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Dynamics of the 1990 winter/spring bloom in Chesapeake Bay

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ABSTRACT: The winter/spring bloom of 1990 in Chesapeake Bay, USA, was prolonged and well developed, relative to other recent years, along the axis of the Bay. However, the bloom did not occur uniformly along the axis of the Bay, but rather developed and dissipated at different times in different regions of the Bay. The peak of the bloom progressed northward and was observed in late March in South Bay, early April in Mid Bay, and not until mid May in North Bay. We measured biomass and nutrient concentrations and the rates of carbon, nitrogen, phosphorus, and silicon utilization during the development and dissipation of the bloom, and compared ratios of these rates to the elemental ratios of the incoming nutrients and the resulting particulate material. In North Bay, bloom development was probably delayed due to light limitation of carbon uptake. Nitrogen was delivered and utilized in excess of stoichiometric proportions in the northern part of the Bay, eventually leading to phosphorus and/or silicon limitation. In the mid portion of the Bay, the mean stoichiometric proportions of the particulate nutrients were similar to Redfield proportions, but ratios of uptake of nitrogen and phosphorus exceeded Redfield proportions by more than 20-fold, reflecting both the high uptake rates of nitrogen and low uptake rates of phosphorus in that region. However, only at the peak of the bloom in mid April did transient phosphorus limitation of growth occur at Mid Bay. In contrast, ratios of nitrogen to phosphorus uptake rates in South Bay were considerably below Redfield proportions, primarily due to the low availability and low uptake rates of nitrogen. Concentrations of $Si(OH)_4$ in South Bay were also extremely low through the bloom period, and thus $Si(OH)_4$ and nitrogen, as well as PO_4^{3-}, limited growth there. In addition, temperature appeared to play a key role in the collapse of the diatom assemblage in mid May. During the early stages of the bloom in South Bay, $NO_3^- + NO_2^-$ contributed >60% of the total nitrogen utilized, but by the end of the spring bloom period in May, over 50% of the nitrogen utilized was urea alone. These data underscore the need to understand how freshwater flow, ambient nutrient concentrations, temperature, and light differ along the axis of the Bay to understand the differential timing and magnitude of bloom development in different regions of the Bay.

KEY WORDS: Phytoplankton · Spring bloom · Chesapeake Bay · Nutrient dynamics · Nutrient ratios

INTRODUCTION

Spring blooms dominated by diatoms are common in temperate aquatic systems, and the coupling between such blooms and seasonal patterns in freshwater flow, nutrients, mixing, and temperature, among other variables, are of interest both in terms of marine ecology in general and water quality management. Spring diatom blooms are often particularly pronounced in estuaries and have been well described in San Francisco Bay (Peterson et al. 1975, Cloern et al. 1989), Delaware Bay (Sharp et al. 1982, Pennock 1985, Pennock & Sharp 1986), the St. Lawrence estuary (Therriault & Levasseur 1985), and the Hudson River estuary (Malone & Chervin 1979, Malone et al. 1983).

A spring diatom bloom is also a common feature of the annual phytoplankton cycle in Chesapeake Bay, where considerable research in recent years has been devoted to understanding how, and on what time

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scales, nutrient input is related to nutrient recycling and primary production (Boynton et al. 1982, Malone et al. 1983, Fisher et al. 1988, 1992, Conley & Malone 1992). The major source of nutrients to Chesapeake Bay is the Susquehanna River, which supplies > 80 % of the total nitrogen to the upper Bay (McCarthy et al. 1977, Harding et al. 1986), and most of this input occurs during the spring freshet (Schubel & Pritchard 1986). It has previously been shown that annual phytoplankton production is better correlated with freshwater nitrogen loading than with freshwater phosphorus loading (Boynton et al. 1982), and most of the assimilation of this external nitrogen occurs downstream of the turbidity maximum in the mesohaline reach of the Bay.

In Chesapeake Bay, Malone et al. (1988, 1991) have documented that there is typically a rapid transition in late spring from a diatom-dominated community to a cyanobacteria- and microflagellate-dominated summer community. While nitrogen loading to the Bay is highly correlated with the amount of chlorophyll (chl *a*) that accumulates in the spring, it has been suggested that both phosphorus and silicon may limit the rate of phytoplankton growth in spring in most of the Bay (Fisher et al. 1992) and that the depletion of silicate is highly correlated with the change in floristic composition (Conley & Malone 1992). Dissolved silicate limitation results in large increases in sinking rates of diatoms (Titman & Kilham 1976, Bienfang et al. 1982), and thus increases in diatom sedimentation rate may well be an important factor in the termination of the Chesapeake Bay spring diatom bloom (Schelske & Stoermer 1971). The increased diatom sedimentation in turn contributes to the seasonal anoxia which typically occurs in bottom waters at the end of the bloom (Malone 1992).

The goal of this study is to describe the dynamics of the spring bloom in Chesapeake Bay. Whereas the studies cited above have provided a seasonal context of the coupling between nutrient input, the development of spring phytoplankton biomass, and the rapid shift to a summer plankton community, the processes responsible for the collapse of the spring bloom are in fact poorly understood. Yet, this information is critical for the development of effective nutrient management strategies for the Bay. On the one hand, the rich phytoplankton biomass of spring supports high secondary production in the Bay; on the other hand, the sedimentation of this organic material in late spring fuels high rates of microbial metabolism which lead to oxygen depletion below the pycnocline (Boynton et al. 1982, Seliger et al. 1985, Malone et al. 1988, Malone 1992). Our study was conducted during spring of 1990, during which there was a bloom which was large relative to other recent years (Harding 1994). We examine both the time series of the bloom development and decline in the mesohaline reach of the Bay and the development of the bloom along the axis of the Bay.

METHODS

There were 3 types of sampling efforts in Chesapeake Bay during spring 1990 from which we have analyzed data. Our process-oriented studies emphasized measurements of production and nutrient uptake at 3 stations: North, Mid and South Bay (Fig. 1). Low altitude aerial overflights using NASA's Ocean Data Acquisition System (ODAS) were used to estimate high frequency, synoptic chl *a* distributions, and monitoring cruises by the Chesapeake Bay Program on a biweekly basis provided additional nutrient and biomass data with good spatial resolution.

Process-oriented studies. Cruises were conducted aboard the RV 'Warfield' at intervals of 2 to 4 wk during April and May. During the cruises, each station was occupied for approximately 13 h. At a minimum, hydrocasts and profiles of conductivity, temperature, and fluorescence were made near midnight, dawn, and noon to describe water column structure and variability over a diel cycle. On selected cruises more extensive diel sampling was conducted. The pycnocline region was defined by changes in $\sigma_t > 0.2\ m^{-1}$. Water was collected using 10 l Niskin bottles from 2 or 3 depths (usually surface-mixed, pycnocline, and near-bottom layers), and the parameters analyzed are summarized in Table 1. Near-bottom samples were collected ~1 m above the sediment interface and care was taken to ensure that the sediment was not disturbed during sampling.

Table 1. Methods used for biomass and uptake rate determinations

Measurement	Technique (Source)
Chlorophyll	Fluorescence (Yentsch & Menzel 1963)
Accessory pigments	HPLC (Van Heukelem et al. 1993)
Particulate carbon and nitrogen	Control Equipment elemental analyzer
Particulate phosphorus	1 M HCl following combustion (Anderson 1976)
Biogenic silica	NaOH digestion (Krausse et al. 1983)
Inorganic nutrient concentrations	Technicon AutoAnalyzer
Primary production	^{14}C-bicarbonate (Malone et al. 1988)
Uptake of NH_4^+, NO_3^-, NO_2^-, urea	^{15}N-tracer (Glibert et al. 1991)
Uptake of PO_4^{3-}	$^{32}PO_4^{3-}$-tracer (Fisher & Lean 1992)
Uptake of $Si(OH)_4$	$^{30}Si(OH)_4$-tracer (Nelson & Goering 1977)

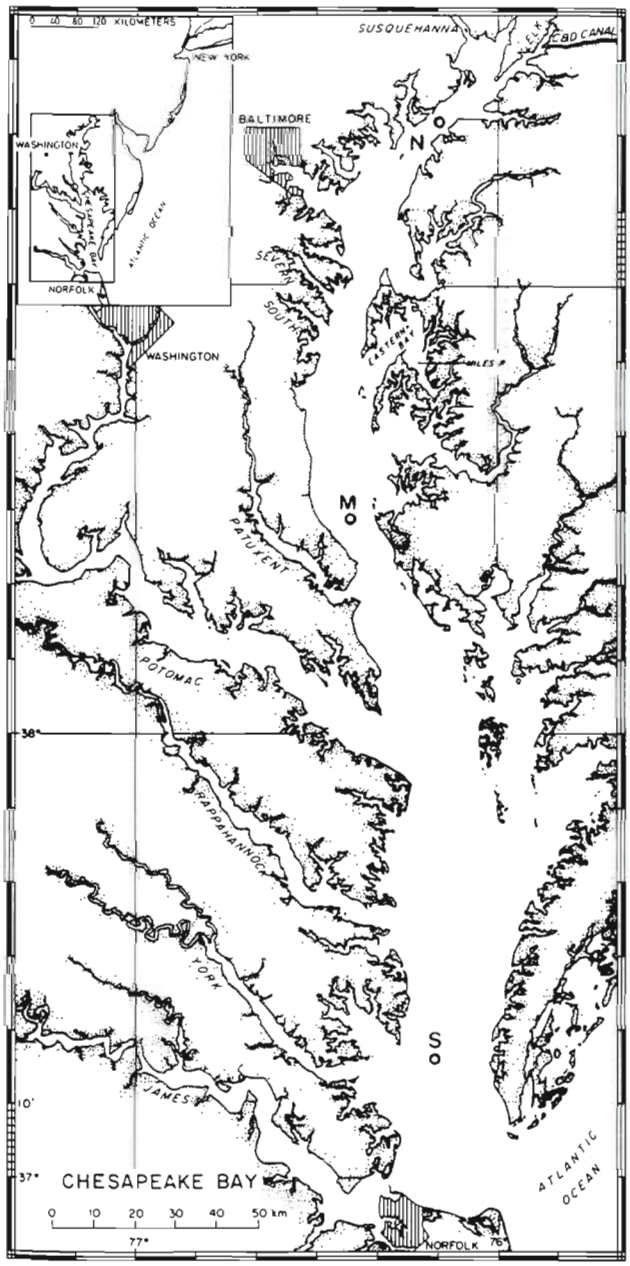

Fig. 1. Chesapeake Bay, USA. (O) Locations of the North (N), Mid (M) and South (S) Bay stations

