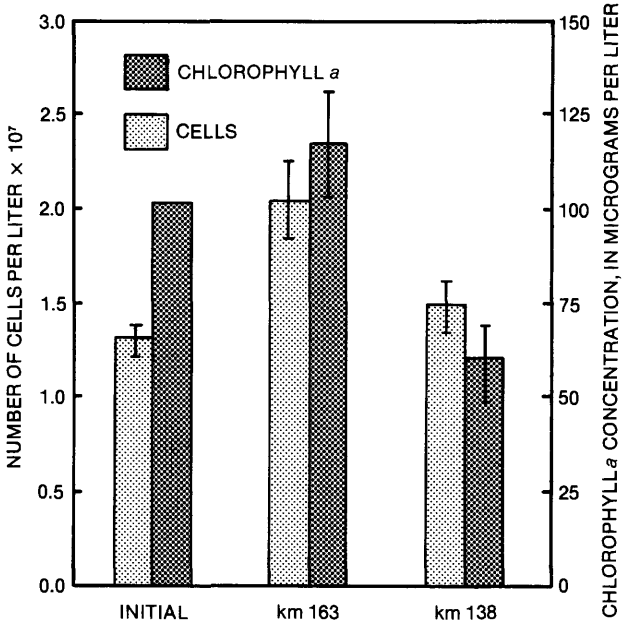

Figure 5. Concentration of phytoplankton cells and chlorophyll *a* in initial samples, and concentrations in samples incubated 4 days in water taken between Rosier Bluff and Hatton Point and between Hallowing Point and Indian Head. There were five chambers incubated in water from each station. Standard deviation = 1. Mean cell counts and chlorophyll a concentrations were significantly different (significance level, $\alpha = 0.005$) after incubation in water from the different stations. Vertical bars are standard error of the mean.

the vertical extent of euphotic zone decreases. The depth of 1 percent of the surface light is an approximation of the limit of the euphotic zone when the euphotic depth is defined as the depth at which GPP is equal to respiration (net primary productivity equals zero) (Parsons and others, 1977). The depth of the euphotic zone is determined by the magnitude of the water-column extinction coefficient for irradiance (also known as the beam attenuation coefficient). The higher the extinction coefficient is, the less light can penetrate the water and the shallower the euphotic zone.

Figure 8 shows how July-August maximum rates of productivity (P_{max}) and mean depth-integrated productivity per unit biomass vary with the extinction coefficient at these stations in the main stem of the fresh, tidal Potomac River.

Hallowing Point not only has the lowest assimilation number, the lowest maximum GPP per unit chlorophyll, and the lowest growth rate in the Potomac River, but it has the highest extinction coefficient for solar radiation. The results presented in this paragraph and in the paragraph before suggest that phytoplankton productivity and growth in the fresh, tidal Potomac River may be limited by light.

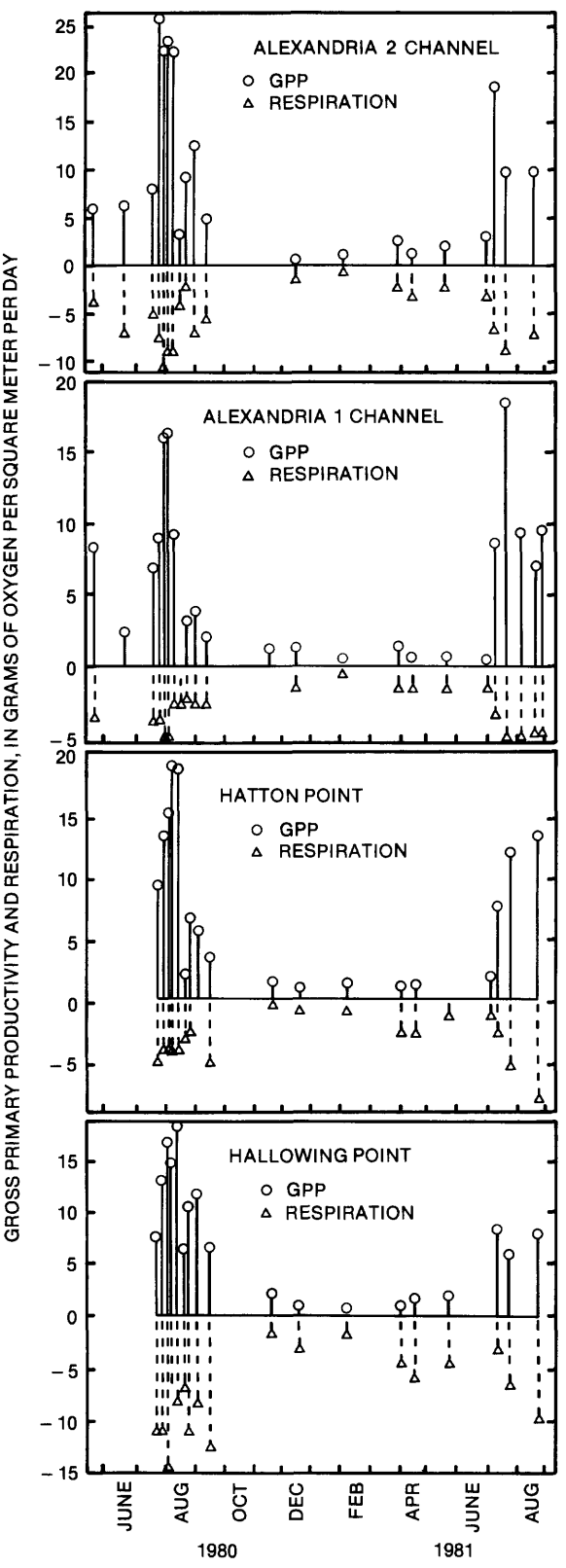

Figure 6. Depth-integrated gross productivity and respiration at four productivity stations from May 22, 1980, to August 25, 1981. Productivity is represented by solid lines; respiration by dashed lines.

Table 3. Gross primary productivity per chlorophyll *a* (the assimilation number) and chlorophyll-to-cell ratios for the productivity stations in the summers of 1980 and 1981

[The assimilation number is (depth-integrated gross primary productivity per depth-integrated chlorophyll mass) grams of molecular oxygen per day per milligrams of chlorophyll *a*. The second column is the average (mean) chlorophyll-to-cell ratios (μg per cell) for the productivity stations in the summers of 1980 and 1981.]

Station	Assimilation number	Chlorophyll-to-cell ratios
1980		
Alexandria 1	0.10	—
Alexandria 2	0.10	—
Hatton Point	0.11	—
Hallowing Point	0.025	—
1980 and 1981 combined		
Alexandria 1	0.09	0.0034
Alexandria 2	0.09	0.0034
Hatton Point	0.09	0.0045
Hallowing Point	0.025	0.0030

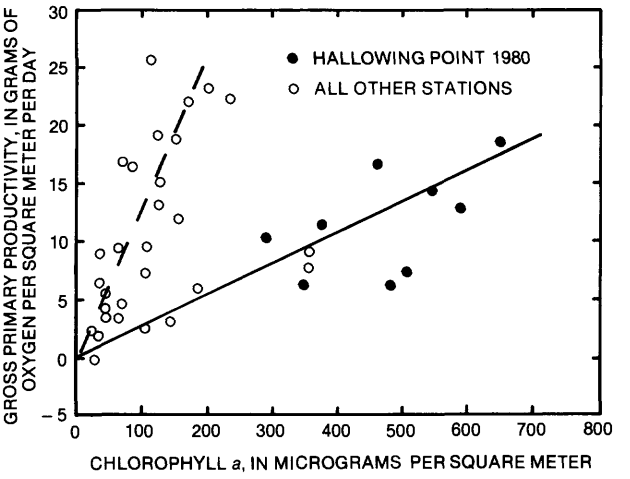

Figure 7. Variation in depth-integrated gross productivity with depth-integrated chlorophyll *a* mass at Alexandria 1 and 2, Hatton Point, and Hallowing Point during the summers of 1980 and 1981. Hallowing Point is represented by closed circles.

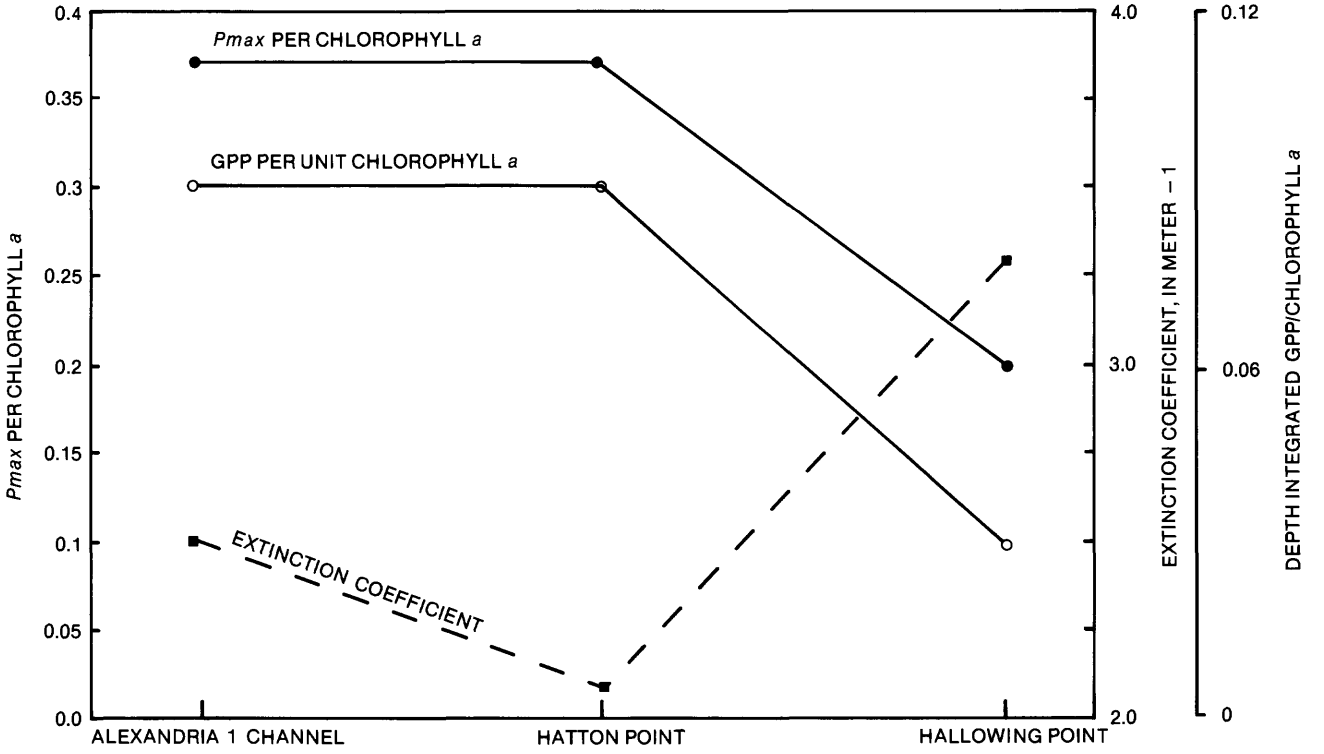

Figure 8. The maximum rate of gross primary productivity as determined from the relationship of productivity to light intensity, P_{max}, per unit chlorophyll *a*; depth-integrated gross productivity per unit chlorophyll *a*; and the extinction coefficient of photosynthetically active radiation in the water column at three stations on the Potomac River.

To quantify the response of the assimilation number to light available to phytoplankton in a well mixed water column, depth-integrated light must be calculated. This depth-integrated light can be calculated by integrating the Lambert-Beer-Bouger equation

$$I_z = I_0 e^{-kz} \tag{5}$$

that determines light at a particular depth (Parsons and others, 1977); and integrating

$$I_0 \int_0^z e^{-kz} dz = \frac{I_0}{k}(1-e^{-kz}) \tag{6}$$

where

I_z = light intensity at a particular depth, z,
I_0 = light intensity at the surface of the water column,
k = water-column extinction coefficient in units of inverse length, and
z = depth.

The relationship of the assimilation number (and growth) to light intensity can be described by an inverse hyperbolic function (Steeman-Nielsen and Jorgensen, 1968). If the relationship is approximately linear, then the productivity-light relationship is on the rapidly rising part of the hyperbolic curve and phytoplankton productivity is light limited (Steeman-Nielsen and Jorgensen, 1968). Figures 9*A*, *B*, *C*, and *D* demonstrate that the relationship of assimilation number and growth rate to light and to the depth of the euphotic zone is approximately linear. The graphs using all 1980 summer data show pronounced heteroscedasticity (figs. 9*A* and 9*C*). This result holds when all of the 1980 data are plotted on one graph and for the individual stations except Hallowing Point. Hallowing Point is not shown because data scatter precludes meaningful analyses. The regression of gross productivity per unit chlorophyll *a* versus light for Hatton Point yields a slope different from that found for Alexandria 1 and 2 and has a coefficient of determination of 0.39. The datum in the lower right quadrant of the graph (fig. 9*C*) may be an outlier. Without that point, the r^2 value is 0.89 and the slope is identical to that of Alexandria 1 and 2 (slope = 0.001).

The assimilation numbers were plotted against depth-integrated light and not just surface light or euphotic depth. The amount of light intercepted by phytoplankton is determined by the combined effects of surface intensity, extinction of light in the water column, and depth of water column.

