Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary*

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ABSTRACT: The mesohaline reach of Chesapeake Bay (USA) receives most of its allochthonous nutrient input from a single source, the Susquehanna River. Seaward of the turbidity maximum, concentrations of dissolved inorganic nutrients decrease rapidly as phytoplankton biomass increases along the salinity gradient. The annual cycle of riverine nutrient input is in phase with phytoplankton biomass but out of phase with phytoplankton productivity in this region. Riverine nutrient input and phytoplankton biomass peak during spring, but phytoplankton productivity peaks during summer. Seasonal variations in biomass are correlated with riverine nitrate input while seasonal variations in productivity are correlated with light and temperature. Evidence is presented which suggests that the spring flux of nitrogen from the watershed and the summer productivity maximum are coupled via the accumulation and sedimentation of phytoplankton biomass during spring and subsequent recycling of regenerated nitrogen into the euphotic zone during summer. We conclude that the occurrence of maximum productivity during summer in the mesohaline reach of the Bay is a consequence of the recycling of nitrogen delivered to the system during the previous spring. Inter-annual variations in the magnitude of the summer productivity maximum appear to be related to variations in vertical stratification which influences the vertical flux of regenerated ammonium from the benthos to the euphotic zone. In this context, the extent of seasonal oxygen depletion during summer appears to be determined by riverine nitrate input during the spring freshet and the strength and variability of vertical stratification during summer.

INTRODUCTION

The response of plankton communities to nutrient enrichment in coastal ecosystems is of major significance in marine ecology and has broad implications in terms of both water quality and fisheries. Anthropogenic nutrient inputs to estuaries have increased rapidly over the last 3 to 4 decades (e.g. Walsh et al. 1981, Nixon & Pilson 1983). Such increases have been shown to stimulate phytoplankton production in estuarine systems (Nixon 1981, Boynton et al. 1982, Cadée 1986). Partially stratified estuaries are likely to be particularly responsive to nutrient enrichment as a consequence of 2-layered flow regimes which potentially increase the retention and recycling of nutrients (Redfield 1955, Ketchum 1967, Taft et al. 1978). The high productivity and temporal and spatial lags

between nutrient inputs and phytoplankton production which often characterize estuarine systems have been attributed to this phenomenon (Nixon 1981, Boynton et al. 1982, Nixon & Pilson 1983, Kemp & Boynton 1984, Flint et al. 1986). However, the time and space scales on which nutrient inputs are related to nutrient recycling and primary productivity are not well documented. Thus, while it is generally observed that nutrient inputs from external sources can cause nonlinear increases in phytoplankton production (Eppley & Peterson 1979, Platt & Harrison 1985), time-dependent relations between the input of nutrients and phytoplankton productivity are poorly understood in estuaries.

Annual phytoplankton production in Chesapeake Bay appears to be more sensitive to nitrogen than to phosphorus loading. In summarizing data on estuarine production and nutrient loading, Boynton et al. (1982) found a better correlation between annual phytoplankton production and nitrogen loading than between

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production and phosphorus loading. More recently, Fisher et al. (in press) observed that nitrogen input to the Bay is removed more efficiently than phosphorus input. While most of the input of dissolved inorganic nitrogen was assimilated and transformed to organic nitrogen within the Bay, total phosphorus and the partitioning of phosphorus among dissolved inorganic and total organic phases showed little net change between freshwater and seawater end members on average. Liss (1976) has interpreted such phosphorus distributions in estuaries as an indication of rapid recycling and the 'buffering' effect of adsorption-desorption reactions which partition phosphate between dissolved and particulate phases.

The major external source of nitrogen to Chesapeake Bay is the Susquehanna River (Carpenter et al. 1969, Flemer et al. 1985), which supplies more than 80 % of the total nitrogen input to the upper Bay (Fig. 1), mainly in the form of nitrate (McCarthy et al. 1977, Harding et al. 1986, Schubel & Pritchard 1986). As is typical of mid-latitude rivers, the annual cycle of fresh water discharge exhibits a spring maximum and a summer minimum. Consequently, 50 to 60 % of the annual nitrogen input to the upper Bay occurs during the spring freshet (Schubel & Pritchard 1986). Most of this external supply of nitrogen is assimilated downstream of the turbidity maximum in the mesohaline reach of the Bay where phytoplankton productivity and chlorophyll *a* concentration also achieve their spatial maxima (Harding et al. 1986, Fisher et al. in press), a pattern which probably reflects light-limited nutrient uptake and productivity (Flemer 1970, McCarthy et al. 1974, 1977, Harding et al. 1986). Seasonal variations in phytoplankton productivity also appear to be light dependent with a winter minimum and a summer maximum (Flemer 1970, Taft et al. 1980, Boynton et al. 1982). Thus, the annual cycle of nutrient delivery and phytoplankton productivity are seasonally out of phase with maximum phytoplankton productivity occurring 2 to 4 mo after the spring freshet (Flemer 1970, Taft et al. 1980, Boynton et al. 1982).

Primarily on the basis of this lag and on assumptions concerning the decay rate of organic matter in Chesapeake Bay, Taft et al. (1980) and Officer et al. (1984) concluded that seasonal oxygen depletion in Chesapeake Bay is a response to the previous years' phytoplankton production. In contrast, based on observations which suggest that the annual cycles of phytoplankton productivity, temperature and nitrogen regeneration are in phase (Kemp & Boynton 1981, Boynton & Kemp 1985), Boynton et al. (1982) and Kemp & Boynton (1984) proposed a conceptual model relating summer phytoplankton productivity to spring nitrogen supply via organic deposition and temperature-dependent nitrogen regeneration. However, the mechanisms

by which nutrients are recycled between sources and sinks on a seasonal time scale are not known. Malone et al. (1986) proposed a mechanism by which nutrients regenerated below the pycnocline could be returned to the euphotic zone at sufficiently high rates to support high summer productivity. This involves lateral oscillations of the pycnocline and associated variations in vertical mixing and advection. A second aspect of the problem is how the spring delivery of nitrate is related to summer ammonium regeneration.