Samples for nutrient analysis were filtered (GF/F), frozen, and analyzed on shore within a few weeks (Table 1). We routinely measured the biomass and rates of uptake in an unfractionated sample; and, for the noon cast, rates of uptake of carbon, nitrogen, and phosphorus in the <1 µm fraction (fractionated using 1 µm Nuclepore filters) were also determined. On selected cruises, measurements of the biomass and rates of nitrogen uptake in the <20 µm size fraction (fractionated using 20 µm Nitex netting) were also made. Particulate material for biomass determinations, and for the measurement of rates of uptake, was collected using GF/F filters with vacuum pressures of <50 mm mercury. Phytoplankton production was estimated by the ^{14}C technique from 24 h shipboard incubations under natural light.

Rates of uptake of nitrogen were determined using ^{15}N substrates, and uptake experiments were performed on all the inorganic nitrogen forms (NH_4^+, NO_3^-, NO_2^-) plus urea. In order to enrich our ^{15}N uptake experiments with a 'trace' quantity of ^{15}N (~10% of ambient, or 0.03 µmol l^{-1} if ambient concentrations were non-detectable), it was necessary to measure the concentration of ambient nitrogen substrates on board, just prior to making the enrichment, using manual methods. This was done by collecting water from a separate cast approximately 1 h before the water for experimentation was collected. Incubations for ^{15}N uptake were typically 1 h in duration. Filters were prepared for mass spectrometry following the general protocol described by Fiedler & Proksch (1975). The mass spectrometer used was a Nuclide 3" 60° sector analyzer with dual mass collection, as described in Glibert et al. (1991).

Uptake of PO_4^{3-} was measured using $^{32}PO_4^{3-}$ additions of 5000 to 10000 dpm ml^{-1} generally following the protocol of Fisher & Lean (1992). Subsamples were taken to assess the incorporation of isotope in a time series of 4 to 5 points at intervals varying from 1 to 30 min, depending on the turnover time of PO_4^{3-}. Subsamples were counted on a Packard Tri-Carb 4530 liquid scintillation counter calibrated with internal and external standards. Particulate samples were counted in fluor with an efficiency of >99%; Cerenkov radiation was counted in aqueous samples with an efficiency of ca 50%. Biologically available PO_4^{3-} (BAP; Rigler 1968), as opposed to the total pool of PO_4^{3-} that was reactive with acid molybdate (soluble reactive PO_4^{3-}or SRP), was assessed using P-limited cultures of *Chlorella* sp. (T. Fisher, E. Peele & T. Coley unpubl.). Rates of PO_4^{3-} reported here were unaffected by interference from the biologically unavailable fraction of SRP.

The rates of uptake of $Si(OH)_4$ were determined on a much less frequent schedule than those of the other nutrients, and only limited data are available. As was the case for the nitrogen uptake experiments, we conducted onboard analyses of $Si(OH)_4$ concentration just prior to our experiments. Based on those data, samples were enriched with a quantity of $^{30}Si(OH)_4$ sufficient to elevate the ambient concentration by ca 10% (Nelson & Goering 1977). Incubations ranged between 1 and several hours, at which time samples were filtered through 1 µm Nuclepore filters, then frozen. They were subsequently analyzed for

isotopic enrichment using a Balzers QMS 240 mass spectrometer.

ODAS overflights. Algal biomass was estimated more frequently and in greater detail using NASA's ODAS in overflights from a small airplane. These overflights were conducted biweekly in a grid over the mainstem of the Bay at an altitude of 150 m for acquisition of upwelling radiances at 460, 490, and 520 nm. Chl *a* was computed from the radiances using a spectral curvature algorithm calibrated with matching ship data (Harding et al. 1992).

Monitoring cruises. Data from the U.S. Environmental Protection Agency (EPA) database on Chesapeake Bay were also analyzed to provide finer spatial resolution of nutrient concentrations than our sampling allowed. These data were collected by the Maryland Department of the Environment and the Virginia Water Quality Control Board in ongoing monitoring efforts and were generously made available to us to support our process measurements.

RESULTS

Timing and extent of the bloom

The extensive EPA database, combined with the broad spatial coverage of the ODAS flights, allowed us to determine that the winter/spring bloom of 1990 developed early in the year, such that by early February, integrated water column chl *a* values exceeding 700 mg m^{-2} were observed in Mid Bay (Fig. 2). However, the peak of the bloom occurred in early April, between the mouths of the Rappahannock and Patuxent Rivers in the mainstem of the Bay, with chl *a* values reaching 800 to 1000 mg m^{-2} (Fig. 2). As indicated by the spacing of the isopleths, concentrations of chl *a* began to decline in mid April; however, the most rapid decline occurred in mid May (Fig. 2). From mid May, values remained <200 mg m^{-2} for the balance of the year.

Whereas the ODAS overflights permitted near-synoptic depth-integrated chl *a* distributions to be determined, water column sampling permitted size fractionation of chl *a* which the overflights could not. Water samples collected from the North Bay station indicated that surface water chl *a* concentrations remained several-fold lower than those in the Mid and South Bay regions, and, with the exception of a brief period in early April, virtually all of the measured chl *a* was in the <20 µm fraction (Fig. 3). In the Mid Bay region, in sharp contrast, chl *a* not only reached concentrations ca 4-fold higher than those in North Bay, but also about 60% of the chl *a* measured in the surface waters during April in the Mid Bay region was phytoplankton <20 µm in size (Fig. 3). The >20 µm fraction declined steadily during April and May, leaving a phytoplankton assemblage that was composed almost entirely of cells <20 µm in size in both surface and bottom waters. The relationship between chl *a* concentration and the fraction of that chl *a* in the <20 µm fraction strongly suggests that large diatoms were sinking out of the water column during this time. In South Bay, while we have fewer shipboard observations from which to draw, it appeared that chl *a* concentrations did not reach levels as high as those in Mid Bay (Fig. 3).

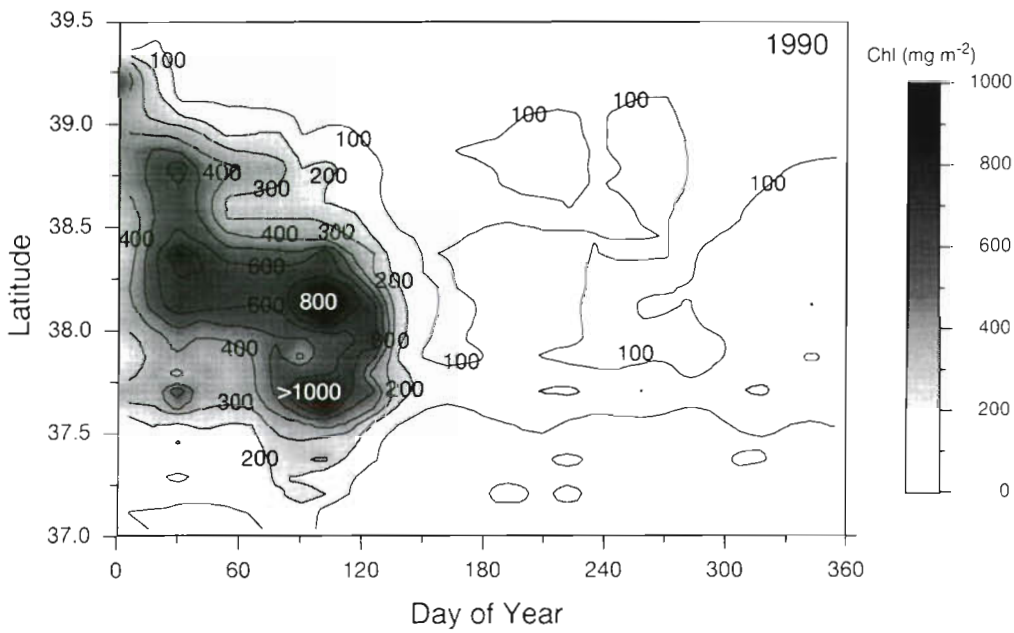

Fig 2. Depth integrated chlorophyll *a* (chl *a*) concentrations in Chesapeake Bay during 1990 based on low altitude aerial surveys using NASA's Ocean Data Acquisition System, and vertical chl *a* profiles from the Chesapeake Bay Monitoring Program