Phytoplankton in the Potomac River can be light limited due to suspended sediment, light-absorbing dissolved substances, and self-shading. As phytoplankton biomass increases, more photosynthetically active radiation is intercepted and the euphotic depth decreases. The effect of self-shading on the euphotic zone and on productivity can be determined quantitatively by calculating the effect that phytoplankton biomass has on the water-column extinction coefficient. In equation 5, k represents the water-column extinction coefficient of photosynthetically active radiation (PAR) due to the combined effects of the nonliving matter (dissolved and particulate) and the phytoplankton. The parameter k can be divided into the following two components: γ, all components other than phytoplankton such as sediment, pure water, dissolved substances; and δ times chlorophyll *a* concentration, which is some coefficient times the chlorophyll concentration, such that

$$\frac{I}{I_0} = e^{-(\gamma+\delta C)z} \quad \text{(Lorenzen, 1980).} \tag{7}$$

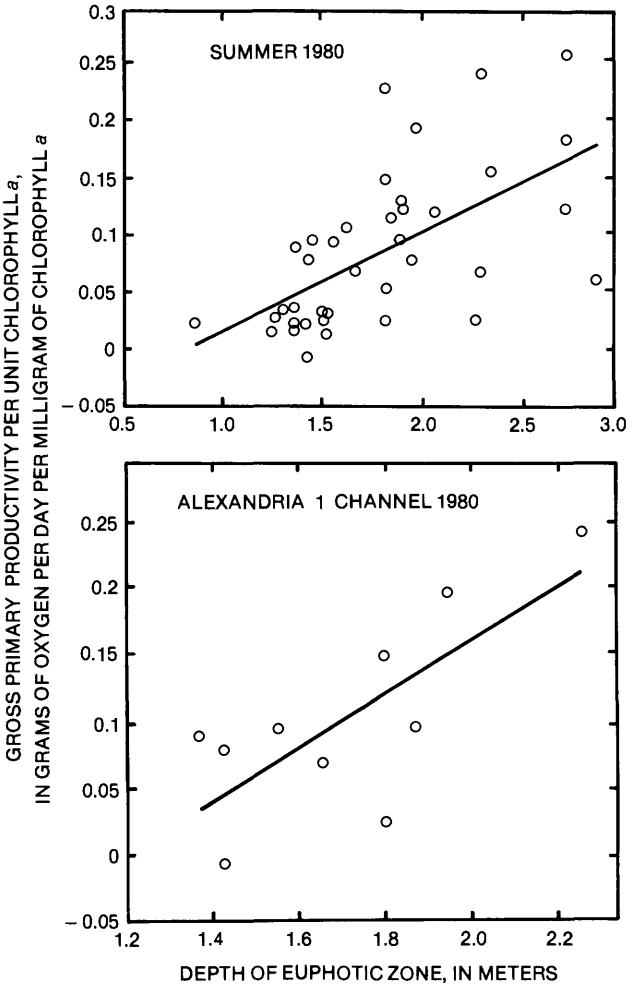

Figure 9A. Variation of gross productivity per unit chlorohyll with depth of euphotic zone for all stations in the summer of 1980 and for Alexandria 1 in the summer of 1980.

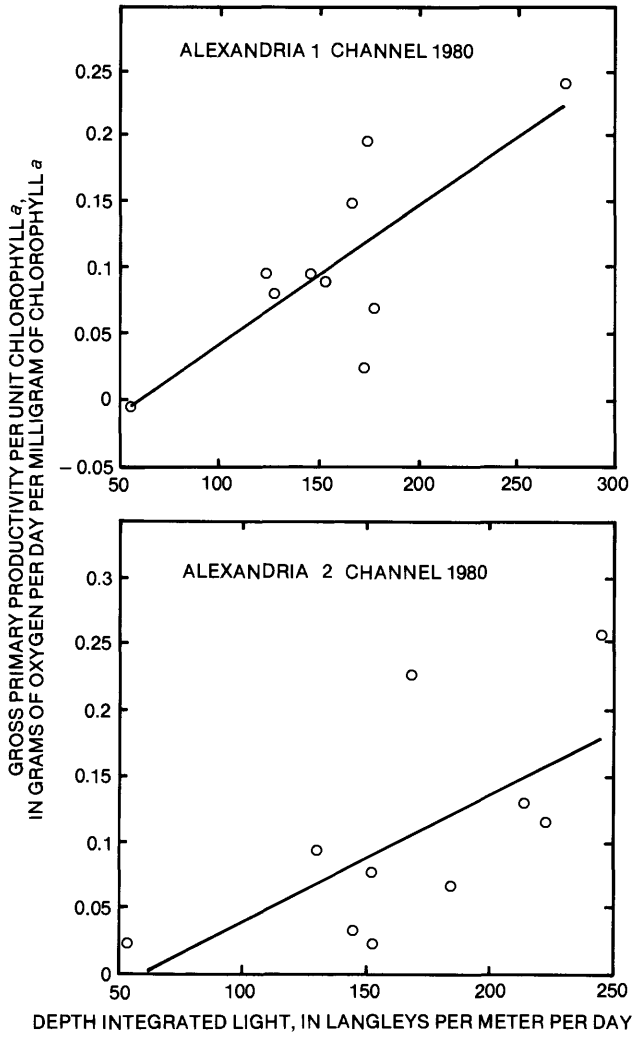

Figure 9B. Variation of gross productivity per unit chlorophyll *a* with depth-integrated light for Alexandria 1 and 2, summer 1980.

The estimated depth of the euphotic zone yields

$$k = \frac{ln\ 0.01}{z} = -\frac{4.605}{z} = -(\gamma + \delta C). \qquad (8)$$

A plot of $4.605/z$ (which is, in this instance, k) as a function of chlorophyll concentration will yield a slope, δ, and an intercept, γ. The γ and δ for the productivity stations Alexandria 1, Alexandria 2, Hatton Point, Md., and Hallowing Point, Va., along with Marshall Hall, Md., are shown in table 4. These parameters were calculated from quantum radiometer measurements taken on the dates of the productivity analyses. Values of δ reported in the literature are between 0.006 and 0.02 m^2 mg chlorophyll a^{-1} (Westlake and others, 1980) and are generally between 0.01 and 0.02 in marine systems. For the fresh, tidal Potomac River in July and August of 1980, the values at the stations discussed in this paragraph range from 0.011 to 0.014 m^2 mg chlorophyll a^{-1}. The mean value of δ for all the stations was 0.014 m^2 mg chlorophyll a^{-1} (table 4). Thus, when chlorophyll *a* concentration was 97 $\mu g\ L^{-1}$ ($\mu gL^{-1} = mg\ m^{-3}$) at Hallowing Point on August 7, 1980, δC (the contribution of chlorophyll to the extinction coefficient) was 1.26 when k was 3.03. When the chlorophyll *a* concentration was 306 $\mu g\ L^{-1}$ at the same station on August 24, 1977 (Clark and Roesch, 1978), δC was 3.98 when the extinction coefficient was 5.58 (estimated from Secchi depth as 1.7/Secchi depth, m^{-1}).

Phytoplankton growth rates in the fresh, tidal Potomac River can be calculated from light and chlorophyll data. If summer 1980 and 1981 net primary productivity (*NPP*) data are regressed against the depth of

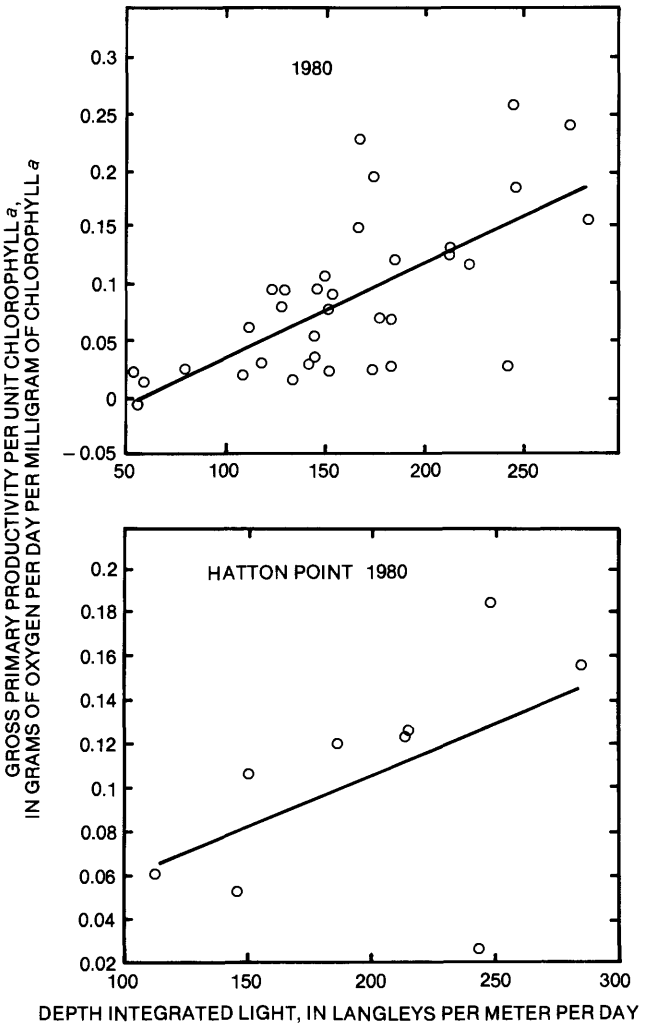

Figure 9C. Variation of assimilation ratio (gross primary productivity per unit chlorophyll *a*) with depth-integrated light for the summer of 1980 and Hatton Point, 1980.

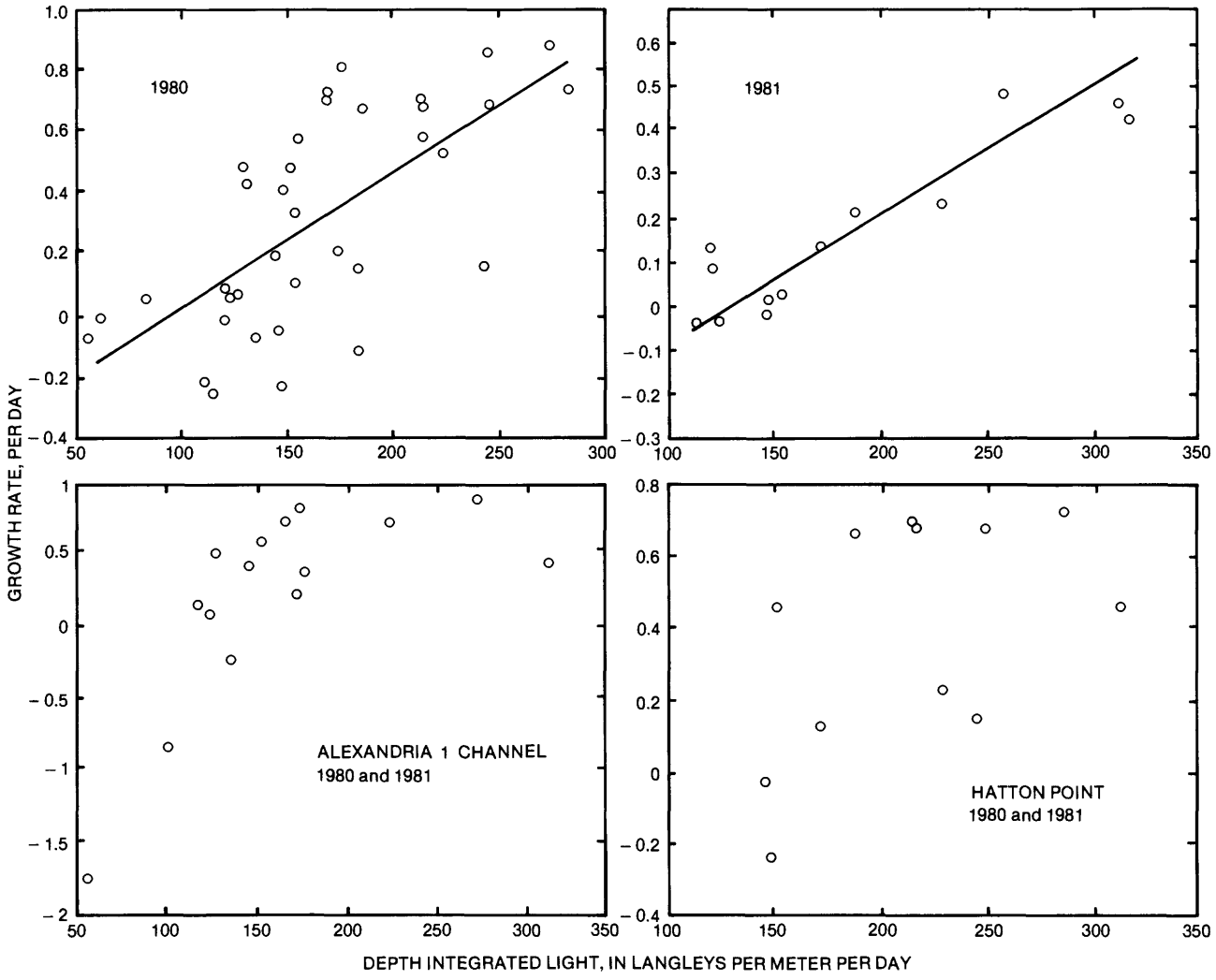

Figure 9D. Variation of growth rate with depth-integrated light for the summers of 1980, 1981, and for 1980 and 1981 summer data at Alexandria 1 and Hatton Point.

1 percent light, the relationship is linear and is described by the equation,

$$NPP = -0.214 + 0.245(Z_{1\%}) \,, \qquad (9)$$

where $Z_{1\%}$ is the depth of 1 percent light.

This equation can replace *NPP* in equation 2. From equation 8, the depth of 1 percent light can be represented as $4.605/(\gamma + \delta(\text{chlorophyll } a \text{ concentration}))$ and combined with equations 9 and 2 to yield:

$$K_G = ln\left(\frac{[B_0 + (A + B\,(\,\frac{4.605}{\gamma + \delta C}\,))]}{B_0}\right)/t \,, \qquad (10)$$

where:

A and B = regression coefficients for the relationship of primary productivity per unit chlorophyll to the depth of 1 percent light.