Since phytoplankton account for most of organic input downstream of the turbidity maximum (Biggs & Flemer 1972), the most likely process is phytoplankton assimilation and the accumulation of sufficient biomass to fuel summer regeneration. However, this seems to be contrary to the notion that the annual cycles of phytoplankton productivity and biomass are in phase (Flemer 1970, Taft 1980, Boynton et al. 1982, Harding et al. 1986). Kemp & Boynton (1984) speculate that dissolved inorganic nitrogen input is transformed to particulate nitrogen via sorption, flocculation and assimilation in the region of the turbidity maximum and that downstream sedimentation provides the source of nitrogen for subsequent summer recycling. However, the spatial distribution of nitrate and salinity indicate that most of the nitrate flux is assimilated downstream of the turbidity maximum in the mesohaline reach of the Bay (McCarthy et al. 1977, Harding et al. 1986, Schubel & Pritchard 1986). Most field programs in the Bay have been more concerned with spatial variations along the longitudinal salinity gradient than with lateral or seasonal variations. Our purpose here is to address the problem of how seasonal variations in phytoplankton biomass and productivity in the mesohaline reach of the Bay are related to the riverine input of nitrogen and to nitrogen recycling within the Bay.

METHODS

Samples were collected at 16 stations along 4 transects of the mesohaline reach of Chesapeake Bay (Fig. 1). Three transects were oriented normal to the main axis of the Bay (east-west). The 4th transect was located in the channel of the main axis of the Bay (north-south). Channel stations ranged in sonic depth from 25 to 42 m. Sampling rate varied with time of year, ranging from a minimum of 1 cruise per month during fall and winter to a maximum of 4 cruises per month during spring. The Chop-Pax transect (T2 in Fig. 1) was sampled more frequently than the transects to the north and south. Stations were often occupied more than once per cruise, in which case results were averaged for the purposes of this analysis. Vertical profiles of

temperature, salinity, dissolved oxygen, dissolved inorganic nutrients, chlorophyll *a*, and particulate organic carbon and nitrogen were determined at all stations. Phytoplankton productivity was measured at Stations 01, 03, and 05 of the Chop-Pax transect. Data on the freshwater discharge of the Susquehanna River were provided by the United States Geological Survey based on gauged flow at the Conowingo Dam located 90 km upstream of the study area.

This sampling scheme emphasizes temporal and lateral variability for a variety of reasons: (1) Effects of nutrient enrichment are greatest in the mesohaline reach of the Bay between 39°N and 38°20'N where phytoplankton productivity and biomass are highest and summer oxygen depletion is most extensive (Flemer 1970, McCarthy et al. 1977, Taft et al. 1980, Harding et al. 1986, Schubel & Pritchard 1986, Fisher et al. in press). (2) Significant lateral (east-west) variations occur in the distributions of nutrients and chlorophyll which appear to be related to depth and to time-dependent variations in density structure normal to the main axis of the Bay (Tyler 1984, Malone et al. 1986). (3) Spatial variations in chlorophyll concentration account for most variability in phytoplankton productivity along the salinity gradient of the Bay (Harding et al. 1986).

Water samples were collected with a submersible well pump equipped with a 2.5 cm diameter hose. Temperature, salinity, dissolved oxygen and *in vivo* chlorophyll fluorescence were measured at 1 m intervals. *In vivo* chlorophyll fluorescence were measured with a Turner Designs fluorometer. Temperature, salinity and dissolved oxygen were measured in 1985 using a YSI model 57 DO meter and YSI model 33 salinity meter and, in 1986, using a thermosalinograph equipped with a Sea-Bird Electronics model 3-01/S temperature sensor and model 4-01/0 conductivity meter. Water samples for particulate organic and dissolved inorganic nutrient analyses were collected at 2 to 6 depths depending on depth and the vertical profiles of salinity and *in vivo* chlorophyll fluorescence. Particulate organic carbon and nitrogen were determined with a Controlled Equipment model 240-XA elemental analyser, chlorophyll *a* with a Turner Designs fluorometer following extraction with 90% acetone, and dissolved inorganic nutrients with a Technicon autoanalyser following filtration. Particulates were collected by filtration under low vacuum (<130 mm Hg) on GF/F glass fiber filters (pre-combusted for organic carbon and nitrogen). Biomass ratios of carbon, nitrogen, and chlorophyll were estimated as described by Chervin et al. (1981).