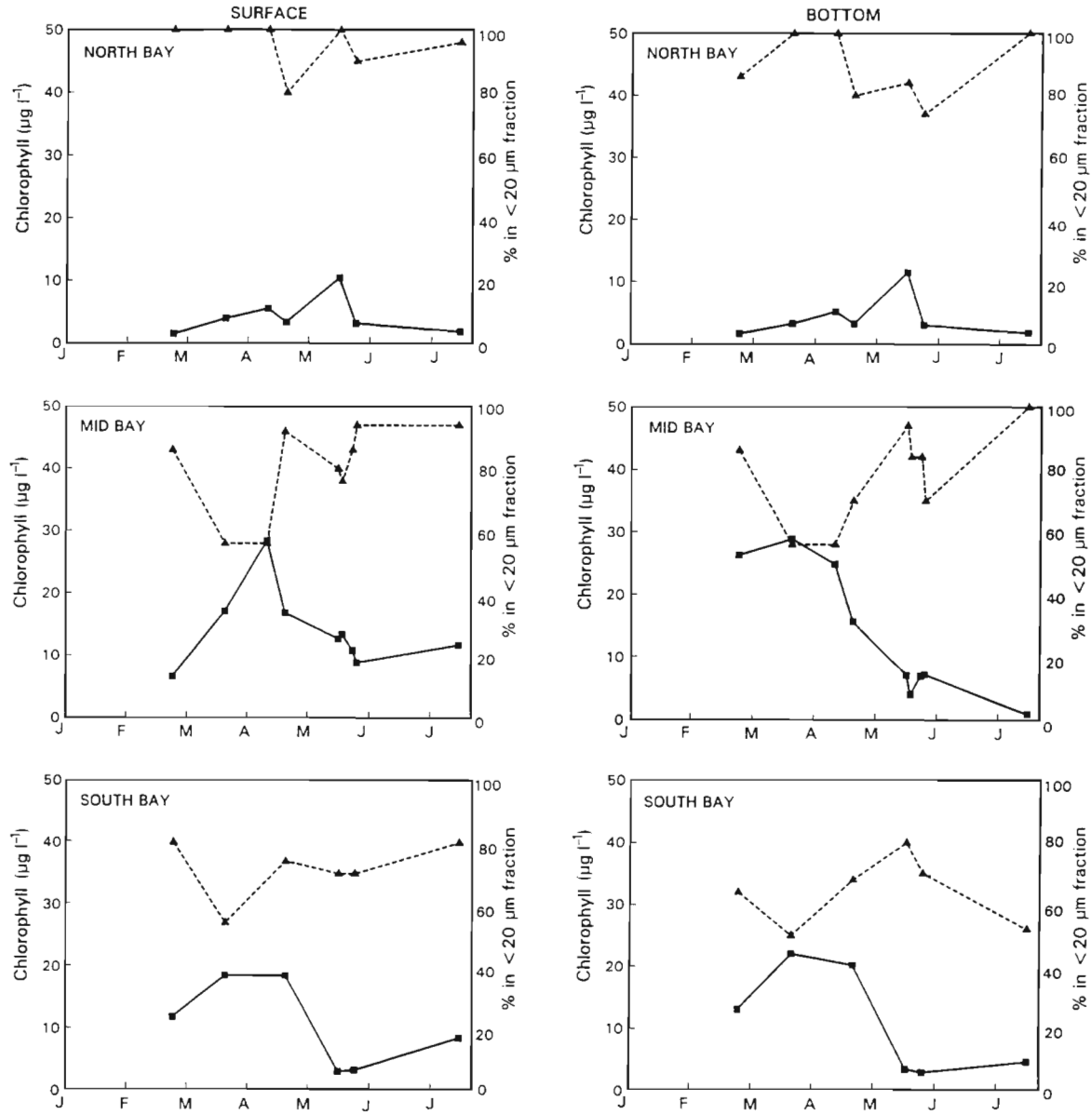

Fig. 3. Surface and bottom water chl *a* concentrations (■—■) and the percentage of chl *a* in the <20 µm size fraction (▲- - -▲) from the North, Mid, and South Bay stations

Although enumerations of phytoplankton were not routinely performed during this period, changes in floristic composition based on pigment biomarkers are consistent with previous descriptions of phytoplankton succession in the Bay (e.g. Van Valkenburg et al. 1978). High fucoxanthin concentrations (data not shown) for Mid Bay during April suggest that diatoms were a major component of phytoplankton assemblage. Fucoxanthin (µmol l^{-1}) concentrations were significantly correlated with concentrations of biogenic silica (µmol l^{-1}) [fucoxanthin = 0.20 (biogenic silica) + 0.65; r^2 = 0.48]. Although the pigment peridinin was present during April, a large increase in peridinin concentration was observed in bottom waters in late May (data not shown), indicative of photosynthetic dinoflagellates (Wright et al. 1991).

In North Bay, the fraction of total chl *a* that was <1 µm in size represented <1% of the total chl *a* throughout April and May (data not shown). At Mid Bay, approximately 5%, on average, of the total chl *a* was <1 µm in size. In South Bay, the contribution of <1 µm chl *a* to total chl *a* increased from <1% in mid April to 10% in late May (data not shown). This likely reflects the increase in cyanobacterial biomass which typically follows the decline of the diatom-dominated bloom (Malone 1992).

River flow, stratification, and temperature

Susquehanna River discharge was slightly below the long-term mean in spring 1990. Daily mean flow of the Susquehanna River measured at the Conowingo Dam in 1990 reveals 3 broad peaks with mean flow rates in excess of 200×10^6 m^3 d^{-1} in February, April, and May (Fig. 4A). A comparison with other recent years provides a context for assessing the magnitude of freshwater input prior to the spring bloom of 1990 (Harding 1994). Susquehanna River flow on a seasonal basis, when expressed as the percentage difference from the long-term (1950 to 1992) mean seasonal flow rate, shows 5 successive seasons of low flow from winter 1988 through winter 1989 (Fig. 4B). Two seasons of high flow, >50% above the long-term mean, followed in 1989, after which 3 seasons of near-average flow occurred from fall 1989 through spring 1990. Summer and fall 1990 had flow rates from 60 to 130% above the long-term mean, followed by a prolonged period of low flow from spring 1991 through spring 1992. Although Fig. 4B demonstrates considerable seasonal and interannual variability, the spring 1990 period under consideration here was one of near-normal hydrologic inputs.

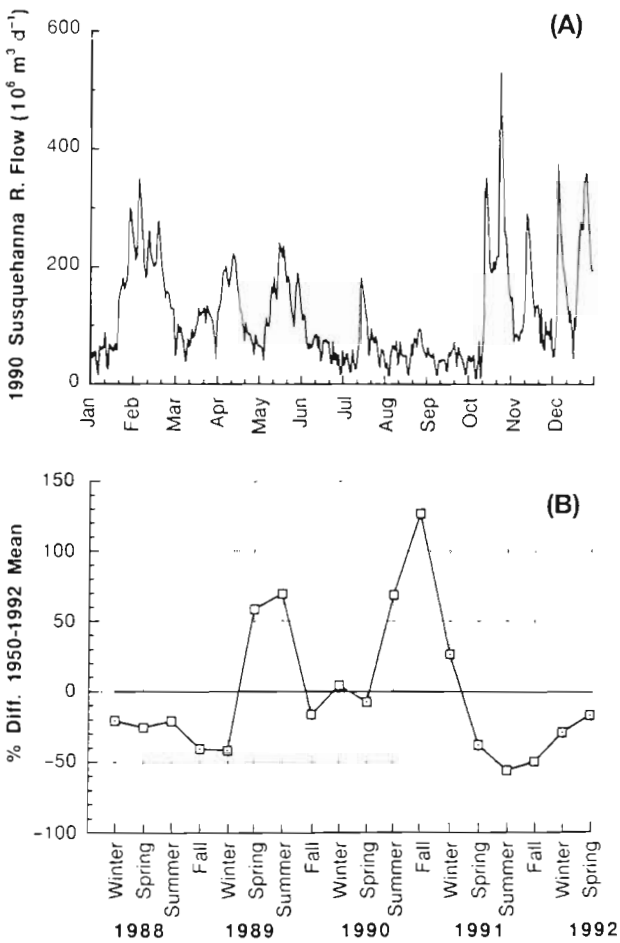

Fig. 4. (A) Daily mean flow of the Susquehanna River during 1990, and (B) the percentage difference in Susquehanna River discharge over seasons from the long-term (1950 to 1992) mean

The degree of stratification of the water column was different at the 3 stations. At North Bay, where the mean depth is ca 10 m, the water column was unstratified during the sampling period. At Mid Bay, where the mean depth is ca 19 m, the water column was continually stratified during the study period. The pycnocline was usually at about 10 m, but shoaling to 6 to 8 m was observed at the peak of the bloom in mid April and a rapid steady shoaling to approximately 3 m occurred at the end of May. The South Bay station, likewise, was continually stratified. Its mean depth is ca 11 m, and the typical depth of the pycnocline was 5 to 8 m, although shoaling to 5 to 6 m was noted at comparable times in April and May. There were no direct relationships between pycnocline depth and monthly river flow. However, the depths of the euphotic zone at Mid and South Bay were comparable to the depths of stratification during this period, but in the turbid North Bay, the euphotic zone was much shallower than the 10 m mean depth.