If carbon is assumed to be 30 times the chlorophyll *a* concentration (Parsons and others, 1977) and initial biomass is in terms of carbon, then K_G (the growth rate) would be -0.019 day^{-1} (a net loss of biomass) when chlorophyll *a* concentration is 300 μg L^{-1}, 0.012 day^{-1} (a net gain) when chlorophyll *a* concentration is 100 μg L^{-1}, and 0.23 day^{-1} when chlorophyll *a* concentration is 25 μg L^{-1}. Hallowing Point had the highest concentrations of chlorophyll *a* of all the main stem productivity stations and had the lowest assimilation numbers and growth rates calculated from productivity data (fig. 7; table 1).

Table 4. Phytoplankton (δ) and nonphytoplankton (γ) components of extinction coefficients in the fresh, tidal Potomac River, Md., calculated for the dates of the July through September productivity experiments
[γ in units of m^{-1}, δ in units of m^2 mg chlorophyll a^{-1}]

Parameters	Data for all stations	Alexandria 1	Alexandria 2	Hatton Point	Hallowing Point	Marshall Hall
γ	2.05	2.51	1.87	1.55	2.43	1.95
δ	0.014	0.011	0.013	0.025	0.013	0.015

If the parameters, γ,δ, (table 4) and A and B (-0.214 and 0.245, respectively) determined for the fresh, tidal river, are used in equation 9 along with the mean, summer chlorophyll *a* concentration at each station for the productivity experiments, then equation 9 generates a K_G for each station that closely matches those calculated from productivity analysis (fig. 10). It should be noted that the only variable in the equation is chlorophyll *a*.

If surface light remained constant day to day, then the growth rate would be observed to increase with increasing depth of the euphotic zone. A plot of growth rate against depth-integrated light intensity takes into consideration the depth of euphotic zone and the amount of surface light. Figure 9*D* shows examples of such plots. The scatter in the data is due to the assumptions made calculating the growth rates from productivity data. The graphs of growth rate against light for the stations with the highest levels of depth-integrated light—Alexandria 1 and Hatton Point—may show some saturation of growth rates at high light intensities (fig. 9*D*). Thus, self-shading is an important regulator of phytoplankton growth rate in the fresh, tidal Potomac River.

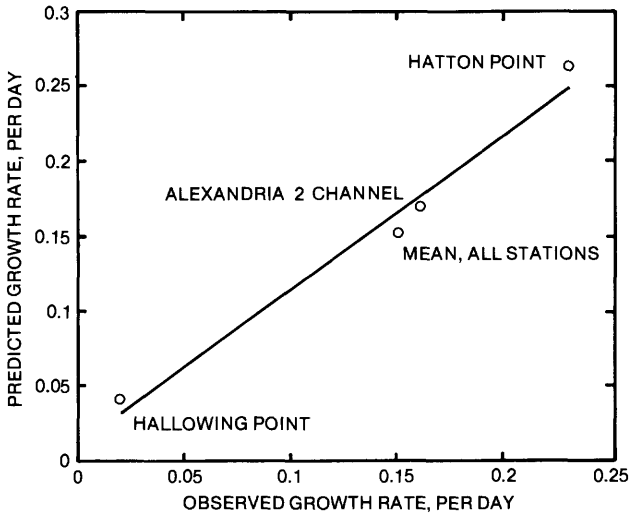

Figure 10. A regression of predicted growth rates on observed growth rates in the main channel of the fresh, tidal Potomac River. Station names are listed next to the data point.

Self-shading can determine the maximum supportable biomass of phytoplankton of the Potomac River. As the euphotic zone becomes very shallow due to phytoplankton biomass, the nonliving component of the extinction coefficient, δ becomes insignificant, and $ln\ 0.01 \approx \delta C_{max}$ (the maximum concentration of chlorophyll when the euphotic-depth approaches zero). For the Hallowing Point to Indian Head reach, the mean value of δ for 1980 was 0.014 m^{-1} (S.D. = 0.004), and the predicted C_{max} was 288 $\mu g\ L^{-1}$. Talling (1960) and Westlake and others (1980) reported an empirical equation to determine maximum supportable chlorophyll biomass:

$$C_{max} = \frac{3.7}{\delta}.$$

For the Hallowing Point to Indian Head reach, the C_{max} predicted by the Talling equation is 231 $\mu g\ L^{-1}$. The mathematical model (equation 9) shows that growth rate will be zero when chlorophyll *a* concentration is 260 $\mu g\ L^{-1}$. Thus, the maximum concentration of chlorophyll supportable by the tidal, fresh Potomac River is between 231 and 288 $\mu g\ L^{-1}$. Clark and Roesch (1978) reported that August 1977 chlorophyll *a* concentrations (uncorrected for phaeopigments) ranged from 300 to 312 $\mu g\ L^{-1}$ in the Hallowing Point to Indian Head reach. If phaeopigments are assumed to be 10 percent of the chlorophyll *a* and $\delta = 0.014\ m^{-1}$, it is demonstrated by three independent methods that in 1977, the fresh, tidal Potomac River supported the maximum possible concentration of chlorophyll *a* which was limited only by self-shading.

Assimilation numbers depend on the chlorophyll content of cells, which in turn are regulated by environmental conditions (Paasche, 1968; Tolstoy, 1979). The chlorophyll-to-cell ratio in the tidal, fresh Potomac River varies from station to station in a predictable manner. Figures 11 and 12 show the station to station distribution of chlorophyll-to-cell ratios for individual days, July 30, 1980, and July 21, 1981 (a.m.); the mean ratio during the summer of 1980 and the summer of 1981; and

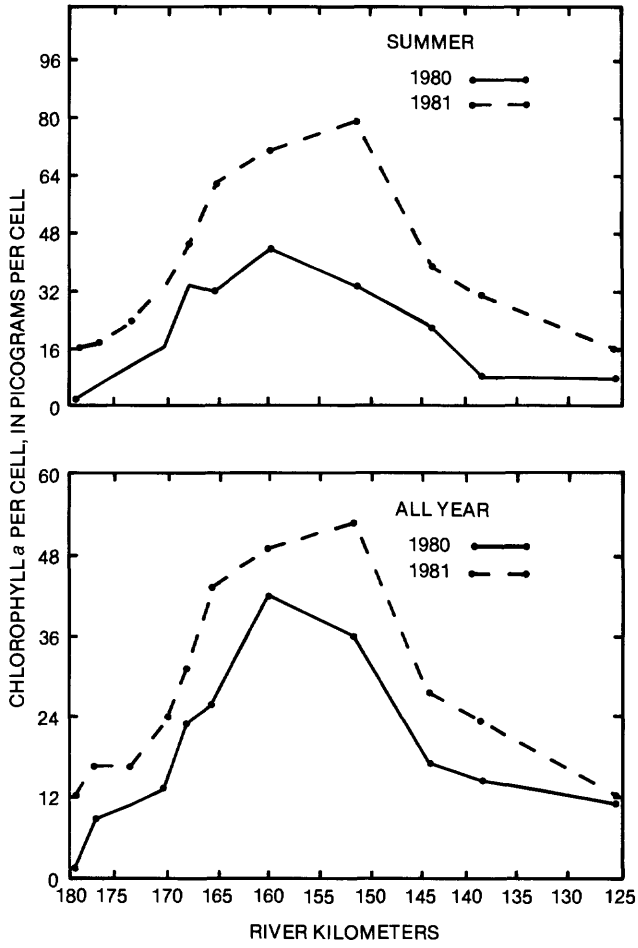

Figure 11. Variation of chlorophyll *a* per cell for all fresh, tidal Potomac River data that have matching chlorophyll *a* and cell-count determinations for the summer of 1980 and 1981 and all of years 1980 and 1981.

the mean ratio for all of 1980 and 1981. The highest ratios occur at Hatton Point, Rosier Bluff, and Marshall Hall. As previously seen in figure 3, these three stations had the lowest concentrations of phytoplankton in the fresh, tidal Potomac River during 1980 and 1981. Hatton Point has the highest assimilation numbers of the productivity stations and, along with Marshall Hall, the highest chlorophyll-to-cell ratios. Therefore, Hatton Point has the highest GPP per cell of all the productivity stations. Phytoplankton in the Hatton Point to Marshall Hall reach receive the highest levels of depth-integrated light intensity as evidenced by the lower extinction coefficient (table 5). In contrast, Hallowing Point receives the lowest quantity of depth-integrated light and shows the lowest assimilation numbers and chlorophyll-to-cell ratio of the primary productivity stations.

The chlorophyll mass-per-cell estimates can be biased if the phytoplankton significantly differ in size, taxonomic composition, and proportion of colonies with respect to station location or date of sampling. For instance, a large number of colonies (where a small colony is counted as one cell) would underestimate phytoplankton cell numbers (and perhaps biomass), whereas a large number of small, single cells might overestimate phytoplankton biomass. This does not seem to be the case in the Potomac River if closely spaced stations are compared. Table 6 lists the percent composition (by genera) and cell volume of phytoplankton at Alexandria 1, Hatton Point, and Marshall Hall on July 28, 1981. The volumes are based on estimates by Wetzel (1975) and Sicko-Goad and others (1977). The taxonomic compositions at the three stations are similar, the total cell volumes are similar at Alexandria 1 and Hatton Point, and small colonies compose approximately 10 percent of each. The chlorophyll-per-cell ratios, however, differ: 0.004 μg cell^{-1} at Alexandria, 0.010 μg cell^{-1} at Hatton Point, and 0.010 μg cell^{-1} at Marshall Hall. Several other dates (July 23, 1980, October 21, 1980, and November 18, 1980) that show widely varying chlorophyll-to-cell ratios were examined. Alexandria,

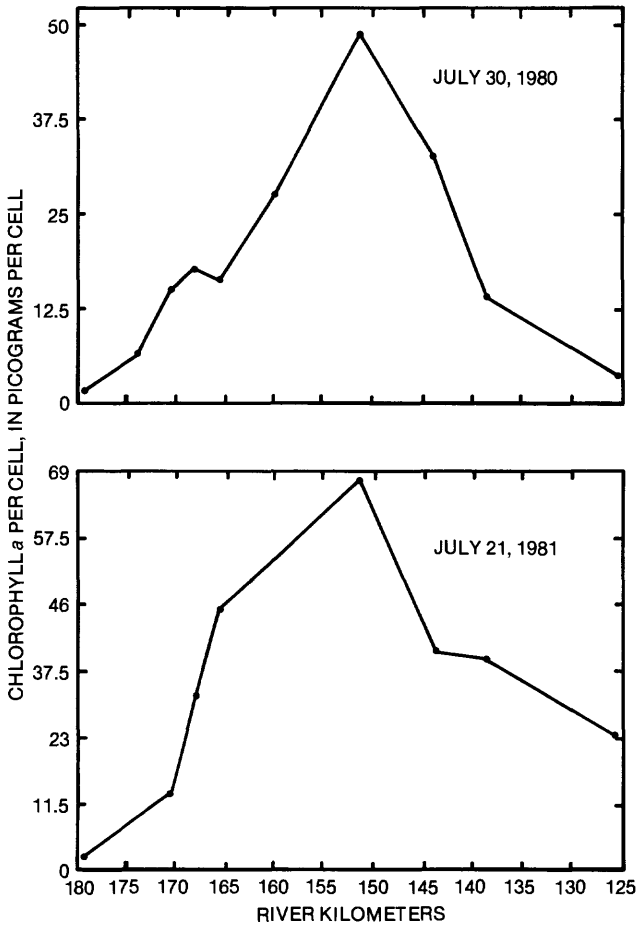

Figure 12. Variation of chlorophyll *a* per cell on July 30, 1980, and July 21, 1981.

Table 5. Solar radiation extinction coefficients (K) and depth-integrated light (DIL) in langleys m^{-1} day^{-1} in the water column at selected sites on the Potomac River

[Alexandria, Virginia channel (Al VA); Alexandria, Maryland channel (Al MD); Hatton Point (Hatton); Hallowing Point (Hal); Mount Vernon (MtV); Quantico (Q); and Douglas Point (Dg) stations. Extinction coefficients were determined using quantum sensor measurements of the depth of 1 percent light except where marked: * = K determined by Secchi disc; t = K determined by quantum sensor measurement 50 percent light. Dashes indicate that no data are available.]