Phytoplankton productivity was estimated by the ^{14}C technique from 24 h incubations under natural sunlight. Total dissolved inorganic carbon was measured with a

Beckman model 864 infrared analyser after acidification. Samples were collected from a depth of 1 m and incubated at surface water temperature under light levels of 100, 50, 25, 9, and 1% of surface irradiance. Incubations were initiated within 2 h of sunrise. Samples were filtered onto GF/F filters under low vacuum, rinsed with filtered estuarine water, acidified with 30 μl of glacial acetic acid, and placed in scintillation vials with 10 ml of Ready-Solv. ^{14}C activity was measured with an LKB 1212 RackBeta liquid scintillation counter. Euphotic zone productivity was calculated as described by Malone et al. (1986). Briefly, the 1% light depth, determined with a Secchi disc and a LICOR submarine quantum meter, ranged from 3 to 12 m (mean = 5 m) and was located in or above the pycnocline. Given the difficulties of collecting samples from precise light depths in such shallow euphotic zones, phytoplankton productivity at the above percent light depths was calculated as the product of chlorophyll specific productivity at each light level and chlorophyll concentration at the corresponding light depths. Euphotic zone productivity was then calculated by integrating between the surface and 1% light depth. This procedure ignores the influence of adaptation to low light levels near the base of the euphotic zone. However, it has been our experience that vertical variations in productivity are primarily a function of light and chlorophyll concentration and that light adaptation is a secondary effect. As discussed by Malone (1982a), 24 h incubations provide reasonable estimates of net particulate organic productivity in nutrient-rich environments.

ANNUAL CYCLES OF FRESHWATER FLOW AND NITRATE SUPPLY

The volume transport of freshwater into the mesohaline reach of the Bay influences the production of phytoplankton biomass through its effects on (1) supply of allochthonous nutrients, (2) gravitational circulation and residence time of water in the system, and (3) vertical stability of the water column (cf. Stefansson & Richards 1963, Malone 1977, Cloern et al. 1983, Pennock 1985, Peterson et al. 1985, Ward & Twilley 1986). The long-term mean annual cycle of freshwater flow from the Susquehanna River is characterized by a spring maximum during March–April of $2.1 \times 10^8 \text{ m}^3 \text{ d}^{-1}$, and a summer minimum during August–September of $0.3 \times 10^8 \text{ m}^3 \text{ d}^{-1}$ (Schubel & Pritchard 1986). River discharge was below average throughout 1985 and close to average in 1986 (Fig. 2). The 2 yr also differed in the duration and magnitude of the spring freshet. The 1985 freshet peaked during 12 March to 9 April with a mean of $1.6 \times 10^8 \text{ m}^3 \text{ d}^{-1}$ compared to the 1986 freshet which peaked during 11

Fig. 2. Annual cycles of freshwater flow (●) of the Susquehanna River and mean nitrate concentration in surface (○) and bottom (■) water of the mesohaline reach of Chesapeake Bay; flow data provided by the U. S. Geological Survey

to 25 March with a mean of $3.2 \times 10^8 \text{ m}^3 \text{ d}^{-1}$. These variations in flow were reflected in the annual cycles of nitrate and salinity. Nitrate concentration was highest in the surface layer where annual maxima of 34 and $55 \mu\text{g-at l}^{-1}$ were observed in mid-April of 1985 and

1986, respectively. Downstream displacement of surface isohalines was also greater in 1986 than in 1985 and lagged peak freshwater flow by 20 to 30 d (Fig. 3). Given the resolution of our observations, the distributions of both nitrate and salinity indicate that the mesohaline reach of the Bay responded to variations in freshwater flow with a lag of about 1 mo.

ANNUAL CYCLES OF CHLOROPHYLL AND PHYTOPLANKTON PRODUCTIVITY

Like nitrate, seasonal variation in the chlorophyll *a* (Chl) content of the water column of the main channel was characterized by a pronounced spring maximum (Fig. 4). The temporal sequence of events occurred 2 to 4 wk later in 1986 than in 1985. Following a transition period of rapid decline during late May, 1 to 2 small peaks developed during summer. The spring bloom peaked in mid-April 1985 compared to mid-May 1986 and declined to a minimum by late May and early June, respectively. Likewise, summer peaks greater than 125 mg m^{-2} developed in mid-June and in mid-July 1985, and in early August 1986. Comparison of euphotic zone and water column Chl shows that while the collapse of the spring bloom occurred over the entire water column, Chl below the euphotic zone accounted for most of the decline (Fig. 4). In contrast, summer peaks were mainly due to increases in the Chl content of the surface layer. Thus, most Chl was located in the bottom layer below the euphotic zone during the spring bloom and in the surface layer within the euphotic zone during summer.

Maximum Chl content of the water column during

Fig. 3. Seasonal variations in the distribution of surface salinity at channel stations along the main axis of the Bay

Fig. 4. Annual cycles of mean chlorophyll content of the water column ($\circ$) and euphotic zone ($\bullet$)

spring exceeded 2000 mg m^{-2} and was centered near the 10 ‰ isohaline about 20 km downstream of the northernmost station during both years (Fig. 5). During 1985, the spring bloom peaked in mid-March at the southern end of the study area and progressed

upstream to a peak in late April at the northern end of the study area (Fig. 5). A similar progression occurred during 1986 but began in mid-April and ended in mid-May. Chl content of the euphotic zone, which was typically confined to the surface layer above the halocline, generally paralleled these variations with spring maxima greater than 200 mg m^{-2} and summer peaks greater than 50 mg m^{-2} (Fig. 6).

Lateral distributions normal to the main channel were documented most frequently along the Chop-Pax transect located in the central region of the study area. For comparison, we present only integral euphotic zone Chl since the euphotic zone typically reached the bottom at the shallow stations along the flanks of the main channel (Fig. 7). Chl content of the euphotic zone was similar to the annual cycle described for the channel station except during 1986 when mean Chl peaked in mid-April rather than in mid-May due to the earlier development of high Chl over the flanks and the later development of the spring bloom upstream of the Chop-Pax transect. Peaks in Chl were highest on the flanks and appeared to be associated with the development of high Chl over the channel during both spring and summer blooms. The spring bloom began to collapse in mid-May during both 1985 and 1986. Together, the distributions shown in Figs. 4 to 7 indicate a temporal sequence of seasonal events which characterized the entire mesohaline reach of the Bay.