Throughout the first 6 mo of the year, surface water temperature at Mid Bay increased in a near-linear fashion with time ($r^2 = 0.97$). During the peak of the bloom, surface temperature was approximately 12°C; this was 1 to 2°C cooler than predicted from the regression of temperature as a function of day of the year [Temp. = 0.16(Julian Day) – 4.27]. Temperatures were approximately 18°C during the rapid decline of the bloom in late May.

Incoming dissolved nutrients and their resulting distribution

Concentrations of dissolved inorganic nitrogen were relatively high during the study period. In the unstratified North Bay, the average concentration of NO_3^- + NO_2^- during spring exceeded 80 µmol l^{-1} (Fig. 5), and at Mid Bay, where stratification was observed, the average concentrations of NO_3^- in the less saline, surface-mixed layer were high (ca 25 µmol l^{-1}) but lower than in the bottom layer. Concentrations of NH_4^+, on the other hand, averaged ca 4 µmol l^{-1} in North Bay, while at Mid Bay, average concentrations of NH_4^+ ranged from ca 2 µmol l^{-1} in the surface to ca 7 µmol l^{-1} in the bottom waters (Fig. 5). The concentration of NH_4^+ in bottom water continued to rise through the summer, exceeding 20 µmol l^{-1} by July. In South Bay, concentrations of the inorganic nitrogen nutrients were always <5 µmol l^{-1} throughout the spring period, and from April through May were <0.5 µmol l^{-1}.

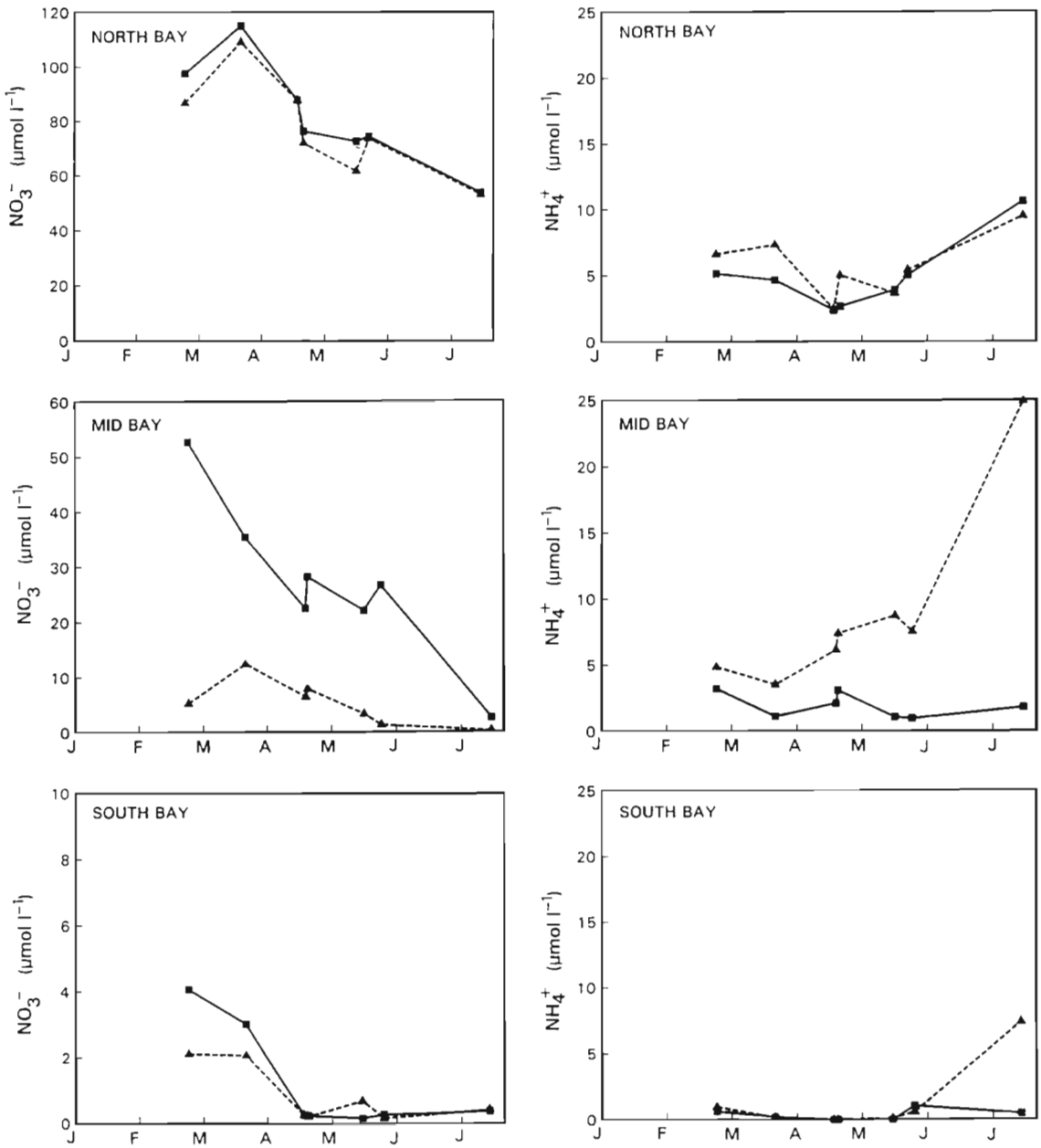

Fig. 5. Concentrations of NO_3^- and NH_4^+ in surface waters (■—■) and bottom waters (▲- - -▲) from the North, Mid, and South Bay stations

In contrast to inorganic nitrogen, concentrations of PO_4^{3-} were very low during spring throughout the Bay. In the surface water, concentrations of SRP averaged ca 0.24 µmol l^{-1} at the North Bay station, and declined to <0.1 µmol l^{-1} at the Mid and South Bay stations (Fig. 6). Bottom waters were slightly higher at the Mid and South Bay stations (Fig. 6). The BAP fraction was 20 to 40% of SRP at the North and Mid Bay stations, and was essentially equivalent to SRP at the South Bay station (data not shown).

As was the case for NO_3^-, $Si(OH)_4$ concentrations were very high in North Bay waters throughout spring, about 4-fold lower at Mid Bay during this period, and were near detection limits in South Bay (Fig. 6). In North Bay there was a brief period of lowered concentrations of PO_4^{3-}, $Si(OH)_4$, and NO_3^- during early May. During the same period, there was a 5-fold elevation in chl *a* concentration in North Bay. During mid April, concentrations of $Si(OH)_4$ dropped to near analytical detection limits at Mid Bay, concomitant with the peak in the

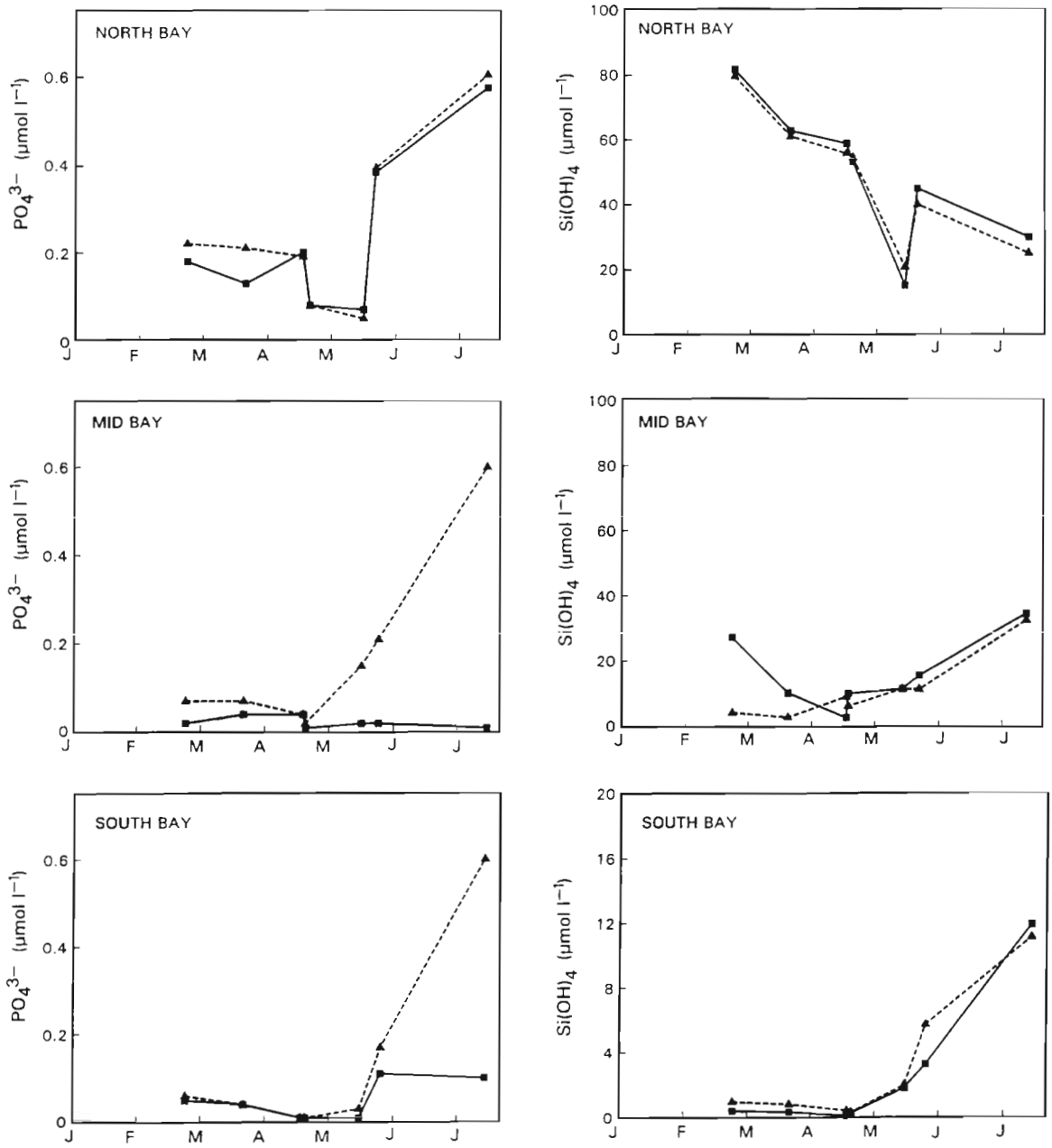

Fig. 6. Concentrations of PO_4^{3-} and $Si(OH)_4$ in surface waters (■—■) and bottom waters (▲- - -▲) from the North, Mid, and South Bay stations

>20 µm chl *a*. During late May, concentrations of $Si(OH)_4$ increased to nearly twice the average concentration (Fig. 6), and in South Bay increased significantly from late spring to summer in both surface and bottom waters.