Dates of Productivity Analysis	Al VA		Al MD		Hatton		Hal		MtV	Dg	Q
	K	DIL	K	DIL	K	DIL	K	DIL	K	K	K
1980											
May 22	-2.52	—	-2.33*	—	—	—	—	—	-3.70*	—	—
May 29	—	—	—	—	—	—	—	—	—	-2.30*	-3.70*
June 23-24	-2.52	176	-3.04*	146	—	—	—	—	-2.66*	—	—
June	—	—	—	—	—	—	—	—	-2.65*	-2.79*	25-26
July 23-24	-2.74	180	-3.21*	154	-2.02*	245	-3.66*	135	—	—	—
July 29-30	-2.53	169	-2.53	170	-2.83*	152	-5.31*	81	—	—	—
August 4-5	-2.33	177	-3.15	131	-2.21	187	-3.36	123	—	—	—
August 7-8	-1.99	277	-2.48	225	-1.95	287	-3.03	185	—	—	—
August 13-14	-3.34	156	-2.41	216	-2.41	216	-3.61	144	—	—	—
August 20-21	-3.20	57	-3.36	54	-1.59	114	-3.01	60	—	—	—
August 25-26	-3.22	130	-1.68	247	-1.68	249	-3.52*	119	—	—	—
September 3-4	-2.43*	148	-2.35*	154	-1.68	215	-3.02	120	—	—	—
September 15-16	-2.94*	126	-1.99	185	-2.52	147	-3.36	110	—	—	—
November 18-19	-2.58*	—	—	—	-1.57	—	-2.36*	—	—	—	-1.38
December 16-17	-1.82	—	-1.51	—	-2.28	—	2.95	—	—	—	-2.30*
1981											
February 4-5	-1.16	—	-1.16	—	-1.18*	—	-2.54*	—	—	—	-1.16
April 1-2	-2.58*	—	-3.04*	—	-4.72*	—	-6.80*	—	—	—	-3.54*
April 15-16	-3.68	—	-3.44*	—	-3.09	—	-3.44	—	—	—	—
May 19-20	-2.52	—	-2.52	—	-2.48	—	-3.60	—	—	—	-4.90
June 30-July 1	-3.03	138	-2.74	153	-2.88	146	-3.22	130	—	—	-4.15*
July 8-9	-2.43*	229	-2.16	258	-1.78	314	-2.97	188	—	—	-4.15*
July 20-21	-1.33[t]	318	-3.03	148	-1.95	229	-3.62*	124	—	—	-3.21*
August 3-4	-3.52	—	—	—	—	—	—	—	—	—	—
August 19-20	-2.79*	120	-2.78*	121	-1.95	172	-2.98*	113	—	—	—
August 25-26	-2.90	—	—	—	—	—	—	—	—	—	—

Rosier Bluff, Hatton Point, and Marshall Hall were compared. On all but November 18, 1980, the three stations supported the same dominant algae and similar taxonomic compositions. Yet the chlorophyll-to-cell ratios differed by as much as 300 percent between stations on each date. The repetitive nature of the chlorophyll-to-cell ratio distributions precludes random error of cell counts or chlorophyll measurements as a source of the variation in the ratio. Thus, productivity per unit chlorophyll, and chlorophyll-per-cell, differ from station to station in the fresh, tidal Potomac River. An implication is that the sag in phytoplankton abundance observed in 1980 and 1981 may actually be more prominent than indicated by chlorophyll *a* concentrations, because the sag occurs in the region of highest chlorophyll-to-cell ratios.

Light not only regulated the longitudinal distribution of chlorophyll-to-cell ratios (and therefore the chlorophyll distribution), but it also may have determined the vertical profile of chlorophyll *a*. Figure 13*A* shows the morning (a.m.) and evening (p.m.) profiles of chlorophyll *a* at Hatton Point and Alexandria (Virginia channel) on August 13, 1980, and the p.m. profiles at Hallowing Point on September 3, 1980 (data from Blanchard and others, 1982). Afternoon profiles showed maximum chlorophyll concentrations between the surface and 1-m depth.

The chlorophyll concentrations also changed in the productivity bottles during the incubations. The equivalent depths for the 100, 65, 32, 16, and 6 percent of surface light intensities at which productivity incubations were made were calculated by using the extinction coefficient and equation 5. Figure 13*B* shows typical chlorophyll *a* concentrations at the end of the incubations plotted as a function of depth. Initial concentrations of chlorophyll were the same from bottle to bottle, because they were taken from the same, well mixed 20-L carboy. The maximum increases of chlorophyll *a* during the day occurred between 0.1 and 1.0 meters of equivalent depth for all the July to August 1980 productivity studies that were examined. The curves are similar to the results shown in figure 13*A*. Table 7 shows the depths at which the maximum chlorophyll occurred in situ, and the equivalent depths at which the maximum chlorophyll appeared in the productivity bottles for the dates shown in figure 13. The only factor that varied from bottle to bottle

Table 6. Generic composition of phytoplankton on July 28, 1981, percentage of total, total numbers in cells per milliliter, volume estimates from literature, and percentage of small colonial composition for three stations that vary greatly in chlorophyll-to-cell ratio
[Dashes indicate that a particular organism was not present in the sample or that a volume estimate was not available in the literature]

Genera	Alexandria 1		Hatton Point		Marshall Hall		Volume (Estimation from literature)
	Percentage of total	Number of cells per milliliter	Percentage of total	Number of cells per milliliter	Percentage of total	Number of cells per milliliter	μm^3
Melosira	32	3700	28	2900	19	630	70,000
Stephanodiscus	17	2000	16	1600	22	720	5,000
Cyclotella	8	960	11	1100	16	540	10,000
Cryptomonas	4	480	10	1000	14	480	1,500
Ankistrodesmus	2	240	4	420	—	—	250
Scenedesmus	14	1700	5	540	7	240	1,000
Chlamydomonas	3	360	5	480	3	90	250
Chroomonas	5	600	5	480	4	120	35
Anacystis	3	360	5	540	4	120	80
Nitzchia	1	120	2	240	—	—	240
Synedra	—	—	1	120	—	—	700
Navicula	—	—	1	60	—	—	—
Surirella	—	—	1	60	—	—	—
Dictyospherium	1	120	1	60	—	—	—
Kirshneriella	—	—	1	120	2	60	—
Oocystis	2	240	1	120	2	60	400
Coelastrum	1	120	1	60	—	—	—
Oscillaturia	—	—	2	240	1	30	17,500
Glenodinium	1	120	1	120	—	—	—
Tetraedon	2	240	—	—	—	—	40
Agmenellum	3	360	—	—	—	—	—
Tetrastrum	—	—	—	—	3	90	—
Gymnodinium	—	—	—	—	1	30	—
Total volume of dominant 70 percent	2.84×10^8 μm^3		2.3×10^8 μm^3		0.54×10^8 μm^3		
Volume per cell μm^3	3.4×10^4		3.2×10^4		2.4×10^4		
Chlorophyll per cell, μg cell	0.004		0.010		0.010		

Table 7. Depth below water surface, in meters, of maximum chlorophyll a concentrations measured in situ and determined from productivity experiments
[All in situ chlorophylls are from the afternoon]

Date	Station	Depth of in situ maximum chlorophyll a concentration, in meters	Depth of maximum chlorophyll a concentration as determined experimentally, in meters
August 13, 1980	Hatton Point	0.6	0.7
August 13, 1980	Alexandria 1	0.9	0.3–0.6
September 3, 1980	Hallowing Point	0.9	0.9
August 20, 1980	Alexandria 1	1.8	0.9

in the productivity experiments was light intensity. Thus, light generated the differential chlorophyll concentrations in the productivity experiments and may have been the forcing function for the vertical profiles observed.

The maximum rate of primary productivity (P_{max}) always occurred between 0 and 1 meter depth, the region of maximum chlorophyll *a* concentration increase (0.1 to 1 meter). Figure 14 shows depth profiles of primary productivity at Alexandria 1. During the summer months, P_{max} is typically at the surface of the water column. Surface P_{max} was observed at 51 of 78 depth profiles from May 22, 1980 to August 25, 1981. P_{max} appeared at the greatest depth below the surface when light penetration into the water column was greatest (when the extinction

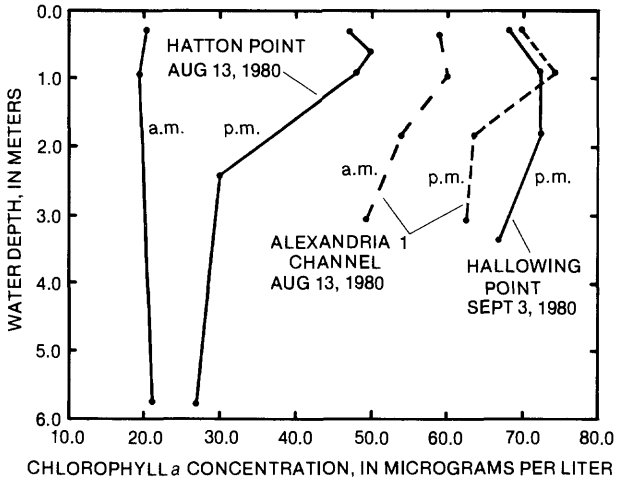

Figure 13A. Variation of in situ chlorophyll *a* concentration with depth for two days in 1980; a.m. are morning measurements, p.m. are afternoon or evening measurements.

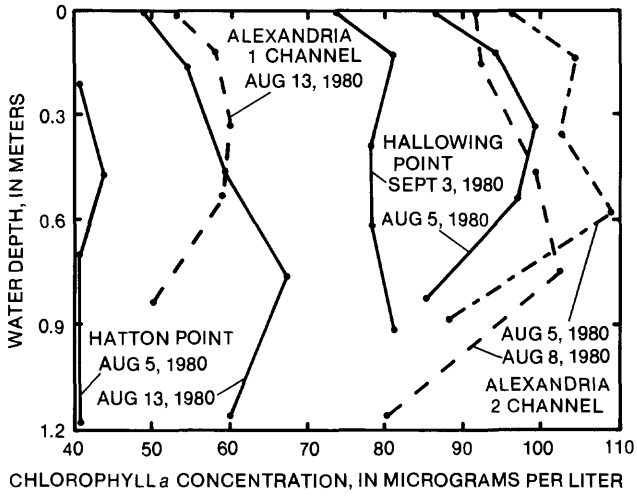

Figure 13B. Variation of chlorophyll *a* concentration in productivity bottles as a function of equivalent river depth. Equivalent depth was calculated by means of the proportion of surface light for the bottle incubations (100, 65, 32, 16, 6 percent) and the extinction coefficient. Initial chlorophyll concentration, in all cases, was equal to or lower than the lowest chlorophyll concentration in each vertical profile.

coefficient was the lowest; figs. 15 and 16). Lower productivity at the surface than at some depth below the surface has been interpreted as light-induced, surface inhibition of productivity (Fee, 1973). The inhibition, however, may be due to the incubation of samples at surface light intensity when the phytoplankton were adapted to a mean or integral light intensity as a result of rapid mixing (Marra, 1978).

The equivalent vertical profiles determined from the productivity incubations may have been the result of an increase in chlorophyll per cell or an increase of both chlorophyll and cells. For the productivity experiments for which there are both cell counts and chlorophyll measurements, the chlorophyll-to-cell ratio at the depth of maximum chlorophyll increased at Alexandria 1 on April 16, 1981, July 9, 1981, August 19, 1981, and August 26, 1981; at Alexandria 2 on July 9, 1981, and August 19, 1981; at Hatton Point on July 9, 1981 and August 19, 1981; at Hallowing Point on May 20, 1981, and August 19, 1981; and at Quantico on July 9, 1981. Cell abundance increased as much as or more than chlorophyll at Alexandria 1 on May 20, 1981, and July 21, 1981; at Alexandria 2 on April 16, 1981, May 20, 1981, and July 21, 1981; at Hatton Point on April 16, 1981, May 20, 1981, and July 21, 1981; at Hallowing Point on April 16, 1981, July 9, 1981, and July 21, 1981; at Quantico on May 20, 1981, and July 21, 1981. Therefore, the increase of chlorophyll in the productivity experiments and in situ was sometimes manifested as an increase of the chlorophyll-to-cell ratio (46 percent of the time) or as an increase in both cells and chlorophyll (54 percent of the time).

Control of K_C by Phosphorus

Phytoplankton growth rates may have been limited by phosphorus under certain conditions during July and August of 1980. One-day bioassays performed in conjunction with primary productivity analysis in the summer of 1980 demonstrate a statistically significant enhancement of productivity by phosphorus in 14 cases ($\alpha = 0.05$) (Cohen and Pollock, 1983). Ammonia additions enhanced productivity in four cases and nitrate did not enhance productivity.

The magnitude of the enhancement due to phosphorus additions was related to the light history of the phytoplankton. The enhancement was linearly proportional to the mean of the light intensity of the day of incubation and the 2 days prior to the incubation (fig. 17). Phosphorus increased productivity by up to 55 percent at Hatton Point, 36 percent at the Alexandria 2 station, and 21 percent at Hallowing Point when phytoplankton were exposed to high light intensity for several days (approximately 500 langleys day^{-1}). When phytoplankton samples were exposed to low light (<300 langleys day^{-1}) for 3 days, there was no increase in productivity.

The in situ concentrations of total dissolved phosphorus measured at the productivity stations at the time of the bioassays were typically higher than the level reported to be limiting to phytoplankton (0.02 mg L^{-1}) or the level required to support a bloom of 5 to 20 mg L^{-1} dry weight (90 to 350 μg L^{-1} chlorophyll *a*) (Rhode,