The annual cycle of phytoplankton productivity was similar to that described by Flemer (1970) and Boynton et al. (1982) and was seasonally out of phase with the annual cycle of euphotic zone chlorophyll (Fig. 8). Productivity began to increase later in 1985 than in 1986 and did not exceed $1 \text{ g C m}^{-2} \text{ d}^{-1}$ until July 1985

Fig. 5. Seasonal variations in the distribution of water column chlorophyll (mg m^{-2}) at channel stations along the main axis of the Bay; timing of the chlorophyll minimum between the spring bloom and secondary summer peaks indicated by stippling

Fig. 6. Seasonal variations in the distribution of euphotic zone chlorophyll (mg m^{-2}) at channel stations along the main axis of the Bay

Fig. 7. Seasonal variations in the distribution of euphotic zone chlorophyll (mg m^{-2}) at stations along the Chop-Pex transect normal to the main axis of the Bay

compared to April 1986. Timing and magnitude of maximum summer productivity also varied between years with a transect mean maximum of $4.2 \text{ g C m}^{-2} \text{ d}^{-1}$ in August 1985 compared to $2.1 \text{ g C m}^{-2} \text{ d}^{-1}$ in July 1986. Thus, phytoplankton productivity was lower during the spring Chl maximum and higher during the summer productivity maximum in 1985 than in 1986 (Fig. 8, Table 1). Annual production was calculated to be 550 g C m^{-2} in 1985, and 430 g C m^{-2} in 1986 – a difference which reflects higher summer productivity in 1985. Both estimates are in the range of values reported by Boynton et al. (1982) for 1972–1977. In contrast to spatial variations in phytoplankton along the salinity gradient of the Bay (Harding et al. 1986), variations in productivity between seasons and years were related to variations in Chl specific productivity (Table 1).

DISCUSSION

Freshwater flow and phytoplankton biomass

Timing and magnitude of the spring bloom in the mesohaline reach of the Bay appear to be related to the delivery of nitrate and to the concentrating effects of 2-layered estuarine circulation. The spring bloom was initiated as salinity began to decrease in response to the spring freshet in late March-early April and declined rapidly in late May as salinity increased (Figs. 3 and 5). Chl peaked earlier downstream than upstream in both years such that maximum Chl coincided with the salinity minimum in 1985 and lagged the salinity minimum in 1986, perhaps as a result of high spring flow in 1986 relative to 1985 (cf. Cloern et al. 1983, Pennock 1985).

Fig. 8. Annual cycles of mean (solid line) euphotic zone chlorophyll (mg m^{-2}) and phytoplankton productivity ($\text{g C m}^{-2} \text{d}^{-1}$) for the stations of the Chop-Pax transect (Stn 01 $\circ$, Stn 03 $\bullet$, Stn 05 $\blacksquare$)

Fig. 9. Seasonal variations in the distribution of bottom salinity at channel stations along the main axis of the Bay

Given the high Chl content of the water column below the euphotic zone during the development of the spring bloom, this progression suggests that much of the accumulated Chl was advected into the region with the upstream flow of bottom water. Mass transport of Chl from downstream is indicated by the upstream displacement of isohalines during this period (Fig. 9). Chl content of the water column began to increase with the intrusion of high salinity bottom water. In 1985, the bloom peaked during the early stages of this intrusion and began to collapse as the intrusion intensified. Minimum Chl following the bloom coincided with a second intrusion of high salinity water in late May. In

1986, the bloom did not peak until salinity began to decrease following the high salinity intrusion and collapsed with the onset of the second high salinity intrusion. This suggests a greater downstream displacement of the high production zone in 1986 due to higher flow and, consequently, a longer lag between riverine nitrate input in the surface layer and subsequent upstream transport of Chl with bottom water. This would explain the lag between the salinity minimum and the Chl maximum observed in 1986. The conceptual model most consistent with these observations involves nutrient uptake and biomass production in the surface layer during seaward transport, sedimentation of biomass

Table 1. Time- and space-averaged chlorophyll (Chl, mg m⁻²), phytoplankton productivity (P, mg C m⁻² d⁻¹), Chl-specific productivity (P_{chl}, mg C mg Chl⁻¹ d⁻¹), carbon-specific growth rate (μ , d⁻¹), dilution rate of the surface layer (D, d⁻¹), and related parameters for the Chop-Pax transect (Chl/C = ratio of Chl to phytoplankton-carbon biomass by weight.) S_b: bottom water salinity; S_s: surface water salinity; Q_t: volume transport of freshwater, 10⁷ m³ d⁻¹; DO: dissolved oxygen content of the bottom layer, g m⁻²)

Year	Month	Chl	P	P _{chl}	Chl/C ^a	μ^b	S _b -S _s	Q _t	D _c	μ/D	DO
1985	Feb-Apr	126	440	3	0.033	0.12	5.9	11.5	0.07	2	78.3
	May-Jun	74	925	12	0.025	0.31	4.5	5.2	0.03	10	19.1
	Jul-Aug	48	4300	90	0.020	1.79	5.1	1.8	0.02	90	8.8
	Sep-Oct	39	3600	92	0.007	0.61	4.3	2.8	0.02	30	14.0
1986	Feb-Apr	119	640	5	0.017	0.09	8.3	18.4	0.08	1	80.6
	May-Jun	93	1760	19	0.014	0.27	5.3	7.1	0.04	7	21.9
	Jul-Aug	52	2100	40	0.017	0.67	6.6	4.5	0.02	34	2.1
	Sep-Oct	50	1540	31	0.020	0.62	5.3	3.0	0.04	16	21.6

^a Calculated for each period as described by Chervin et al. (1981)
^b $\mu = P_{chl} (Chl/C)$
^c $D = Q_s/V$ where $Q_s = Q_t (S_b/[S_b-S_s])$; V = volume of the euphotic zone (5.24×10^9 m³)

into the bottom layer, and upstream transport of biomass with the landward advection of bottom water.