The stoichiometric proportions of the dissolved nutrients in surface water are compared in Table 2. For the North and Mid Bay regions, the mean N:P ratios exceeded the Redfield proportions of 16:1 (Redfield 1958) by nearly 50-fold, and if only the smaller BAP is used instead of SRP, the mean ratios exceeded the Redfield proportions by up to 100- to 200-fold. Only in South Bay, where nitrogen availability was considerably lower, and where SRP was composed almost entirely of BAP, did the ratios of N:P approach Redfield proportions. In fact, as the winter/spring bloom declined in South Bay, the N:P ratio fell below Redfield proportions due to the depletion of nitrogen (data not shown). The mean Si:P ratios also exceeded the Redfield proportions in the North and Mid Bay regions, by factors of 10 to 50 (Table 2), and in South Bay, as for the

Table 2. Mean molar ratios of the concentrations of dissolved nitrogen (NH_4^+, NO_3^-, NO_2^-, urea), PO_4^{3-}, and $Si(OH)_4$ in the near-surface waters of Chesapeake Bay during the spring bloom of 1990. Ratios presented are the average ratios for all available data from late March through late May. The first entry for each station is calculated using the biologically available pool of PO_4^{3-} (BAP), and the second entry is the ratio calculated using the total soluble reactive pool of PO_4^{3-} (SRP). Standard deviations are given in parentheses

Stn	N:BAP N:SRP	Si:BAP Si:SRP	N:Si
North Bay	1500 (860) 620 (360)	730 (430) 350 (180)	2.0 (0.8)
Mid Bay	3200 (1400) 540 (210)	850 (210) 140 (90)	3.8 (1.5)
South Bay	29*(11) 29 (11)	31*(16) 31 (16)	0.9 (0.4)

*BAP equaled SRP at South Bay

N:P ratio, the mean Si:P ratio was within a factor of 2 of Redfield proportions. Concentrations of $Si(OH)_4$ were generally within a factor of 2 of the NO_3^- concentrations (Figs. 5 & 6); thus, the similarity in total dissolved inorganic nitrogen plus urea and $Si(OH)_4$ is also noted in the ratio of these values, which ranged from 0.9 to 3.8 and encompassed the Redfield proportions of 1:1 (Table 2).

Distribution of particulate biomass

The time course of particulate N and particulate C concentrations in the near-surface waters show that from February to June 1990 there were 2 distinct peaks. The largest and most prolonged peak was observed in early April, and was present throughout the length of the Bay (Fig. 7). The second peak, more short-lived in duration, was observed from early to mid May, and was only noted in North and Mid Bay. It is possible, however, that with the limited data in South Bay, a secondary peak developed but was not measured.

Table 3. Mean molar ratios of the particulate nutrients, and weight:weight ratios of C:chl *a* in the near-surface waters of Chesapeake Bay during spring 1990. Ratios presented are the average of all available data from late March through late May. Standard deviations are given in parentheses

Stn	N:P	C:N	C:P	Si:N	C:chl *a*
North Bay	7.3 (1.9)	11 (1.5)	82 (12)	2.8 (1.1)	290 (120)
Mid Bay	16 (0.9)	7.1 (0.6)	114 (14)	1.0 (0.4)	73 (14)
South Bay	13 (7.0)	8.7 (1.2)	124 (19)	0.9 (0.3)	67 (76)

In sharp contrast to the stoichiometric proportions of the available nutrients during spring 1990, the mean N:P ratios of the particulate material in the near-surface waters were below Redfield proportions in the North Bay, and were close to Redfield proportions in the Mid and South Bay regions (Table 3). In addition, because of the high proportion of diatom biomass, the mean ratio of biogenic Si : particulate N in Mid Bay was 1.0 ± 0.4. The mean C:N ratios and the C:P ratios also approximated Redfield ratios.

The mean C:chl ratios for the spring were distinctly different for the near-surface waters of the 3 regions of

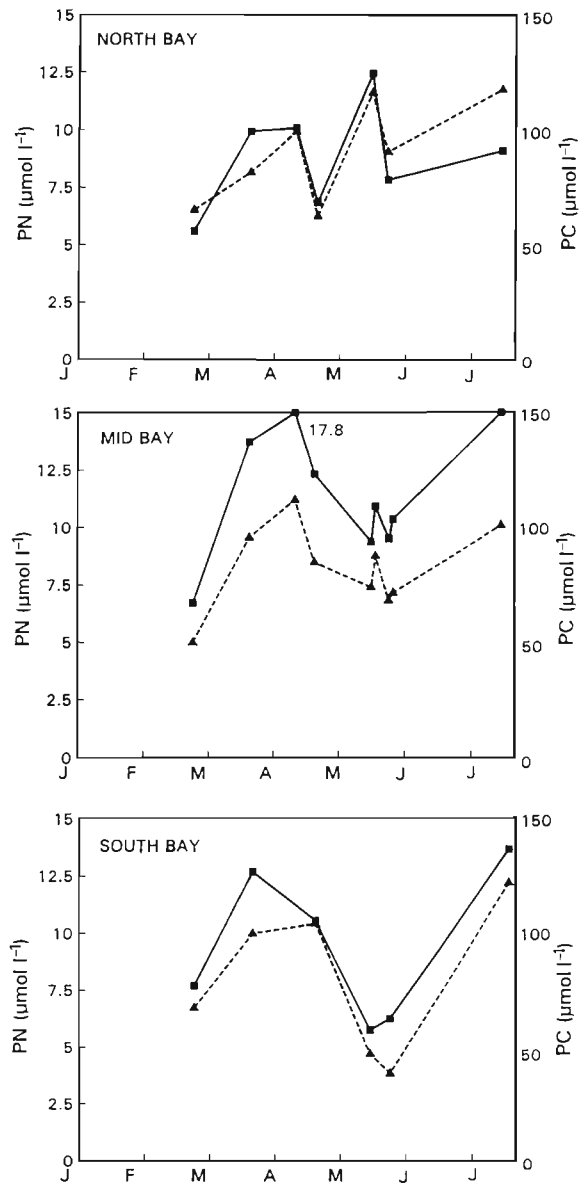

Fig. 7. Concentrations of particulate nitrogen (PN, ■—■) and particulate carbon (PC, ▲- -▲) in surface waters from the North, Mid, and South Bay stations

the Bay (Table 3), and also changed significantly with the time course of the bloom. In North Bay, the mean C:chl *a* ratio was 290 ± 120, but revealed a fairly steady decline from mid February (520) to mid May (140). The mean C:chl *a* ratio for Mid Bay averaged 73 ± 14, and was fairly invariant during the entire study period. In contrast, in South Bay, the C:chl *a* ratio averaged 67 from mid February to mid April, when the bloom was at its peak in this region, then escalated sharply to ca 160 during mid May, reflecting the decline in chl *a* in the surface waters.

Rates of carbon fixation and uptake of dissolved nutrients

Time-averaged rates of carbon fixation during the spring bloom were highest at Mid Bay (4.1 µmol l^{-1} h^{-1}), and 2- to 3-fold lower in North (2.2 µmol l^{-1} h^{-1}) and South Bay (1.4 µmol l^{-1} h^{-1}; Fig. 8A). The shallow euphotic zone at the North Bay restricted carbon fixation to the top 2 m of the water column, unlike Mid Bay or South Bay, where the euphotic zones were 6 and 9 m respectively, so that carbon fixation rates integrated over the water column were considerably lower in the North than in the Mid or South Bay regions. Carbon fixation rates were about 2-fold higher during the peak of the bloom at Mid Bay than during either the development or the decline of the bloom.

Time-averaged rates of uptake of nitrogen (expressed as the sum of the measured substrates) in near-surface waters decreased from North to South Bay during spring (Fig. 8A). At South Bay the measured rates were about 20% those determined for North Bay. The relative proportions in which the different nitrogen substrates were consumed also varied along the axis of the Bay (Fig. 8B). The proportion of total nitrogen utilized as NO_3^- decreased down-Bay, the proportion of total nitrogen utilized as NH_4^+ varied by only a few percent, while the proportion of urea utilized increased from approximately 6% at North Bay to >30% at South Bay (Fig. 8B).