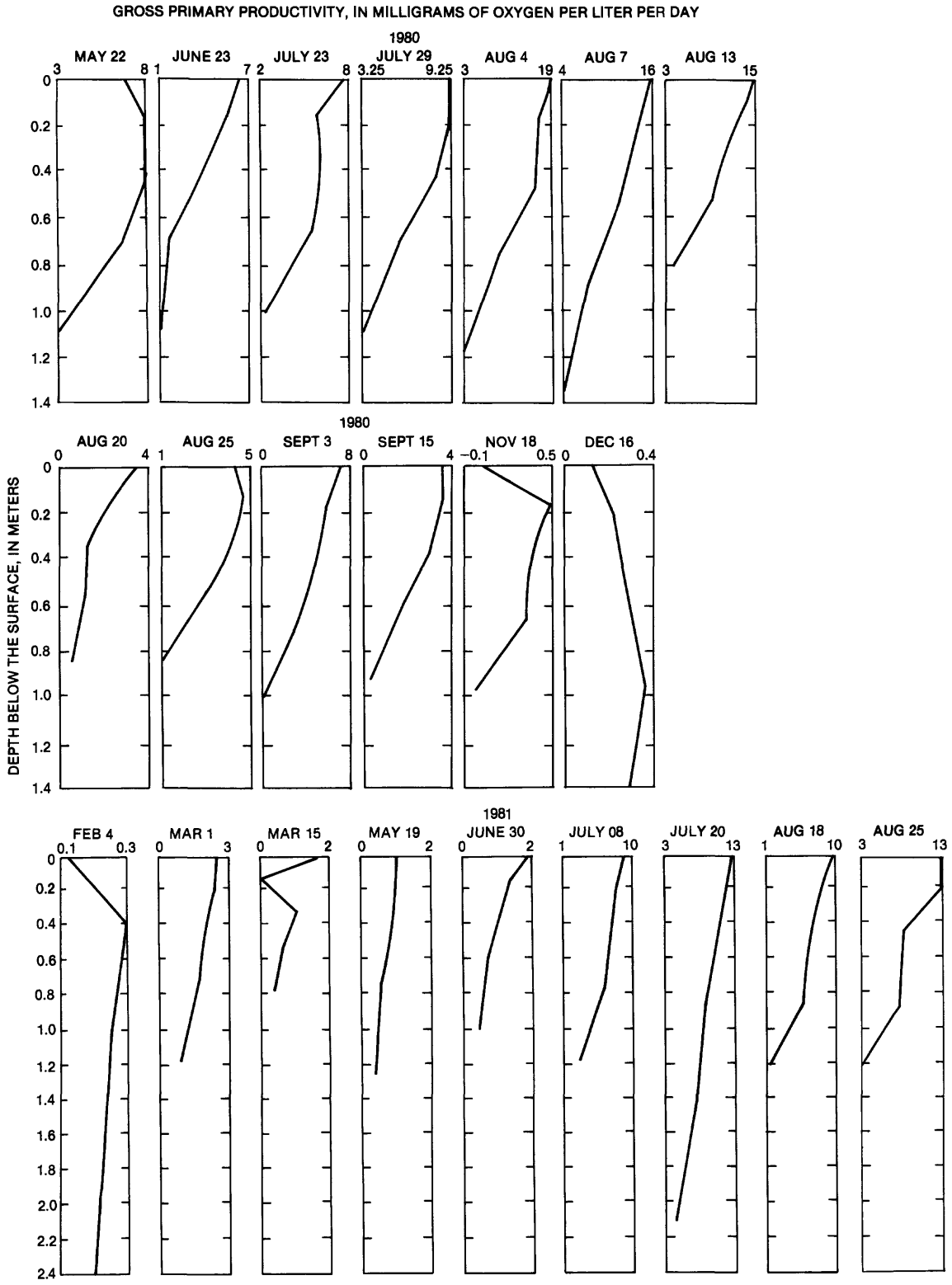

Figure 14. Depth profiles of gross primary productivity from May 1980 through August 1981 at Alexandria 1.

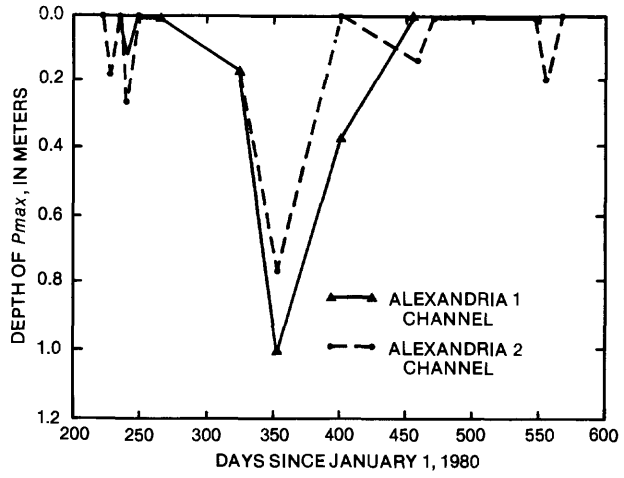

Figure 15A. Variation of the depth of maximum primary productivity, P_{max}, with time at Alexandria 1 and 2.

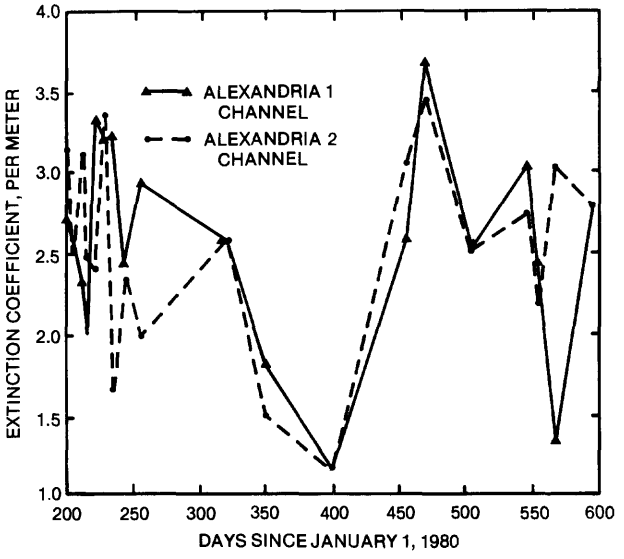

Figure 15B. Variation of extinction coefficients with time at Alexandria 1 and 2.

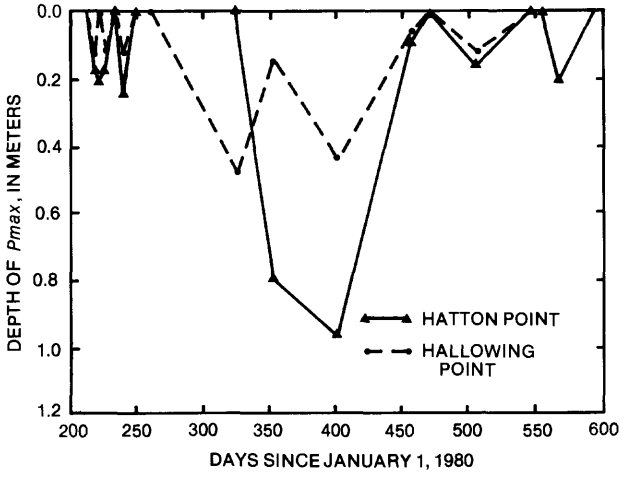

Figure 16A. Variation of the depth of maximum primary productivity, P_{max}, with time at Hatton Point and Hallowing Point.

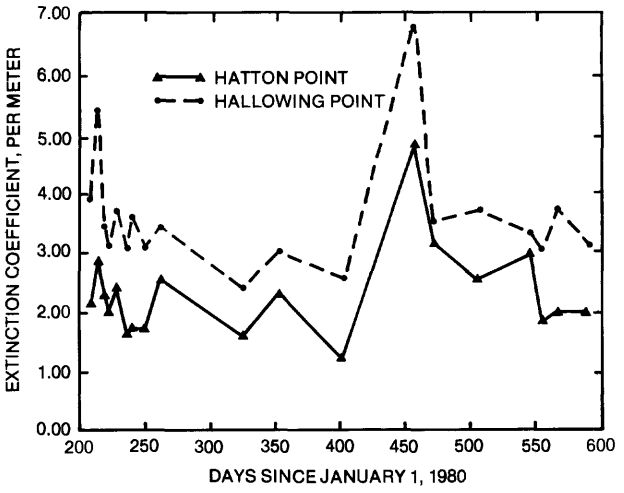

Figure 16B. Variation of extinction coefficients with time at Hatton Point and Hallowing Point.

1948; Fitzgerald, 1972; Fee, 1973), except at Hallowing Point in the last week of August and during September 1980 (table 8). Although phosphorus concentrations during the last two weeks of August 1980 at Hallowing Point were less than 0.02 mg L^{-1}, there was enough phosphorus (an average of 0.006 to 0.008 mg L^{-1} ranging up to 0.019 mg L^{-1}) to support an additional 25 to 75 μg L^{-1} of chlorophyll *a* as calculated from the the Redfield ratio (Borrego and others, 1975). Therefore, either some other environmental factor limited phytoplankton growth, or the phosphorus was not in a form available to the phytoplankton. Phosphorus may have been one of the factors that limited phytoplankton growth in the Hallowing Point to Indian Head reach during the unusually dry September of 1980. The total dissolved phosphorus discussed above includes organic-, poly-, and orthophosphate. The results suggest that the dissolved phosphorus may not have been in a form that was available at rates suitable to support maximum or optimal rates of photosynthesis and growth. The total pool of phosphorus was large enough to support a higher phytoplankton biomass than was observed.

There was little evidence that phosphorus concentration limited primary productivity in the summer of 1981. Phosphorus-enhanced primary productivity was observed only at Hatton Point (km 160) on July 21, 1981. Phosphorus concentration was 0.041 mg L^{-1} on that date. Nitrate enhancement was observed at Hatton Point on July 9, 1981. Ammonia did not stimulate productivity.

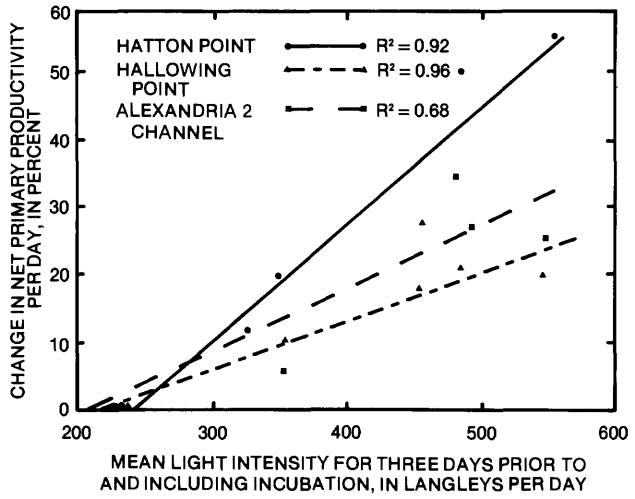

Figure 17. The variation in percent of phosphate-induced enhancement of primary productivity with light intensity. Light is the mean of 3 days—2 days prior to incubation and the 1 day of the incubation.

The above discussion concerns short-term enhancement of productivity by phosphorus. Long-term (6 to 7 days) enhancement of growth was examined in the laboratory. Phosphate stimulated growth in samples taken from Alexandria 1 on August 26, 1981. Dissolved reactive-phosphorus concentration was 0.035 mg L^{-1} in the field on August 26. The growth rate (K_G), with 0.36 mg L^{-1} PO_4 added, was 0.17 and 0.21 day^{-1} measured using nephelometry and chlorophyll *a*, respectively. Growth in the controls was 0.04 and 0.09 day^{-1}. Phytoplankton growth was increased in samples from Hatton Point on July 1, 1981 (ambient concentration was 0.044 mg L^{-1}). The K_G was 0.22 with the addition of 0.36 mg L^{-1} PO_4 and 0.10 day^{-1} in controls (measured by nephelometry). The impact of phosphorus on the phytoplankton growth constant can be estimated with an equation analogous to Michaelis-Menten kinetics (Fogg, 1975).

The equation is

$$K_G = K_{max} \frac{S}{K_m + S} \qquad (11)$$

where

K_G = specific growth rate, day^{-1},
S = nutrient concentration, mg L^{-1},
K_{max} = maximum specific growth rate, and
K_m = half-saturation constant, mg L^{-1}.

An average K_m for freshwater phytoplankton based on literature values is 0.026 mg L^{-1} as P (Lehman and others, 1975; Fuhs and others, 1972). The maximum rate of growth, K_{max} for the fresh, tidal Potomac River phytoplankton, observed in laboratory-enrichment experiments was 0.22 day^{-1} for July 1, 1981 samples. The phytoplankton were grown at light intensities equivalent to surface light in the Potomac River so that K_{max} may be an overestimate. A plot of the equation constructed from these parameters is shown in figure 18.

The average P concentration in the Hallowing Point (km 144) to Indian Head (km 138) area during July and August 1981 (the time and place of the highest phytoplankton concentrations in the fresh, tidal Potomac) was 0.041 (S.D. = 0.029, n = 39) mg L^{-1}—a concentration capable of supporting a growth rate of K_G = 0.14. The growth rate supportable by phosphorus at Hallowing Point is an order of magnitude higher than observed growth rates and may point to limitation of growth by another factor such as self-shading.

The phytoplankton sag between Rosier Bluff and Marshall Hall, discussed earlier, could be the result of nutrient limitation, which would induce low growth rates. The mean concentration of dissolved inorganic nitrogen (as N) and total dissolved phosphorus (as P) in the sag

Table 8. Dissolved phosphorus, as PO_4, in mg L^{-1} for the dates that the productivity samples were taken or, if that was unavailable, for the date closest to the experiments
[If more than one sample per day was available, the mean is presented. Dashes mean that data were not available]

Dates of productivity analysis	Stations			
	Alexandria 1	Alexandria 2	Hatton Point	Hallowing Point
May 22, 1980	0.031	—	—	—
June 24, 1980	0.064	0.22	0.069	—
July 24, 1980	0.078	0.023	0.053	0.022
July 30, 1980	0.068	0.069	0.045	0.025
August 5, 1980	0.057	0.049	0.030	0.011
August 8, 1980	0.037	0.035	0.024	0.025
August 14, 1980	0.062	0.042	0.034	0.019
August 21, 1980	0.073	0.040	0.029	0.008
August 26, 1980	0.049	0.042	0.104	0.006
September 4, 1980	0.018	0.017	0.021	0.002
September 16, 1980	0.033	0.065	0.001	0.000
November 19, 1980	0.076	—	0.061	0.030
December 17, 1980	0.031	0.069	0.055	0.019
February 5, 1981	0.106	—	0.087	0.070
April 2, 1981	—	—	—	—
April 16, 1981	0.059	—	—	—
May 20, 1981	0.126	—	0.045	0.024
July 1, 1981	0.076	—	0.044	—
July 9, 1981	0.042	0.087	0.050	0.029
July 21, 1981	0.040	0.038	0.047	0.027
August 4, 1981	0.048	0.077	0.046	0.113
August 19, 1981	0.046	—	0.041	0.038
August 26, 1981	0.033	0.041	0.029	0.033

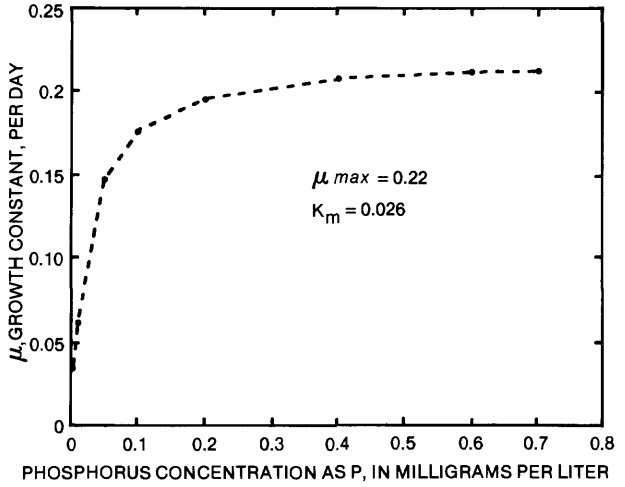

Figure 18. Variation in growth rate with phosphorus concentration. μmax is maximum growth rate and K_m is the half-saturation constant.

reach in July and August 1980 was, respectively, 1.78 mg L^{-1} (S.D. = 0.28) and 0.048 mg L^{-1} (S.D. = 0.016). Smith and Herndon (1980) reported that on August 25, 1977, and September 8, 1977, concentrations of dissolved inorganic nitrogen and phosphorus in the same area (near Broad Creek, km 163) were 1.96 mg L^{-1} (S.D. = 0.13) and 0.065 mg L^{-1} (S.D. = 0.004). Clark and Roesch (1978) measured dissolved inorganic nitrogen and what they call filtered inorganic phosphorus on nine dates between July 18 and August 29, 1977. The mean dissolved nitrogen was 1.75 mg L^{-1} (S.D. = 0.4) and filtered inorganic phosphorus was 0.12 mg L^{-1} (S.D. = 0.04). Thus there was little, if any, difference between the mean nitrogen and phosphorus concentrations when there was a sag in 1980 and no sag in 1977.