Delay of the 1986 spring bloom may also reflect more rapid flushing of the surface layer in response to higher freshwater flow. Assuming conservation of salt on a monthly time scale and that chlorophyll specific productivity is a reasonable index of phytoplankton growth rate, the dilution rate of the surface layer and carbon specific growth rate were calculated as described by Malone (1977) and Malone et al. (1983). Carbon-specific growth rates varied from 0.1 d⁻¹ during spring bloom, to 1.8 d⁻¹ during peak summer productivity (Table 1). Comparison of these growth rates to the dilution rate of the euphotic zone by the non-tidal, seaward flow of surface water indicated that growth and dilution were in approximate balance during the 1986 spring bloom and that growth exceeded dilution by a factor of 2 during the 1985 spring bloom (Table 1). Thus, production within the study area was more important as a source of biomass in 1985 when river flow was low compared to 1986 when river flow was higher and mass transport of biomass from downstream was relatively more important.

High rates of growth relative to dilution suggest the possibility that phytoplankton production in terms of biomass yield could depend on the external supply of new nitrogen. To test this hypothesis, time and space weighted mean monthly Chl was compared to monthly averaged volume transport of freshwater from the Susquehanna River (Fig. 2). By lagging flow by 1 mo to account for the delayed response of the mesohaline reach of the Bay, freshwater flow and Chl were significantly correlated ($p < 0.001$) with variations in flow accounting for 82 % of the Chl variance. This relationship was not solely a consequence of the seasonal variation in Chl and flow as indicated by the correlation

Table 2. Coefficients of determination (r^2) and least square regressions of particulate organic nitrogen (PN, μ g) on chlorophyll (Chl, μ g) (PN = a Chl + b)

Year	Month	n	r^2	a (SE)	b (SE)
1984 ^a	Jul-Aug	21	0.66	9.9 (1.1)	88 (69)
1985	Feb-Apr	18	0.64	5.5 (1.0)	64 (54)
	May-Jun	32	0.57	6.1 (1.0)	76 (50)
	Jul-Oct	32	0.56	9.1 (1.5)	105 (84)
1986	Feb-Apr	20	0.64	8.4 (1.5)	82 (51)
	May-Jun	20	0.72	6.2 (0.9)	79 (65)
	Jul-Oct	56	0.73	10.0 (0.7)	76 (48)

^a Data from Malone et al. (1986)

between Chl and flow rate when the high flow months of spring were excluded ($r = 0.75$, $n = 14$, $p < 0.01$). For a quantitative comparison of nitrate input (Q-N) and total phytoplankton biomass in the study area, biomass as nitrogen (Ph-N) was estimated from the product of monthly mean Chl, N/Chl ratios (Table 2), and a surface area of 1.1×10^9 m². Note that the N/Chl ratio estimated for the 1986 spring bloom period is higher by a factor of 1.5 than during the same period in 1985. Freshwater flow and nitrate concentration were higher by a similar factor (1.6). Thus, while Chl levels did not differ substantially between years, nitrogen-biomass varied in proportion to freshwater flow and nitrate concentration. Nitrate input from the Susquehanna was assumed to be the sole source of allochthonous nitrogen and was estimated as the product of freshwater volume transport and nitrate concentration of the freshwater end member. The latter was estimated to be 100 μ g-at l⁻¹ based on the conservative mixing line for flows greater than 10⁸ m³ d⁻¹ (least-square, linear regression of nitrate on salinity: $NO_3 = 112 - 6.5 S$, $r^2 =$

Fig. 10. Relationships between monthly mean phytoplankton biomass (10^8 g N; euphotic zone ●, water column ○), nitrogen assimilation (10^8 g N d^{-1}) and riverine nitrogen input for the mesohaline reach of the Bay between $38^{\circ}59'$ N and $38^{\circ}20'$ N (area = 1.078×10^9 m 2); includes data from 1984 (Malone et al. 1986)

0.99) and $50 \mu\text{g-at l}^{-1}$ for lower flows (Smullen et al. 1982). These are obviously rough approximations, but will suffice for the purposes of these calculations. Biomass was estimated for the euphotic zone and for the entire water column, both of which were found to be significantly correlated ($p < 0.001$) with nitrate supply (Fig. 10) by the least square regressions:

(1) (Water Column):

$$\text{Ph-N} = 4.6 + 7.7 (\text{Q-N}) \quad (r^2 = 0.86, n = 24)$$

(2) (Euphotic Zone):

$$\text{Ph-N} = 3.5 + 3.9 (\text{Q-N}) \quad (r^2 = 0.78, n = 24)$$

As indicated by the slopes of these regressions, a unit increase in nitrate input resulted, on average, in a 4 fold increase in phytoplankton biomass in the euphotic zone and an 8 fold increase in the water column as a whole. While these calculations are subject to large errors, they are indicative of the effects of 2-layered estuarine circulation and nutrient recycling on the accumulation of phytoplankton biomass within the mesohaline reach of the Bay. As discussed above, the development of the spring Chl maximum appears to be due to sedimentation and accumulation of Chl within the study area and to the advection of Chl into the study area with bottom water from downstream. Varia-

tions in the magnitude of the spring biomass maximum were related to the amount of nitrate delivered to the system during the spring freshet. Our results indicate that the lag between the spring freshet and the magnitude of the spring accumulation of phytoplankton biomass increase in relation to the volume transport of freshwater during late winter-early spring. Evidence is discussed below which suggests that the seasonal and vertical separation of phytoplankton production in the surface layer and benthic ammonium regeneration from that production allow for the high productivity characteristic of summer.