In addition to the overall decrease in nitrogen uptake rates from North to South Bay, temporal differences were also noted. At North Bay, NO_3^- initially contributed >60% of the total nitrogen utilized, but this proportion fell to roughly 30% by the end of the bloom (data not shown). The contribution of NH_4^+ to the growth of plankton in the North Bay increased from approximately 25% to 50% during the course of the spring. In the Mid Bay region, however, NO_3^- and NH_4^+ contributed about equal proportions to the total nitrogen utilized, and these proportions varied by no more than a few percent during the development and dissipation of the bloom (Fig. 9). Rates of NO_3^-

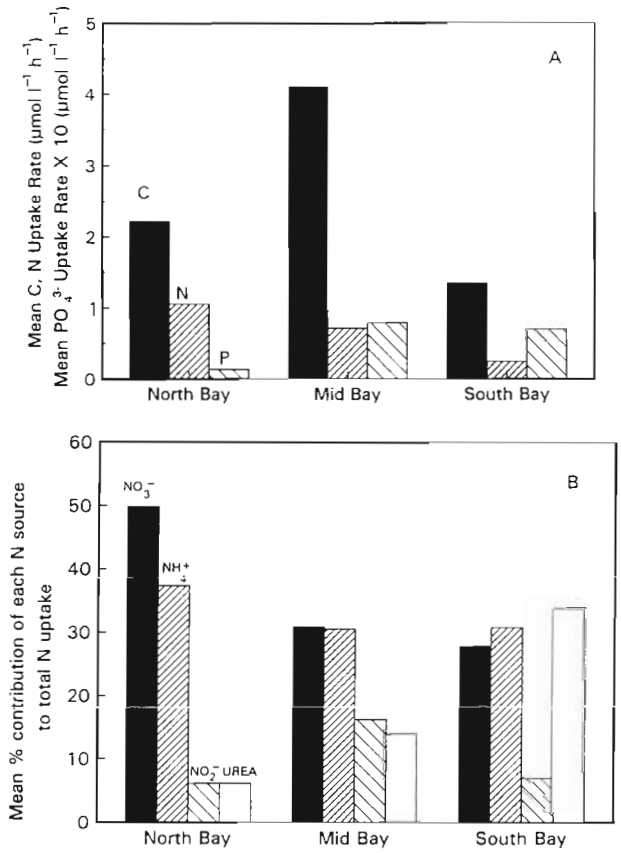

Fig. 8. (A) Mean uptake rates of C, N, and P (PO_4^{3-}), and (B) mean percent contribution of each nitrogen source (NO_3^-, NH_4^+, NO_2^-, urea) to the total N uptake averaged over spring 1990 from the surface waters of the North, Mid, and South Bay

uptake declined rapidly after the decline of the bloom at Mid Bay, paralleling the decrease in chl *a* from mid April to late May (r^2 of NO_3^- uptake and chl *a* = 0.92), whereas the rates of NH_4^+ uptake increased then decreased over the same time period (Fig. 9). Further, for both substrates, the <20 µm fraction utilized these substrates at rates that were on average 40% those of the whole fraction. In neither North nor Mid Bay did NO_2^- or urea contribute more than 15% of the total nitrogen utilized. In sharp contrast, at South Bay, the contribution of NO_3^- dropped from 40% of the total nitrogen utilized to 20%, NH_4^+ utilization dropped from roughly 20% to 15%, while the contribution of urea to total nitrogen utilized increased from 14% to 54% from mid April to mid May (data not shown).

Rates of PO_4^{3-} uptake (Fig. 8) were very low throughout this period, but were higher in Mid and South Bay than in the North Bay region. This spatial pattern noted in the rates of PO_4^{3-} uptake is almost the inverse of that observed for rates of nitrogen uptake, which were highest at the North and Mid Bay stations.

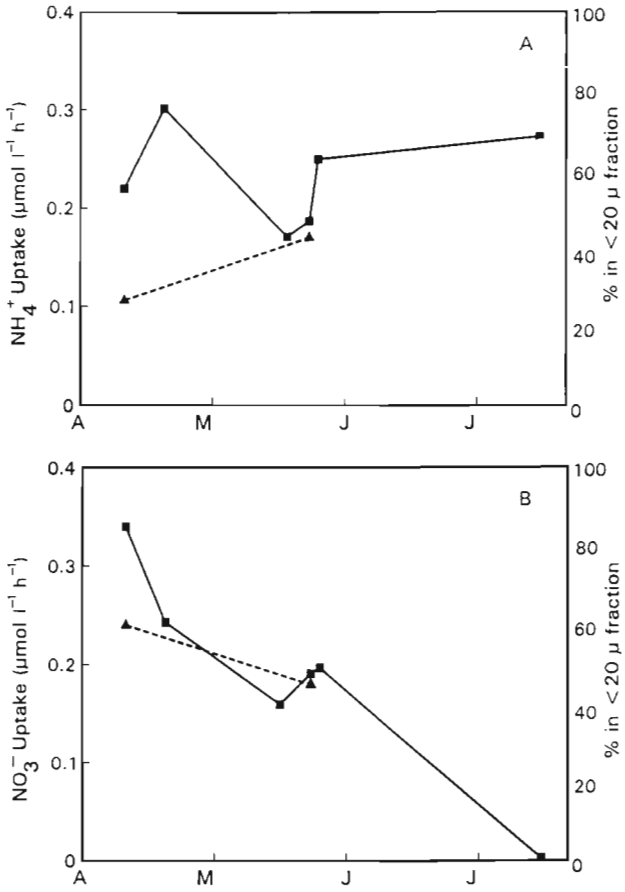

Fig. 9. Surface uptake rates of (A) NH_4^+ and (B) NO_3^- as a function of time during spring 1990 at the Mid Bay station. (▲- - -▲) Uptake rates of the <20 µm fraction

Also contrasting with the rates of nitrogen uptake, which were relatively invariant with time, the rates of uptake of PO_4^{3-} increased 2- to 4-fold from mid to late May (data not shown).

The stoichiometric relationships between the rates of assimilation of different nutrients are also informative and are particularly interesting to compare with those of both the available dissolved nutrients and the particulate material. The mean N:P ratio of uptake rates decreased about 100-fold down-Bay, and this pattern was similar regardless of whether rates were expressed for near-surface mid morning only (µmol l^{-1} h^{-1}), or integrated over the water column over a 24 h period (µmol m^{-2} d^{-1}; Fig. 10A). In North Bay, the mean N:P uptake ratio (based on volumetric rates) exceeded Redfield proportions by more than 20-fold, reflecting both the high uptake rates of nitrogen and the low uptake rates of PO_4^{3-} in that region. This ratio approximated Redfield proportions at Mid Bay, but fell considerably below Redfield proportions at South Bay. This reflected the inverse patterns of N and P uptake; rates of total N uptake decreased considerably from North to South Bay, while rates of PO_4^{3-} increased. Note that this downward trend in N:P uptake ratios down-Bay mirrors the downward trend in the molar ratios of N:P concentrations (Table 2), whereas the molar ratios of the resulting particulate biomass were

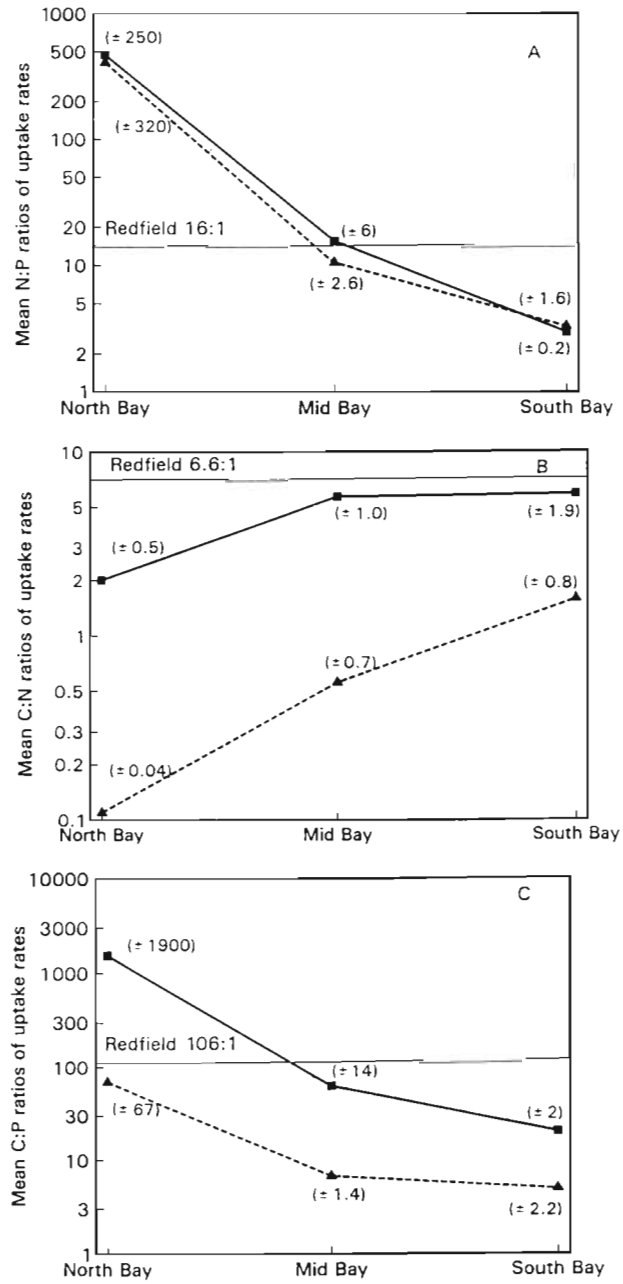

Fig. 10. Mean molar ratios of the rates of (A) N:P uptake, (B) C:N uptake, and (C) C:P uptake, where the N uptake rate is the sum of all substrates measured (NO_3^-, NH_4^+, NO_2^-, urea). (■—■) Rates determined for mid morning, near-surface waters (µmol l^{-1} h^{-1}); (▲- - -▲) rates integrated over the water column and full day period (µmol m^{-2} d^{-1}). Standard deviations are given in parentheses