The concentration of nutrients in the Rosier Bluff to Marshall Hall sag reach in July to August 1980 and 1981 (stated above) was higher than that found in the high biomass reach near Hallowing Point—0.86 mg L^{-1} (S.D. = 0.25) of dissolved N; 0.019 mg L^{-1} (S.D. = 0.012) of dissolved P in 1980. Growth rates determined by three independent methods show that the sag area supported the highest growth rates in the fresh, tidal Potomac River.

Relationship of Phytoplankton Abundance to Discharge

The sag similar to that between Rosier Bluff and Hatton Point observed in 1980 and between Rosier Bluff and Marshall Hall in 1981 was observed on August 14, 1969, by Clark and Jaworski (1972). There were peak discharges on August 6 (382 $m^3 s^{-1}$) and August 10, 1969 (356 $m^3 s^{-1}$), measured at km 190. The peak discharges would have arrived at Hatton Point (km 160) and Marshall Hall (km 152) at the time the chlorophyll *a* measurements were made because the hydraulic residence time at km 190 to 160 at a discharge of 300 $m^3 s^{-1}$ is 2 to 3 days. Two weeks earlier, on July 29, 1969, no sag was observed, suggesting that peak discharge washed phytoplankton out of the reach. In fact, continuously high flow results in low phytoplankton concentrations throughout the tidal, fresh Potomac River as shown for September 1979 in figure 2 (flow remained above 115 $m^3 s^{-1}$ from July to September 1979). Only one peak discharge (286 $m^3 s^{-1}$) occurred in July and August 1980 (July 11) and would not have affected any longitudinal transects or induced any sags. A peak discharge of 323 $m^3 s^{-1}$ on July 6, 1981, may have induced the sag observed on July 8. A 1-km-long sag has been reported between Marbury Point and Alexandria, Va., in June 1969 (Jaworski and others, 1969). We do not know the cause of this sag. The highest phytoplankton biomass in June 1969 was observed between Rosier Bluff and Marshall Hall, the area of the 1980 and 1981 sags.

Inhibition of Phytoplankton by Toxic Substances

The reduction of the number of phytoplankton and the phytoplankton sag may have been due to toxic substances in the water. Sewage treatment and power plant effluents may contain substances, such as chlorine, that are toxic to algae (Toetz and others, 1977). Byproducts of microbial nitrification may result in production of hydroxylamine, a strong inhibitor of phytoplankton growth (Gunner, 1980). The 1980 and 1981 loss of phytoplankton occurred in the reach 3 to 9 km downstream from the Washington, D.C., major sewage treatment plant (Blue Plains) and a steam electric station. In 1980 and 1981, the highest concentrations of phytoplankton below the sag reach were observed between Hallowing Point and Quantico (fig. 3). Phytoplankton samples, collected from the region of highest phytoplankton biomass, were placed in the 100-mL, Plexiglas phytoplankton chambers after zooplankton were filtered from the water. Five chambers were incubated for 4 days in depth- and time-integrated water samples collected from km 138 (30 km downstream from the sewage treatment plant) and five chambers of the same phytoplankton were incubated in water collected from km 163 (the sag region), 5 km downstream from the sewage treatment plant. Phytoplankton abundance at the end of the 4-day incubation was greater in water taken from the sag reach than from the segment that supported the highest in situ biomass of phytoplankton (fig. 5). Chambers were inoculated with 90 mL of a sample that had a concentration of 1.38×10^4 cells mL^{-1}. The mean number of cells at the end of the incubation in chambers incubated in water

from km 163 was 2.06×10^4 cells mL^{-1} (S.D. = 2.12×10^3); in water from km 138 it was 1.50×10^4 cells mL^{-1} (S.D. = 1.56×10^3). The final number of cells observed in the chambers incubated in sag area water was significantly higher than the final number of cells incubated in water from the reach supporting the high biomass ($\alpha = 0.005$).

Effect of Invertebrates on Phytoplankton

Clam Distribution

The Asiatic clam, *Corbicula fluminea*, was first observed in the fresh, tidal Potomac River in 1977 (Dresler and Cory, 1980). The average density at Rosier Bluff was 1.2 clams m^{-2} (fig. 19). From the size of the clams, Dresler and Cory (1980) estimated that the clams first invaded the tidal Potomac River in 1975. By August 1978, *Corbicula* density had increased to 200 clams m^{-2} at km 166. The number at Rosier Bluff had increased to 425 clams m^{-2} (159 grams of wet weight per square meter) by 1979, 1400 clams m^{-2} (959 g m^{-2}) by 1980 and 1467 clams m^{-2} (3139 g m^{-2}) by July 1981 (fig. 19). A die-off of the clams began the last week in July 1981 (indicated by floating, decaying clam tissue) and continued for at least 3 weeks. The October 1981 abundance of clams at Rosier Bluff was 93 percent less than in July 1981 (fig. 19). *Corbicula* biomass in the Rosier Bluff to Marshall Hall reach was reduced by 62 percent. *Corbicula* biomass remained high at Marshall Hall. In 1980 and 1981, the highest biomass of clams occurred in the same reach as the phytoplankton sag. *Corbicula* have been reported capable of clarifying phytoplankton-laden water (Greer and Ziebell, 1972; Haines, 1979; Rogers and others, 1979; Lauritsen and Mozley, 1983). The *Corbicula* may have been responsible for the loss of phytoplankton between Rosier Bluff and Marshall Hall and may account for the reduction of phytoplankton biomass in the entire fresh, tidal river in 1980 and 1981. Therefore, we examined if (1) there was a biomass of *Corbicula* large enough to reduce phytoplankton abundance levels, (2) *Corbicula* were capable of filtering phytoplankton from Potomac River water, and (3) there was evidence that *Corbicula* were filtering phytoplankton in the river.

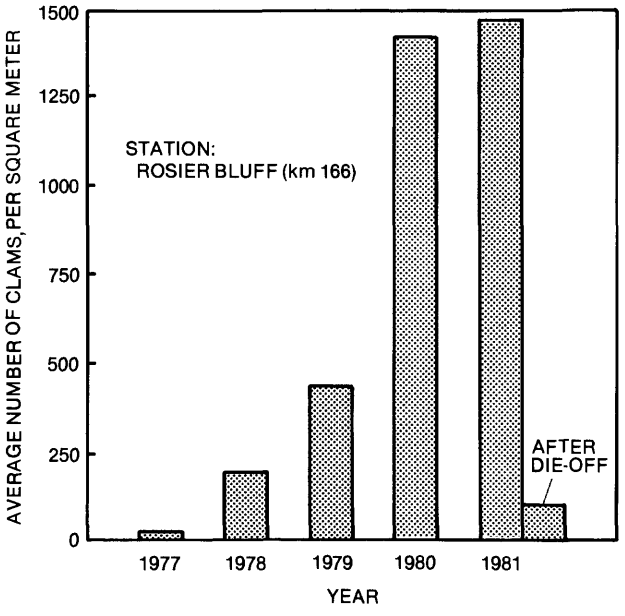

Figure 19. Mean number of *Corbicula fluminea* at Rosier Bluff (km 166) from 1977 to 1981. Units are clams per square meter.

The abundance, biomass, and age-class data for *Corbicula* collected in July 1981 was used to estimate the *Corbicula* distribution for July 1979 and 1980 at stations not included in the 1979–80 surveys. Clams in all samples collected during the July 1981 reconnaissance survey were counted, measured, and weighed. The clams were categorized into four size classes based on size-frequency distribution reported by Dresler and Cory (1980): class 1, 0 to 13 mm; class 2, 13 to 18 mm; class 3, 18 to 25 mm; class 4, >25 mm. Each size class represents a year class[5] for *Corbicula* (Gunning and Suttkus, 1966). The observed wet weight (with shell) for each size (year) class is presented in table 9.

Table 9. Mean wet weight per clam and estimated year class of *Corbicula fluminea* in the Potomac River, July 1981
[Classification according to Gunning and Suttkus (1966)]

Year class	Mean wet weight per clam, in grams	Standard deviation	Number of samples
1	0.48	0.23	36
2	1.47	0.50	50
3	4.30	0.98	50
4	10.37	2.76	41

In order to test our ability to predict wet-weight biomass of *Corbicula* (with shell) based on the observed number and year class of the clams, we estimated the wet-weight biomass for July 1981 and compared the estimates to observed biomass. The estimated biomasses were within 15 percent of observed values (table 10). The observed wet weights of *Corbicula* in July 1981 are shown

[5]A year class is a group of organisms that were the result of all reproductive cycles for a year. They may not be one year old if there was more than one reproductive cycle that year.

Table 10. A comparison of observed and estimated biomass (wet weight) of *Corbicula fluminea* in July 1981
[Estimates were based on the number of clams within each year class and the mean weight for each class]

Station (km from Chesapeake Bay)		Observed wet weight of clams, in grams per square meter	Estimated wet weight of clams, in grams per square meter	Difference in percent
Hunting Creek	(167)	797	885	11.4
Rosier Bluff	(166)	3193	2810	-12.0
Broad Creek	(163)	1543	1378	-10.7
Swan Creek	(160)	723	828	14.6
Piscataway Creek	(158)	1232	1101	-10.6
Machley Point	(157)	310	264	-14.8
Mt. Vernon	(155)	1482	1497	1.0
Dogue Creek	(153)	493	516	4.7
Gunston Cove	(148)	352	397	12.8

in figure 20, along with the phytoplankton distributions (from figs. 2 and 3). Subtracting the number of clams in year class one from the total number of clams present at each bank-to-bank transect in July 1981 yielded estimates of the number and wet weight of clams at the transects in July 1980 (fig. 20). When year class one and two were subtracted from the July 1981 *Corbicula* distributions, an estimate for July 1979 was obtained (fig. 20). The estimated clam abundances for 1979 and 1980 are minimum numbers for the periods. The calculations described above do not account for the large mortality of year class one clams (Dresler and Cory, 1980; Rogers and others, 1979).

Britton and others (1977) suggest that *Corbicula fluminea* produces two spatfalls per year (spring and fall) and that they complete their life cycles in 2 years or less. Three factors suggest that this interpretation is not valid for the Potomac River:

1. The 1980 size-frequency histograms of Dresler and Cory (1980) do not show bimodal size-class peaks.
2. If the life cycle of *Corbicula* were 2 years, most of those found at Rosier Bluff in 1977 would be dead by 1979 or 1980. No dead clams (empty shells) were found in the 1979 or 1980 surveys at Rosier Bluff. In 1981, however, the dead-to-live ratio at Rosier Bluff was 1.6 suggesting an increased mortality in the fourth year.