Nitrogen cycling and phytoplankton productivity

Regeneration, the major source of ammonium in the Bay, supports on the order of 60 to 70 % of annual phytoplankton production (Flemer et al. 1985). For nutrient regeneration to have such an effect, the production and decomposition of organic matter must be separated in time on scales which are long relative to phytoplankton generation times. Most regeneration on these time scales appears to occur in the benthos where ammonium regeneration rate varies seasonally with a summer maximum and a winter minimum (Kemp & Boynton 1981, Smullen et al. 1982, Boynton & Kemp 1985). Experimental results summarized by Nixon & Pilson (1983) indicate that benthic rates of ammonium regeneration per unit of organic nitrogen input are on the order of 100 times slower than regeneration rates in the water column. The inverse relationship between phytoplankton productivity and nitrate transport into the Bay (Fig. 10) may reflect the importance of ammonium regeneration and the seasonal lag between nitrogen input and regeneration as indicated by annual cycles of ammonium concentration (Fig. 11). In contrast to nitrate which exhibited a spring maximum in the surface layer, ammonium exhibited a summer maximum in the bottom layer. Bottom-water ammonium began to increase following the spring Chl maximum, and peaks in concentration of 20 to $40 \mu\text{g-at l}^{-1}$ were observed throughout the summer. Decreases in ammonium concentration during summer appeared to be related to intrusions of high salinity bottom water in that upstream displacements of isohalines coincided with decreases in ammonium concentration (Fig. 9). The ammonium content of bottom water at the time of the peaks varied from 5.6 g N m^{-2} in 1985 to 2.8 g N m^{-2} in 1986. This compares to phytoplankton biomass maxima of 1.8 to 2.9 g N m^{-2} during spring of 1985 and 1986, respectively. Thus, the spring accumulation of phytoplankton biomass had the potential of providing about 30 and 100 % of the ammonium which reappeared in the water column during the summers of 1985 and 1986, respectively.

Fig. 11. Annual cycles of mean surface (○) and bottom (●) ammonium concentration of the mesohaline reach of the Bay

Table 3. Seasonal balance between the input of nitrate-nitrogen (I, 10^9 g) and phytoplankton assimilation (A, 10^9 g N) in the mesohaline reach of the Bay

Year	March–May			June–August		
	I	A ^b	I/A	I	A ^b	I/A
1984 ^a	25.7	—	—	8.7	19.6	0.4
1985	12.2	7.9	1.5	2.8	38.5	0.1
1986	21.5	12.0	1.8	3.9	27.5	0.1

^a Data from Malone et al. (1986)

^b Calculated from the product of phytoplankton productivity and an N/C = 0.14 estimated from the slope of the least square regression of particulate organic nitrogen on carbon ($r = 0.92$, $n = 177$)

These results are consistent with seasonal and interannual changes in the balance between nitrate supply and phytoplankton demand calculated from phytoplankton productivity assuming a N/C assimilation ratio of 0.14 (Table 3). During the spring bloom when growth and dilution rates were roughly equivalent, nitrate input exceeded demand within the study area by a factor of 1.5 to 1.8. During summer when growth rates were high relative to dilution rates, nitrate

input accounted for 7 to 44 % of demand. Assuming that the excess nitrate input during spring was assimilated downstream and returned to the study area as phytoplankton biomass as discussed above (i.e. that all nitrate delivered during the spring freshet was recycled as ammonium during summer), regeneration of the spring bloom potentially supported about 30 % of the summer demand during 1985 and 80 % during 1986 (Table 3), in good agreement with the spring biomass to summer ammonium ratios calculated above. Such agreement further illustrates the importance of recycled nitrogen during summer and indicates the potential of the spring bloom in satisfying a significant fraction of the summer phytoplankton demand. This is consistent with calculations which indicate that eutrophication in Chesapeake Bay is a function of recent nutrient inputs rather than of long-term nutrient storage over periods of a year or more (Nixon 1987).

It is unlikely that direct sedimentation of summer phytoplankton production is a major source of additional organic nitrogen for benthic metabolism. The phasing of annual cycles of phytoplankton biomass and productivity (Fig. 8) indicates a seasonal progression from high production relative to losses during spring to a tightly coupled balance between production and losses during summer (cf. Malone & Chervin 1979, Pennock 1985). This trend is illustrated by the relationship between Chl content of the euphotic zone and the balance between the rates of growth (μ) and dilution (D). Mean euphotic zone growth rate increased relative to dilution rate from a minimum during the spring bloom when rates of growth and dilution were in approximate balance to a maximum during July–August when growth greatly exceeded dilution (Table 1). If the Chl content of the euphotic zone were a simple function of the balance between growth and dilution, Chl should increase as μ/D increases above 1 as observed in the Hudson Estuary (Malone 1982b). However, euphotic zone Chl in Chesapeake Bay was inversely related to μ/D by the least-square regression:

$$\text{Chl} = 124 - 20.9 \ln (\mu/D) \quad (r = 0.93, n = 8)$$

Such a rapid decline in Chl as μ/D increased strongly implicates grazing as the major process controlling phytoplankton biomass in the surface layer during summer. This is consistent with previous observations in the Bay which indicate that most of the summer flux of POM into the benthos is in the form of organic detritus derived from phytoplankton (Malone et al. 1986).