Table 4. Mean turnover times (h) for the dissolved nutrients in the near-surface waters of Chesapeake Bay during spring 1990. Standard deviations are given in parentheses. nd: no data available

Stn	NH_4^+	NO_3^-	PO_4^{3-}	$Si(OH)_4$
North Bay	12 (6.0)	180 (38)	12 (3.1)	nd
Mid Bay	6.4 (4.4)	100 (45)	0.22 (.04)	20 (14)
South Bay	0.7 (0.3)	1.6 (1.0)	2.1 (1.1)	nd

lower at North Bay than at Mid or South Bay (Table 3). The temporal change in N:P uptake rates for Mid Bay was considerably smaller than the spatial change. Ratios of N:P uptake were 8.9 in mid April and increased to 17.9 by late May.

In contrast to the downward trend in N:P uptake ratios from North to South Bay, ratios of C:N uptake (based on volumetric rates) increased seaward along the axis of the Bay (Fig. 10B). Ratios of C:N uptake for near-surface, mid morning only, averaged 2.0 for North Bay, and 5.7 and 5.9 for the Mid and South Bay stations, respectively. Thus, these ratios were below Redfield proportions for phytoplankton and bacterial biomass at North Bay, while nearing Redfield proportions down-Bay. When these rates are integrated over the water column and over a daily period, average C:N uptake ratios were well below Redfield proportions at all stations (Fig. 10B). These low overall ratios, and the increase in these ratios from North to South Bay, likely reflect several contributing factors. At the North Bay, where the lowest C:N uptake ratios were observed, phytoplankton carbon fixation rates were likely suppressed by the shallow euphotic zone and the resulting low light availability, and nitrogen uptake rates were in excess of phytoplankton growth requirements. At all stations, uptake of nitrogen below the euphotic zone, or at night, may have contributed to the depression in these ratios when integrated with depth and time. Reports of relatively high uptake rates of NH_4^+ in the dark are not uncommon, and uptake appears to be regulated more by substrate availability then irradiance on a diel basis. Furthermore, while measurements of carbon fixation account for uptake by phytoplankton, measurements of NH_4^+ (and possible NO_3^-) reflect consumption by both phytoplankton and bacteria. Our measured rates of nitrogen uptake in the <1 µm fraction — obtained only in near-surface Mid Bay waters — averaged 25% of the uptake in the whole fraction. However, the GF/F filters used for collection of biomass in the uptake studies typically capture only about 50% of the bacterial assemblage (authors' unpubl. data), and therefore underestimate the total uptake by bacteria. Independently measured bacterial production rates in near-surface Mid Bay waters were approximately 10% of near-surface carbon fixation rates during spring 1990 (Shiah & Ducklow 1994).

Lastly, C:P uptake ratios for near-surface mid morning decreased about 100-fold down-Bay, exceeding Redfield proportions at North Bay, being slightly below Redfield proportions at Mid Bay, and considerably below Redfield proportions at South Bay (Fig. 10C). When rates were integrated over the water column and full day period, these ratios dropped considerably, with only the North Bay stations revealing ratios near Redfield. The downward trend in this ratio is at least partially a result of the increasing rates in PO_4^{3-} uptake down-Bay. Uptake of PO_4^{3-} was close to biomass requirements for uptake at North Bay, while there was likely luxury consumption at Mid and South Bay. Furthermore, as was the case for C:N uptake ratios, heterotrophic uptake of PO_4^{3-} in waters below the euphotic zone would depress the overall C:P uptake ratios, although the average biomass C:P ratios (Table 3) are more reflective of a rapidly growing phytoplankton community. The temporal change in C:P uptake ratios at Mid Bay were small compared to the change from North to South Bay.

The uptake of $Si(OH)_4$ was measured at Mid Bay on a few occasions during the peak of the bloom. Rates ranged from 0.3 to 1.1 µmol l^{-1} h^{-1} Ratios of $Si(OH)_4$:NO_3^- uptake ranged from 1 to 3, whereas ratios of $Si(OH)_4$:inorganic N plus urea uptake ranged from 0.6 to 1.9. The ratio of $Si(OH)_4$:total N uptake was therefore in proportion to that of Redfield stoichiometry and was also nearly the same as the ratio of biogenic Si:particulate N (Table 3).

The mean turnover times of the dissolved nutrients (Table 4) also underscore the significant down-Bay changes in the utilization of different substrates. Turnover times of NH_4^+ dropped from >10 h at North Bay to <1 h at South Bay. Turnover times of NO_3^- likewise dropped dramatically from North and Mid Bay to South Bay. Turnover times of PO_4^{3-} were very low at Mid Bay (0.2 h), highest at North Bay (12 h), and intermediate at South Bay (2 h). Turnover times for $Si(OH)_4$ could only be calculated for Mid Bay and averaged 20 h for the bloom as a whole.

DISCUSSION

The multiphasic character of the 1990 spring bloom

The spring bloom of 1990 in Chesapeake Bay did not occur uniformly along the axis of the Bay, but rather developed and dissipated at different times in different regions of the Bay. This is apparent not only from the frequent aerial surveys of chl *a*, but also from the size fractionation of shipboard chl *a* measurements. The

bloom apparently began early in the year, between Mid and South Bay, where nearly 50% of the chl *a* biomass was >20 µm in size. In North Bay, virtually all of the chl *a* was <20 µm in size through mid April, and throughout the entire spring, the <20 µm fraction dominated the chl *a* biomass. In the Mid and South Bay regions, at the peak of the bloom nearly 50% and 30%, respectively, of the phytoplankton biomass was composed of cells >20 µm in size. In the North and Mid Bay there were 2 distinct peaks in near-surface chl *a* and particulate N, while in South Bay, the bloom appeared to be a singular, more prolonged event.

As has been noted for other years in Chesapeake Bay (Tyler & Seliger 1978, Seliger et al. 1981, Malone et al. 1988), during 1990 high chl *a* concentrations were observed throughout the water column, and particularly in the Mid Bay region, concentrations of chl *a* in near-bottom waters exceeded those of the surface layer. It has previously been suggested that phytoplankton biomass may accumulate in the mesohaline bottom waters from advection from the lower Bay with high salinity bottom water (Seliger et al. 1981, Malone 1992), and the chl *a* data of 1990 are consistent with this hypothesis.

Environmental variables and physiological responses during bloom development

Based on chl *a*, particulate N and particulate C, it is apparent that the bloom began to develop as early as February. The peak of the bloom was attained in late March in South Bay, early April in Mid Bay, and not until mid May in North Bay due to the more severe light limitation in the north. The euphotic zone was roughly 4 times deeper in South Bay than in North Bay during the early stages of the bloom, permitting the higher initial rates of carbon fixation. The 55 d delay in the timing of the peak of the bloom from South to North Bay also coincided with the rapid increase in daily solar irradiation of the spring. The accumulation of chl *a* in the Mid Bay region is strongly correlated with the input of nitrogen, lagged by 1 mo, and interannual variations in the magnitude of the spring bloom maximum are related to the amount of NO_3^- delivered during the spring freshet (Malone et al. 1988).

Whereas the annual cycles of nutrient availability, production, and biomass accumulation have now been well described for Chesapeake Bay (cf. Boynton et al. 1982, Kemp & Boynton 1984, Malone et al. 1988), the effects of rapidly changing environmental variables on bloom development and dissipation are not well understood. It has been hypothesized for a variety of systems that large cells (i.e. diatoms) tend to bloom when environmental conditions such as upwelling, mixing, or, as in this case, runoff, increase the flux of NO_3^- (e.g. Malone 1980). It has since been argued (Chisholm 1992) that there is no physiological basis for this relationship. However, evidence to support or refute a physiological basis for this is difficult to obtain. Nevertheless, there are many examples in the literature that demonstrate that diatom growth and NO_3^- uptake are favored when concentrations of NO_3^- are high. In Vineyard Sound, Massachusetts, Glibert et al. (1982) reported that during a large winter bloom of the diatom *Rhizosolenia delicatula*, NO_3^- appeared to be used preferentially, and Maestrini et al. (1982) reported that some natural assemblages of phytoplankton (mostly diatoms) in oyster ponds can utilize NO_3^- even when NH_4^+ is present at concentrations which range over an order of magnitude higher than values previously reported to suppress NO_3^- reductase activity and the uptake of NO_3^-. In addition, for the waters of the Antarctic, Koike et al. (1986), as well as Probyn & Painting (1985), have also observed that the larger size fractions of phytoplankton took up proportionately more NO_3^- than did the pico- and nanoplankton fractions. Clearly, additional study on the use of NO_3^- by diatoms is warranted.