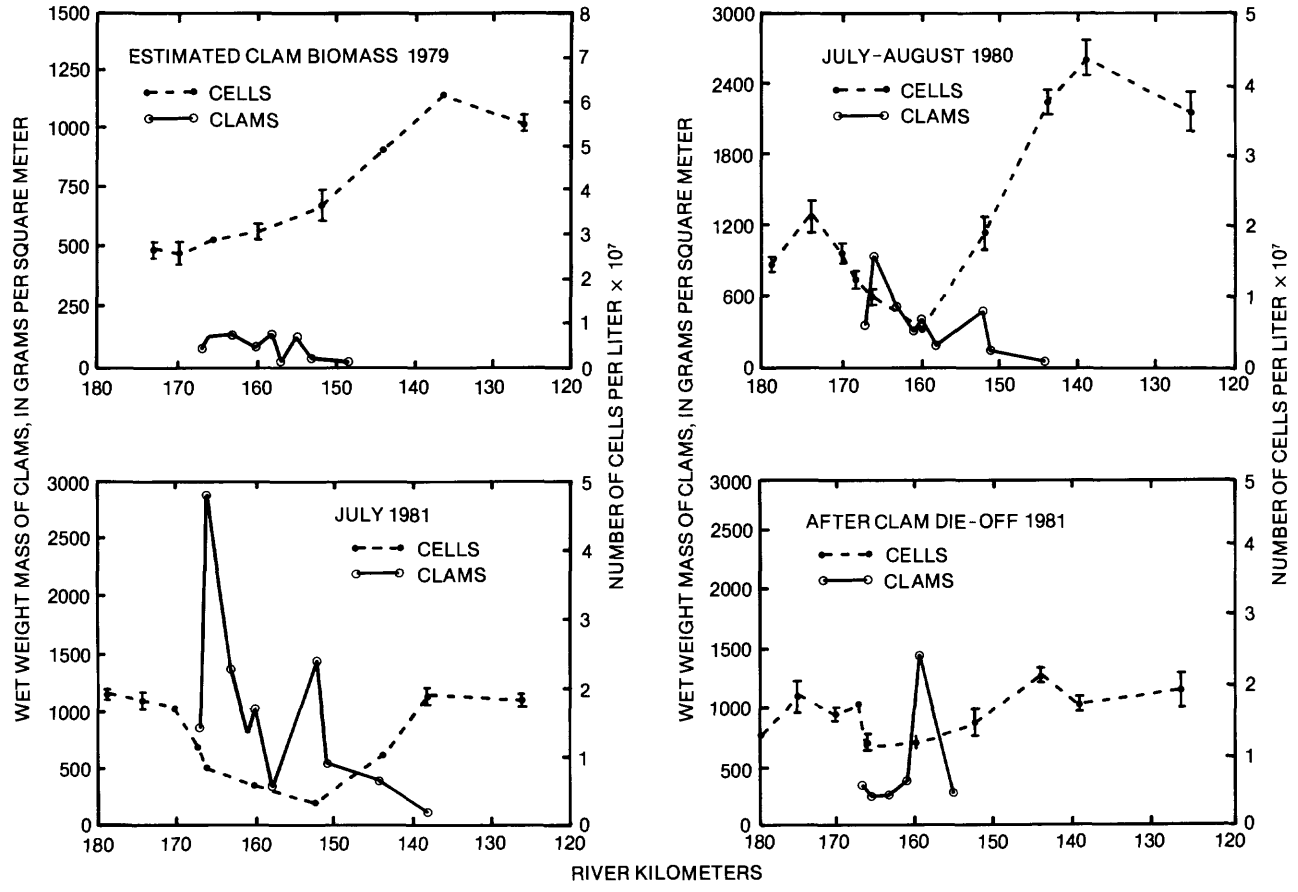

Figure 20. Longitudinal distribution of *Corbicula fluminea* biomass (mean wet weight per transect in grams per square meter) (solid line) and phytoplankton cell numbers per liter (dashed lines) in September 1979, July to August 1980, July 1981, and August 1981. Vertical bars are standard error of the mean.

3. The *Corbicula* biomass at Rosier Bluff in July 1979 was 159 g wet weight m^{-2}. The biomass for the same date calculated from 1981 size-class distribution was 123 g wet weight m^{-2}. The agreement between observed and estimated values for 1979 based on one reproductive period a year supports the contention that *Corbicula* produce one successful spatfall per year in the Potomac River.

Mean discharge was very high in July and August 1979 (155 m^3 s^{-1}). The phytoplankton sag that was observed in 1980 coincides with the location of the highest *Corbicula* abundances (fig. 20). The zone of the phytoplankton sag in July 1981 extended even further downstream than in 1980 (fig. 20).

Distribution of *Corbicula* in October 1981, after the clam die-off, was very different than in July 1981 (fig. 20). A 46 percent reduction in the average number of clams (498 to 270 m^{-2}) and a 62 percent reduction in wet weight (1137 to 510 g m^{-2}) between km 166 to 155 was observed. The number of clams m^{-2} decreased 93 percent at Rosier Bluff, 45 percent at a location midway between Rosier Bluff and Hatton Point and had increased 300 percent at Hatton Point (biomass increased only 17 percent at Hatton Point). The mass of clams between Rosier Bluff and Hatton Point in October 1981 was equal to the estimated mass of clams in July and August 1980.

Filtration by Clams

We measured filtration rates of *Corbicula* by measuring the change of nephelometric turbidity (NTU) in beakers (fig. 21). The slope of the relationship of NTU to time is the filtration rate (table 11). The average pumping rate for all weight classes (wet weight including shell)

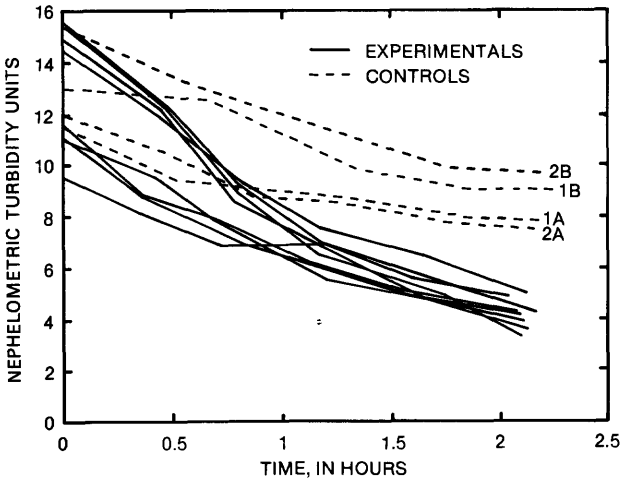

Figure 21. The change of nephelometric turbidity (NTU) with time due to filtration by clams; it includes settling rate (curves 3A,B to 6A,B) and settling rates in control beakers (curves 1A,B and 2A,B).

Table 11. Summary of filtration rates of *Corbicula fluminea*

[To calculate filtration rates, the equation of Prokopovich (1969) was used and settling rates in the controls were subtracted. Two experiments were performed consecutively and labeled A and B. Experiment controls were labeled 1 and 2]

Experiment label	Mean wet weight of clams, in grams (SD)	Number of clams	Filtering rates, in milliliters per hour per gram clam
3A	3.2 ± 0.4	8	32.9
3B	3.2 ± 0.4	8	33.9
4A	4.2 ± 0.6	8	19.4
4B	4.2 ± 0.6	8	22.6
5A	7.1 ± 1.0	6	13.8
5B	7.1 ± 1.0	6	21.3
6A	2.3 ± 0.4	8	17.9
6B	2.3 ± 0.4	8	30.9

was 24.1 (± 7.5) mL g^{-1} hr^{-1} (578.4 mL g^{-1} day^{-1}). Prokopovich (1969) reported that *Corbicula* pumping rate was 20 mL g^{-1} hr^{-1} or 0.5 L day^{-1}. If the pumping rate is assumed to be constant for 24 hours, as reported by Prokopovich (1969), the total volume of water pumped per day in a reach can be calculated as follows:

$$V_t = P \times B \times A$$

where

V_t = volume pumped per unit time,
P = average pumping rate per unit biomass,
B = average clam wet-weight biomass per unit area, and
A = bottom area of river segment.

For the reach between Rosier Bluff and Hatton Point, the average clam biomass in July 1981 was 1337 g m^{-2}, the bottom area was 1.2×10^7 m^2 and the total volume of river water pumped through the clams per day was 8.9×10^6 m^3. The hydraulic residence time of a parcel of water in the Rosier Bluff to Hatton Point reach is 3 days at the July 1981 flow of 112 m^3 s^{-1}. Therefore, the equivalent of the entire volume between Hatton Point and Rosier Bluff, 3.0×10^7 m^3, could be pumped through the *Corbicula* populations in approximately 3 to 4 days. Lauritsen and Mozley (1983) reported that the northern reach of the Chowan River, N.C., was pumped through *Corbicula* in 4 days. They reported pumping rates that were an order of magnitude higher than the above.

Phytoplankton were filtered from the river water during the pumping rate experiments. The data in figure 22 demonstrate that, in 2 hours, chlorophyll increased in the four controls (no clams), but decreased approximately 30 percent when exposed to live clams in the experimental beakers. The hypothesis that chlorophyll concentration in the controls (no clams) was higher than

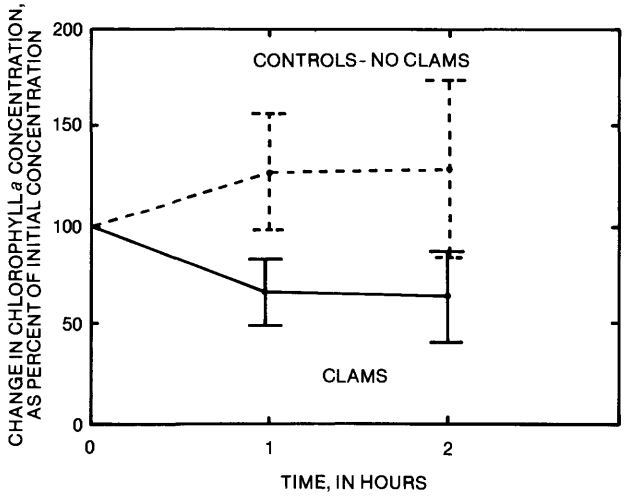

Figure 22. The change of chlorophyll a concentration (as a percentage of initial concentration) with time in control beakers; no clams (dashed lines) and clams present (solid lines). Vertical bars indicate the standard deviation.

in the beakers with clams at the end of 1 and 2 hours was accepted ($\alpha = 0.005$). Many algae may pass through mollusks undigested and may appear in their feces and pseudofeces (Hill and Knight, 1981; Galtsoff, 1977). Pseudofeces trap particles and bind them to the sediment (Prokopovich, 1969). If some phytoplankton pigments pass through the *Corbicula* undigested and appear as feces or pseudofeces (Lauritsen and Mozley, 1983), phytoplankton degradation products in the surficial sediments should be related to clam biomass. Phaeopigment *a* (a degradation product of chlorophyll *a*) , in the surface sediments, was proportional to clam biomass (fig. 23) at stations where both clams and sediment were sampled. The amount of phaeopigment in the surface sediment was not related to the depth of the overlying water. The highest and lowest concentrations of phaeopigment were found at both the shallowest and deepest sampling sites (fig. 23).

Zooplankton Grazing Rates and Impact of *Unionids*

The volume of river water grazed by zooplankton in the tidal, fresh Potomac River was estimated for June 30, July 8, August 18 and 25, 1981 (Buchanan and Schloss, 1983). Grazing rate estimates, in mL hr^{-1}, reported in the literature for each species (table 12), were multiplied by the number of individuals of each species found at each station. Assuming continuous, 24-hour feeding of zooplankton (probably an overestimate), daily grazing rates by volume were estimated. The mean grazing rates of zooplankton at Rosier Bluff, Hatton Point, and Marshall Hall were estimated to be 3.1 (S.D. = 2.0), 3.6 (S.D. = 2.7), and 2.8 (S.D. = 3.2) percent of the river volume each day, respectively. The grazing rates of zooplankton at stations upstream and downstream of the sag area were nearly the same as at Rosier Bluff and Hatton Point, 2.8 (S.D. = 1.0) percent at Indian Head and 3.5 (S.D. = 2.6) percent at Alexandria, Va. The total zooplankton grazing rates by volume were an order of magnitude less than the clam pumping rates in the Rosier Bluff to Indian Head reach. Clam and zooplankton grazing rates were similar upstream and downstream of the sag reach.

Unionid clams were present in the tidal Potomac River. Their biomass was 9.2 percent of the total mollusk biomass (*Corbicula* plus *Unionids*). They ranged from 0.6 percent at Rosier Bluff to 18.5 percent at Dogue Creek.

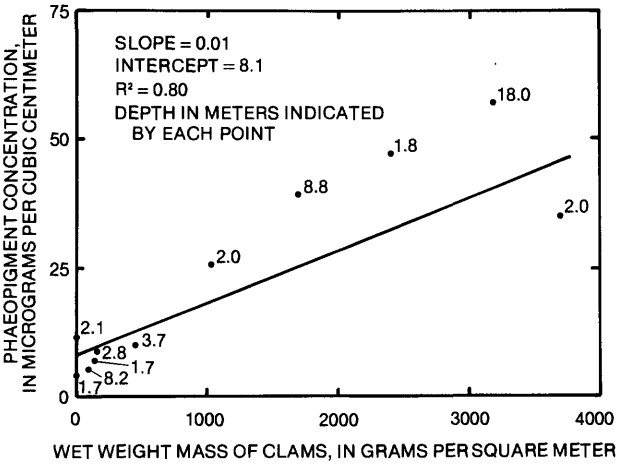

Figure 23. The relationship of phaeopigment *a* concentration to clam biomass (as wet-weight grams per square meter). Depth of water column, in meters, from which surficial sediment sample was obtained is labeled near each point.

DISCUSSION

Phytoplankton growth rates and biomass vary with temperature, amount of solar radiation available in the water column, river discharge, nutrient concentration and availability, and grazing. The phytoplankton, discharge, nutrients, and invertebrates in the fresh, tidal Potomac River in 1979 through 1981 differed from that of the 1960's through mid-1970's. Summer discharges generally were higher than average in 1979 through 1981, nutrient loadings and phytoplankton biomass were lower, and phytoplankton-grazing, benthic invertebrates were more plentiful. The data and experiments in this paper were used to elucidate the processes that control phytoplankton

Table 12. Zooplankton filter rates reported in the literature
[Dashed lines represent no available data]

Organism	Size range in millimeters	Average filtering rate, milliliters per hour	Source
Cladocerans			
Bosmina longirostris	0.4 - 0.6	0.018	Average of night and day, Haney (1973)
Moina species	0.7 - 1.2	0.192	Estimated from rates of *Ceriodaphnia quadrangula*, Haney (1973)
Diaphanosoma brachyurum	0.4 - 0.9	0.067	Haney (1973)
Daphnia parvula	0.7 - 1.2	0.158	Haney (1973)
Copepods			
Eurytemora affinis	1.0 - 1.5	0.25	Allan and others (1977)
Naupli	0.08 - 1.0	0.015	Extrapolated from adult *Eurytemora affinis* filtering rates
Copepodids	0.4 - 0.8	0.035	
Rotifers			
Brachionus calyciflorous	0.4 - 0.8	0.0075	Starkweather and Gilbert (1977)
Brachionus species	0.2 - 0.4	0.0058	Starkweather and Gilbert (1977)
Misc. small rotifers	<0.2	0.005	Haney (1973)
Kelicotio sp.	—	—	
Filinia sp.	—	—	
Conichilus sp.	—	—	

growth and biomass and explain the changes in phytoplankton distribution that have taken place between the 1960's and 1980's.