The annual cycle of phytoplankton productivity is characterized by a winter minimum and a summer maximum, a pattern which is typical of a broad spectrum of estuaries (Malone 1977, Boynton et al. 1982, Cole & Cloern 1984). This suggests the importance of

light and temperature as parameters of phytoplankton productivity as Harding et al. (1986) have shown for Chesapeake Bay. For example, chlorophyll-specific productivity (P_{chl} , mg C mg Chl⁻¹ d⁻¹) during 1987 was significantly correlated ($R^2 = 0.54$, $p < 0.001$) with incident, photosynthetically active radiation (I , E m⁻² d⁻¹) and temperature (T , °C) by the (Type II) multiple regression:

$$P_{chl} = -55 + 2.0 I + 2.3 T$$

Table 4. Interannual variations in mean productivity (P , mg C m⁻² d⁻¹), chlorophyll content of the euphotic zone (Chl , mg m⁻²), chlorophyll-specific productivity (P_{chl} , mg C mg Chl⁻¹ d⁻¹), and vertical salt stratification for July–August

Year	P	Chl	P_{chl}	$S_b - S_s$
1984 ^a	1840	74	25	9.3
1985	4300	48	90	5.1
1986	2100	52	40	6.6
1987 ^b	4425	59	75	5.3

^a Data from Malone et al. (1986)
^b Malone unpubl.

Incident PAR and temperature were of nearly equal importance as indicated by the partial correlation coefficients (0.34 and 0.27 for PAR and temperature, respectively). However, as reported by Boynton et al. (1982), large interannual variations occur in the magnitude of the summer productivity maximum which are related to variations in P_{chl} (Table 4). These variations were correlated ($r = 0.96$, $n = 4$) with vertical salinity stratification (bottom salinity, S_b —surface salinity, S_s) by the (Type II) regression:

$$\ln P_{chl} = 5.85 - 0.292 (S_b - S_s) \quad (r = 0.96)$$

This, and the results of nutrient enrichment studies which indicate that phytoplankton growth is likely to be nitrogen-limited during summer (D'Elia et al. 1986), support the hypothesis that the magnitude of the summer productivity maximum is a function of physical

processes which regulate the recycling of ammonium from subpycnocline depths into the euphotic zone. As described by Malone et al. (1986), lateral 'tilting' of the pycnocline may be particularly important in this regard.

Comparison of these results with those for the coastal plume of the Hudson River illustrate the effects of seasonally pulsed inputs of new and recycled nitrogen (Table 5). Most new nitrogen input to the lower Hudson estuary is exported to the coastal plume where it is rapidly taken up by phytoplankton over an area which is roughly equivalent to the area of high uptake in Chesapeake Bay (Malone 1982b). The annual cycle of water column Chl in the plume is similar to that of the Bay in that maximum Chl occurs during February–April. However, the spring bloom in Chesapeake Bay is 5 times greater than that of the Hudson plume on average. In contrast, the annual cycles of productivity exhibit similar maxima but differ in timing with the productivity maximum of the plume occurring during early spring 5 to 6 mo prior to the productivity maximum of the Bay. These differences appear to be related to patterns of nutrient input and recycling and to the capacity to retain and concentrate biomass. New nitrogen supply to the Hudson plume is mainly derived from sewage and exhibits little seasonal variation relative to input to the Bay which is seasonally pulsed due to the large fraction of nitrogen derived from fertilizers (Malone 1982b, Smullen et al. 1982). High Chl in the Bay during February–April relative to other seasons and to the Hudson plume in general most likely reflects the pulsed nature of nitrogen input and the concentrating effects of estuarine circulation as discussed above. Regeneration and recycling of nitrogen assimilated during spring then supports the development of the summer productivity maximum of the Bay. As a consequence, a unit input of nitrogen to the mesohaline reach of the Bay supports 5 times more Chl during spring and 5 times more productivity during summer than in the plume (Table 5).

Table 5. Seasonal comparison of phytoplankton responses to nitrogen supply in the mesohaline reach of Chesapeake Bay and the coastal plume of the Hudson River

Variable	System	Feb–Apr	May–Jun	Jul–Aug	Sep–Oct
N-input (10 ⁶ g d ⁻¹)	Chesapeake	181	116	40	22
	Hudson	180	155	130	120
Chl (mg m ⁻²)	Chesapeake	723	306	132	107
	Hudson	147	76	60	88
P (mg m ⁻² d ⁻¹)	Chesapeake	480	1224	2824	2570
	Hudson	2833	2362	1724	1240
Chl/N-input	Chesapeake	4.0	2.6	3.3	4.9
	Hudson	0.8	0.5	0.5	0.7
P/N-input	Chesapeake	2.6	10.6	71.0	116.8
	Hudson	15.7	15.2	13.3	10.3

Phytoplankton production and summer oxygen depletion

The seasonal lag between the spring Chl maximum and summer regeneration provides a mechanism not

Fig. 12. Annual cycle of dissolved oxygen in bottom water ($\circ$, ppm) and vertical salinity stratification ($\bullet$, $S_b - S_s$; where S_b = bottom water salinity; S_s = surface water salinity)

only for enhancing summer productivity but also for seasonal oxygen depletion of bottom water. The concentration of dissolved oxygen (DO) in bottom water declined throughout the spring bloom and fell below 2 ppm as the bloom collapsed (Fig. 12). Bottom water was anoxic throughout most of July and August, 1986, but anoxia did not occur in 1985 until late August. The decline in bottom water DO during spring was significantly correlated ($p < 0.01$) with temperature by the regression equations:

- (1) (1985) $DO = 10.14 - 0.49 (T)$ ($r^2 = 0.88$, $n = 7$)
- (2) (1986) $DO = 10.71 - 0.47 (T)$ ($r^2 = 0.96$, $n = 6$)

It is noteworthy that, despite large differences in vertical stratification (Fig. 12, Table 1) and freshwater flow (Fig. 2), the rate of DO depletion with increasing tem-

perature was similar in 1985 and 1986. Mean Chl content of the water column at the peak of the spring bloom was in the range of 1200 to 1300 $mg\ m^{-2}$ during both years. Biomass as nitrogen was apparently greater in 1986 as indicated by higher N/Chl ratio (Tables 2 and 3). Likewise, biomass as carbon, calculated from C/Chl (Table 1), peaked at 72 $g\ m^{-2}$ in 1986 compared to 39 $g\ m^{-2}$ in 1985. Assuming stoichiometry between carbon, oxygen and carbon dioxide, these concentrations correspond to aerobic oxygen demands of about 100 to 200 $g\ O_2\ m^{-2}$, more than sufficient to account for oxygen depletion given reasonable rates of vertical eddy diffusion (Officer et al. 1984).

The occurrence and extent of summer anoxia appeared to be related to both vertical stratification during summer and to nitrate loading during the spring freshet. On time scales of days to weeks, increases in DO coincided with or occurred soon after decreases in vertical stratification once bottom water DO fell below about 2 ppm (Fig. 12). This implies a response to increased vertical mixing or lateral oscillations of the pycnocline (Malone et al. 1986). Interannually, mean bottom water DO during July–August was related to differences in stratification between summers (Table 1) and to differences in nitrate loading during the previous spring (Table 3). Summer productivity did not seem to be a major factor since productivity and DO were inversely related, a finding which is consistent with the conclusion that summer productivity depends on the physically driven recycling of ammonium into the euphotic zone. Contrary to the notion that oxygen demand during any given year is a function of the decomposition of organic detritus formed during the previous year and that summer anoxia is the result of increased stratification during spring (Officer et al. 1984), our results indicate that DO depletion of bottom water during spring was primarily a consequence of temperature-dependent metabolism of recently produced organic matter and is relatively insensitive to variations in vertical stratification over a wide range of salinity gradients. The occurrence and extent of anoxia and the frequency of reoxygenation events during summer appeared to be determined by the magnitude of the spring bloom and the strength and variability of vertical stratification during summer.

CONCLUSIONS

The annual cycle of phytoplankton productivity in the mesohaline reach of Chesapeake Bay is governed by incident PAR, temperature, and nitrogen recycling. Seasonal and interannual variations in phytoplankton biomass occur in response to variations in fresh water flow and associated variations in nitrate flux. Fresh

water flow and nitrate input during the spring freshet govern the timing and magnitude of the spring biomass maximum which determine the amount of nitrogen available for recycling during subsequent summer months. The occurrence of a summer productivity maximum and interannual variations in the magnitude of this maximum reflect the effects of vertical stratification on the return flux of ammonium from the benthos to the euphotic zone. Given the broad spectrum of estuaries which have annual cycles of productivity characterized by a summer maximum (Boynton et al. 1982), such a seasonal coupling between spring nutrient input, benthic regeneration and summer productivity may be a general phenomenon in mid-latitude, partially stratified estuaries.

Two scales of interaction appear to characterize the production of organic matter by phytoplankton in the surface layer and subsequent nutrient regeneration and oxygen depletion below the euphotic zone. Seasonally, sedimentation of the spring bloom fuels the regeneration of nutrients and maintenance of anoxia during summer. On a shorter time scale (days-weeks), sedimentation of phytoplankton production during spring provides the organic substrates for temperature-dependent oxygen consumption which causes the rapid decline in DO during spring. While vertical stratification is a necessary condition for this decline, bottom water DO did not appear to be sensitive to variations in stratification during the spring decline. During summer, phytoplankton productivity and grazing are closely coupled and sedimentation of fecal material and pseudofeces produced by grazing activity supplement the spring supply of phytoplankton (Malone et al. 1986). The effects of vertical stratification are most pronounced during summer when vertical fluxes of ammonium and oxygen respectively limit phytoplankton productivity in the surface layer and oxygenation of bottom water. Thus, the primary determinants of summer phytoplankton productivity in the surface layer and anoxia in the bottom layer are the magnitude of the spring freshet and the strength and variability of the summer halocline.

Finally, it is evident that the relationship between new and regenerated production proposed for the open ocean (Dugdale & Goering 1967, Eppley & Peterson 1979) is more complex in estuarine systems (Kemp & Boynton 1974). In the open ocean, phytoplankton production and nutrient regeneration are either closely coupled in time and space (ammonium assimilation = regenerated production) or separated by very large time and space scales (nitrate assimilation = new production). In estuaries, coupling between production and regeneration occurs over a continuum of time and space scales so that the distinction between new and regenerated production is not as clear and cannot be

made based on such factors as the oxidation state of the nutrient element in question. Perhaps the distinction between new and regenerated nutrients should be based on the scales by which primary production and nutrient regeneration are separated in time and space relative to the generation times of the primary producers. Thus, ammonium in Chesapeake Bay is regenerated nitrogen if it is produced and consumed in the euphotic zone but new nitrogen if it is produced below the euphotic zone where it must be returned into the euphotic zone for uptake to occur.

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