Rates of nitrogen uptake reported here and, more specifically, values for the Relative Preference Index (RPI: McCarthy et al. 1977), support the contention that the capacity for uptake of NO_3^- by diatom assemblages may be greater than that of other phytoplankton and may well impart a competitive advantage during the development of the bloom. The RPI compares the contribution of 1 nitrogen form relative to total nitrogen uptake with the contribution of that nitrogen form to the total nitrogen pool measured. A value >1.0 reflects preference for that nitrogen form, a value <1.0 indicates selection against that form of nitrogen, and a value equal to 1.0 reflects utilization equitable with availability. In the South Bay the RPI for NO_3^- uptake exceeded 5 during the development stage of the bloom, but dropped to 1 as the bloom was in declining stages. At Mid Bay, the preference for NO_3^- was not exhibited as strongly as in South Bay; in fact, NH_4^+ was the preferred nitrogen nutrient at Mid Bay. This may lend further credence to the suggestion that conditions were most favorable for diatom development in South Bay, and their high accumulation in Mid Bay is due to both *in situ* growth and advection. While McCarthy et al. (1977) reported a near universal preference of Chesapeake Bay phytoplankton for NH_4^+, their data do also show that in the South Bay NO_3^- tended to be utilized equitably with availability in early spring. Horrigan et al. (1990) reported a uniform preference for NO_2^- by Chesapeake Bay phytoplankton in late spring. Additionally, Boyer et al. (1994) have reported many

instances when NO_3^- was the preferred nitrogen source in the Neuse River Estuary, with RPI values on occasion exceeding 5.

Temperature, also, seems to be an important correlate with regard to the proportionately greater utilization of NO_3^- by larger phytoplankton. The development of the Chesapeake Bay bloom in 1990 began very early in the year; although our shipboard measurements began in mid February, when water temperatures were ca 5°C, the development of the bloom was clearly well under way. Malone (1977) has shown that below 8°C, the assimilation number of phytoplankton in the New York Bight was higher than would be expected from a relationship between temperature and assimilation for higher temperatures, and some evidence for a similar phenomenon for nitrogen uptake was observed in Vineyard Sound (Glibert et al. 1982). As Malone (1992) has previously summarized for the years 1984 to 1988, the late May decline in diatom biomass coincides with the rapid increase of cyanobacteria, chrysophytes, cryptophytes, chlorophytes, and small dinoflagellates, and this shift appears to occur quite consistently at temperatures near 18°C. In this context, it is interesting to note that during the peak of the 1990 bloom, surface water temperatures remained 1 to 2°C cooler than predicted from the regression of temperature with time of year. However, the rapid demise of the secondary bloom did occur with the warming of near-surface waters above 18°C. Further study is warranted to determine whether diatoms in fact are physiologically better able to exploit high nitrogen availability at lower temperatures than other small phytoplankton.

Factors contributing to bloom decline

The demise of the spring bloom was also not a singular event attributable to a single factor. Our results for 1990 are consistent with reports from previous years that different nutrients limited growth in different regions of the Bay (Fisher et al. 1992, Conley & Malone 1992).

In North Bay, concentrations of nitrogen never dropped below tens of µmol l^{-1} (Fig. 5), well above levels normally taken to saturate uptake by phytoplankton (Wheeler et al. 1982). While light limitation of carbon fixation likely prevented the bloom from becoming established in North Bay as early in the year as at the other stations, once the bloom was established other factors likely contributed to its demise. Levels of PO_4^{3-} and $Si(OH)_4$ dropped dramatically during the brief period of chl *a* accumulation in early to mid May (Fig. 6), and likely continued to decrease after our mid May sampling. Based on these patterns, and the very high ratios of N:P uptake, it is highly likely that PO_4^{3-} and $Si(OH)_4$ were the primary limiting factors controlling further growth of phytoplankton in this region of the Bay at that time. The concentrations of PO_4^{3-} and $Si(OH)_4$ rapidly increased to pre-bloom concentrations or higher almost immediately once the bloom had passed.

In Mid Bay, the mean stoichiometry of the particulate nutrients was in very close agreement with Redfield proportions (Table 3), as were N:P uptake ratios (Fig. 10). This indicates that for most of the spring period, sufficient nutrients were available to sustain growth. In addition, even though chl *a* concentrations in near-surface waters fluctuated by over 3-fold, the C:chl *a* ratio was relatively invariant. Nutrient turnover times at Mid Bay were also relatively long, except for PO_4^{3-}, which were frequently in the range of values associated with phosphorus limitation of growth rates. In mid April concentrations of PO_4^{3-} dropped below detection limits, while ambient nitrogen concentrations were >20 µmol l^{-1} Thus, through the period of biomass accumulation, the bloom at Mid Bay was not nutrient limited, and only at the peak of the bloom (mid April) did transient PO_4^{3-} and/or $Si(OH)_4$ limitation occur, leading to its collapse. In mid May, a secondary bloom developed; however, chl *a* and particulate N concentrations were not nearly as high as in the first bloom period, and as noted above, this bloom likely collapsed as the temperatures warmed.

The factors leading to the demise of the bloom in South Bay were apparently different from those in the North and Mid Bay regions. Conley & Malone (1992), in assessing a 5 yr time series from the Mid-South Bay regions, observed that $Si(OH)_4$ depletion was highly correlated with the change in floristic composition typically observed in late May. While concentrations of $Si(OH)_4$ in Mid Bay only became depleted very briefly in April 1990, concentrations of $Si(OH)_4$ in South Bay were near analytical limits of detection as early as mid February and remained extremely low through mid April. After the collapse of the diatom-dominated assemblage in South Bay, concentrations of $Si(OH)_4$ increased steadily through mid summer. In addition, ambient concentrations of NH_4^+ in South Bay were near detection limits from February through May, and the very rapid turnover times of this nitrogen form are indicative of its high demand and low availability. Concentrations of NO_3^-, while about <4 µmol l^{-1} in February, were consumed by mid April. Also, PO_4^{3-} was depleted by mid April and concentrations remained at or near detection limits through mid May. Thus, it appears that limitation by nitrogen, $Si(OH)_4$, and PO_4^{3-} occurred in this region at different stages of the bloom.

It is also worth noting that, during the declining phase of the bloom in South Bay, urea contributed over 80% of the nitrogen available and over 50% of the

nitrogen consumed. In the coastal plume of the Chesapeake Bay, Glibert et al. (1991) have shown that urea is a major contributor to the nitrogen nutrition of the plankton in early June. Zooplankton biomass and rates of grazing, while usually low in May and June, have been shown to increase rapidly. Both zooplankton release and flux from the bottom could result in accumulations of ambient urea (Bidigare 1982, Lomstein et al. 1989, Miller 1992), but we do not have the data to distinguish these potential sources for our study period. Nevertheless, the high proportion of urea is a further indication of the rapid shift to conditions most closely associated with summer assemblages.

Zooplankton do not appear to play a central role in the decline of the spring bloom. Measured rates of macrozooplankton grazing are typically low throughout the spring (Malone 1992), and only ~5% of phytoplankton biomass is consumed by these grazers during this period (White & Roman 1992). Rates of microzooplankton grazing are somewhat higher, and up to 50% of the phytoplankton biomass may be consumed by these small heterotrophs (mostly heterotrophic flagellates, ciliates, and invertebrate larvae). Thus, the fate of most of the phytoplankton biomass is sedimentation to the bottom, leading to rapid decline in concentrations of dissolved oxygen below the pycnocline.

The spring bloom of the Chesapeake Bay compared to other mid- to high-latitude waters

Assuming a sufficient supply of nutrients, it has long been observed that spring blooms develop when phytoplankton experience an increase in irradiance, and this generally occurs through the development of a seasonal thermocline and the isolation of phytoplankton above a critical depth. Townsend et al. (1992), however, have reported that in the Gulf of Maine, the spring bloom can, in fact, precede the onset of vertical stratification and may even contribute to the development of the thermocline.

Like the Chesapeake, the onset of vertical stratification in the Delaware Bay stimulates phytoplankton growth in late winter, and biomass accumulates during March through May (Pennock & Sharp 1986). The decline of the bloom in the Delaware is also similar to that of the Chesapeake, having been attributed to the depletion of PO_4^{3-} and $Si(OH)_4$ (Sharp et al. 1984) and, to a lesser extent, zooplankton grazing (Pennock & Sharp 1986). In the Baltic, depletion of nitrogen and PO_4^{3-} contributes to the rapid decline of the bloom (Lignell et al. 1993), and sedimentation accounts for most of the loss of phytoplankton biomass.

While nutrient limitation plays an indisputable role in the Chesapeake, as well as the other systems cited above, temperature appears to also play an important role in plankton succession in other systems. Malone & Neale (1981) for the Hudson, and Levasseur et al. (1984) for the Lower St. Lawrence Estuary, for example, have shown that the temperature cycle is critical with respect to the decline in diatoms in late spring in those systems. Laws et al. (1988) also suggested that during the spring bloom in Auke Bay, Alaska, phytoplankton growth rates may have been limited by temperature, whereas biomass in that system was apparently limited by the supply of NO_3^-.

In summary, these data suggest that interactions between freshwater flow, nutrient availability, ambient temperature, and light differ along the axis of the Bay, leading to differential timing and magnitude of phytoplankton biomass in the spring. These data also strongly underscore the need to consider specific strategies for nutrient management for different regions of the Chesapeake Bay system.

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