Light penetration in the water column as a function of self-shading may be the major abiotic process controlling phytoplankton growth rate and biomass in the fresh, tidal Potomac River. The growth rates of phytoplankton in the summer of 1980 determined by productivity analysis and phytoplankton chamber experiments can be simulated by using light-penetration parameters, particularly γ, δ and chlorophyll *a* in equation 9. Nutrient factors are not required. Phytoplankton productivity and assimilation numbers were proportional to depth-integrated light and the depth of the photic zone. The productivity-light relationship is reported to be in the form of an inverse-hyperbolic function analogous to Michaels-Menten kinetics (Smith, 1936; Talling, 1957; Cohen and Pollock, 1983). If the data fall on the linear portion of the productivity-light curve, as in the case for the fresh, tidal Potomac River in 1980 and 1981, then phytoplankton are considered light limited (Steeman-Nielsen and Hansen, 1961; Ichimura and others, 1962). The assimilation numbers and rates of maximum productivity (P_{max}) vary inversely with extinction coefficients. The growth rates increase as primary productivity per unit biomass increases. Thus, all evidence supports the contention that phytoplankton are light limited in the Potomac River. The light limitation is greatest in the area of Hallowing Point and least at the Alexandria and Hatton Point stations. As a result, the primary productivity per unit biomass and growth rate are highest at Alexandria and Hatton Point and lowest at Hallowing Point as determined by several independent methods.

Water-column light not only regulates primary productivity and growth rate, but also the observed station-to-station variation in chlorophyll distribution, the productivity per unit chlorophyll (assimilation number) and the chlorophyll content per cell. Hatton Point has the lowest chlorophyll and cell concentrations, highest growth rates, primary productivity per unit biomass and, with Marshall Hall, the highest chlorophyll per cell. Hallowing Point, with the highest phytoplankton biomass of the productivity stations, has the lowest primary productivity per unit biomass and chlorophyll concentration per cell. These results agree with those of Goldman (1980) who demonstrated that the chlorophyll-to-cell ratio increases with increasing growth rate. Therefore, the observed chlorophyll distributions in the fresh, tidal Potomac River not only were determined by the biomass of phytoplankton present, but by the light history of phytoplankton. The station-to-station variations of chlorophyll *a* per cell can result in chlorophyll *a* concentration not being representative of algal biomass. In the summers (July to August) of both 1980 and 1981, biomass at Hatton Point would be overestimated by 54 percent relative to Hallowing Point, 23 to 42 percent relative to Alexandria 1 and 150 percent relative to Quantico if chlorophyll was used to estimate phytoplankton biomass. Thus, light controls growth rate, actual biomass, and estimated biomass (as chlorophyll *a*).

It also has been shown that, in 1977, the fresh, tidal river near Hallowing Point and Indian Head supported the highest attainable concentration of phytoplankton, limited only by self-shading.

Phosphorus may, at times, be rate limiting but not limiting to final biomass except at Hallowing Point in September 1980. Total dissolved phosphorus concentrations generally were above levels considered limiting to phytoplankton. At high surface-light intensities, however, phosphorus was not available at rates fast enough to support maximum primary productivity. Phosphorus concentrations in September 1980 were too low to support 300 $\mu g\ L^{-1}$ chlorophyll *a* at Hallowing Point. Concentrations of phosphorus were high enough up to the last week in August 1980, at and downstream of Hallowing Point, to support considerably higher biomass of phytoplankton than were observed. Phosphorus concentrations in the sag reach were always higher than those in the reach that supported the highest phytoplankton biomass. Schindler and Fee (1973) reported that a nutrient pool may be large enough not to limit final biomass, but is not available at rates adequate to support maximum productivity. The total dissolved phosphorus and nitrogen concentrations in the high biomass summer of 1977 were not very different than the lower biomass summers of 1980 and 1981. Therefore, nutrient concentrations do not explain the reduced phytoplankton concentrations of 1980 and 1981. Silica was present in 1980 and 1981 in amounts nonlimiting to diatoms. The concentrations were 3 to 30 times higher than the highest half-saturation constants reported in the literature and 30 to 300 times the lowest (Officer and Ryther, 1980). Silica was probably not a factor in reducing phytoplankton biomass from 1977 levels.

High discharge reduces phytoplankton biomass in the fresh, tidal Potomac River. Concentrations in July and August 1979, a period of high discharge (>115 $m^3\ s^{-1}$), were 20 percent of those of 1977 (discharge was 47.8 $m^3\ s^{-1}$ in July through August). Higher mean discharge in July and August of 1980 and 1981 (88 and 91 $m^3\ s^{-1}$ for July through August of 1980 and 1981) than in 1977 may have been a partial cause of lower phytoplankton concentrations in the fresh, tidal Potomac River. However, discharges of August 1981 and August 1977 were similar (53.1 and 40.5 $m^3\ s^{-1}$, respectively), yet the chlorophyll concentrations of 1981 were approximately half of those of 1977. Thus, discharge differences could not explain completely the differences in phytoplankton concentrations between the summers of the 1960's through 1970's and that of 1981 (and perhaps, 1980).

Benthic invertebrates can graze a significant number of phytoplankton from the water column (Cloern, 1982; Wright and others, 1982). Grazing by benthic invertebrates, particularly the Asiatic clam, *Corbicula fluminea*, has had a major impact on the distribution of Potomac River phytoplankton. Although absolute numbers of phytoplankton throughout the tidal, fresh Potomac were lower in 1980 and 1981 compared to the 1960's and early 1970's due to a combination of one or more of the above factors, the phytoplankton sag in 1980 and 1981 is explained best by the presence of *Corbicula*.

Examination of discharge records demonstrated that a phytoplankton sag could be generated between Hatton Point and Rosier Bluff 2 to 4 days after a high-flow event. Only one such event occurred within 2 to 4 days of river phytoplankton profiles for July through August 1980 and 1981, that of July 6, 1981, yet the sag persisted through the summers of both years.

Calculation of pumping rates from experiments performed in 1981 demonstrated that *Corbicula* populations could filter a volume of water equivalent to the entire volume of Rosier Bluff to Hatton Point in 3 to 4 days.

The hydraulic residence time of a parcel of water between Rosier Bluff and Hatton Point was approximately 3 days in 1980. The 3- to 6-km tidal excursion carries the phytoplankton over the clam beds many times during the residence time of the parcel. These clams are capable of removing phytoplankton from river water and phaeopigment concentration in the sediment was proportional to clam biomass. There was no relationship between depth of the water column and benthic sediment pigment concentration. Thus, clams removed phytoplankton from river water that passed over them and deposited some partially digested phytoplankton on the bottom as feces or pseudofeces. Prokopovich (1969) found that the mucoidlike mass of the pseudofeces of *Corbicula fluminea* was a strong binding agent of sediment. It would probably require a bottom-scouring storm to resuspend the excreted, partially decomposed algae.

If toxic substances from the sewage treatment or power plants caused the phytoplankton sag between Rosier Bluff and Hatton Point, then water collected from that reach of the river should support less growth than water from segments downstream from the sag. Yet water from the 160- to 166-km reach supported greater growth than that obtained from the segment that typically supported the highest phytoplankton biomass.

There may have been no toxic substances discharged into the reach when the water samples were collected. The hydraulic residence time of the parcel between Rosier Bluff and Hatton Point during this study was 3 days. Because the reach is well mixed (less than 1 hour top to bottom (Hetling and O'Connell, 1966)), its characteristics were representative of not only the day that the depth- and time-integrated sample was collected, but also of the combined properties of the previous 2 days. Thus, the evidence suggests the existence of a physical process and not an inhibitory or toxic substance that removed the phytoplankton from km 166 to 160.

Zooplankton-grazing pressure was not as significant a factor as clam-grazing pressure. Herbivorous zooplankton were present and exerting grazing pressure on the phytoplankton. With average grazing rates by volume reported in the literature (see table12 for reference), the impact of zooplankton on the phytoplankton was calculated for the Rosier Bluff to Hatton Point reach. The estimated rate was approximately one order of magnitude less than the estimated rate of grazing by *Corbicula*. Grazing pressure by zooplankton in August 1981 was similar upstream and downstream of and in the sag reach.

Nutrient concentrations (nitrogen and phosphorus) in the sag reach were similar in the years the sag was present and in the years the sag was not observed.

Lower growth rates in the Rosier Bluff to Hatton Point reach than in upstream or downstream reaches could account for the sag. However, growth rates measured using several independent methods were highest in the sag reach. Growth rates calculated from productivity experiments demonstrated that growth rates at Hatton Point were higher, not lower than at other stations.

Dissolved inorganic N and total dissolved P concentrations between Rosier Bluff and Hatton Point were higher than at Hallowing Point, the reach supporting the highest biomass of phytoplankton. The water in the sag reach was capable of supporting a higher phytoplankton biomass than was observed in the summers of 1980 and 1981.

The evidence supports the hypothesis that the depression of phytoplankton abundance between Rosier Bluff and Hatton Point in the summers of 1980 and 1981 was due to the Asiatic clam *Corbicula fluminea*. The evidence does not support the alternative hypotheses that zooplankton, *Unionid* clams, toxic substances, nutrient limitations, or peak discharges were responsible for the 1980 and 1981 sag.

In 1977, 1980, and 1981 the mean July through August chlorophyll *a* concentrations at stations including and upstream of km 168 (Alexandria 1) ranged from 20 to 50 $\mu g\ L^{-1}$ for each year. They ranged from 20 to 65 $\mu g\ L^{-1}$ in 1969, 1973, and 1974 at Haines Point (km 179) (Pheiffer, 1976). Thus, the phytoplankton concentrations above the reach containing the *Corbicula* did not show the dramatic decline observed from the 1960's to 1980 and 1981 at Rosier Bluff to Quantico. Thus, the *Corbicula* may have been the primary factor responsible not only for the sag, but may have contributed to the lower phytoplankton concentration in the entire fresh, tidal river.

The reach that had the highest phytoplankton growth rates (Hatton Point to Marshall Hall) had the highest loss of phytoplankton due to *Corbicula*. There were fewer cells being transported downstream to the reach of lowest growth rate (Hallowing Point). This would explain much of the lower concentrations of phytoplankton downstream of the sag reach in July through August 1980 and 1981 compared to the 1960's and 1970's.

Phytoplankton have a major impact on dissolved oxygen concentrations in the Potomac River. Productivity typically was much higher than respiration and there was a net gain of oxygen to the water column. Because the net gain of oxygen to the water column could be as high as 15 mg L^{-1} day^{-1} above levels already present (Hatton Point in the summer of 1980), much of the phytoplankton-produced oxygen must have been lost to the sediment and to the atmosphere.

SUMMARY

The factors that have had the greatest impact on the growth and biomass of summer phytoplankton of the fresh, tidal Potomac River were: (1) grazing by *Corbicula fluminea* (Asiatic clam); (2) the effect of phytoplankton self-shading on penetration of solar radiation into the water column; and (3) wash-out due to high discharge. These same factors also account for the differences in the distribution of phytoplankton biomass in the period 1980 to 1981 and the period 1960 to 1979.

Solar radiation available in the water column controlled the growth rate of phytoplankton. Average growth rate for the fresh, tidal river in 1980 and 1981 was 0.15 day^{-1}. Differences between experimentally determined growth rates at productivity stations can be explained by differences in the depth of the photic zone, which, in turn, can be explained by phytoplankton self-shading. The highest concentrations of phytoplankton attained in the Potomac River in the 1960's and 1970's could be shown to be the maximum supportable concentration limited only by self-shading. Light also regulated the chlorophyll-to-cell ratio. Chlorophyll concentration per cell varied in a repeatable pattern from station to station. The station with the highest light penetration and the lowest phytoplankton concentrations had the highest chlorophyll concentration per cell in both 1980 and 1981.

The differences in relative distribution of phytoplankton in the fresh, tidal Potomac River between the 1960–1977 period and the 1979–1981 period was probably due to the Asiatic clam *Corbicula fluminea*. The lower absolute concentrations of phytoplankton in 1979–1981 compared to 1960–1977 were probably due to the combined effects of the *Corbicula* and high discharge. Nutrient concentrations were usually above levels reported to be limiting to phytoplankton even at times and places of highest phytoplankton biomass and productivity. Nutrient concentrations were very low late in August and in September, after blooms had been established. On

clear, sunny days, phosphates may not have been available at rates high enough to support maximum productivity during the summer of 1980. Concentrations of total dissolved phosphorus were high enough to support higher phytoplankton concentrations than were observed.

There was evidence to reject the hypotheses that toxic substances reduced phytoplankton biomass and growth in 1980 and 1981 as compared to the 1960's and 1970's. Zooplankton were shown to graze phytoplankton, but their impact was an order of magnitude less than that of the *Corbicula*.

Phytoplankton primary productivity varied with phytoplankton biomass. Therefore, larger diel excursions of dissolved oxygen would be expected from increases in phytoplankton biomass.

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CONVERSION FACTORS

For readers who prefer to use inch-pound system of units, the data may be converted by using the following factors:

Multiply SI unit	By	To obtain inch-pound units
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
kilometer (km)	0.5400	nautical mile (nmi)
gram (g)	0.0022	pound (lb)
cubic meter per second ($m^3\ s^{-1}$)	35.31	cubic foot per second (ft^3/s)

Concentration Conversions

Constituent	From	To	Divide by
Nitrate	micromoles per liter	milligrams per liter (as N)	0.014
Ammonia	micromoles per liter	milligrams per liter (as N)	0.014
Phosphate	micromoles per liter	milligrams per liter (as N)	0.031