

Long-term trends in the distribution of phytoplankton in Chesapeake Bay: roles of light, nutrients and streamflow

Lawrence W. Harding Jr *

University of Maryland, Sea Grant College, 0112 Skinner Hall, College Park, Maryland 20742, USA

ABSTRACT: This paper synthesizes >40 yr of data on phytoplankton abundance in the Chesapeake Bay, USA, spanning the period 1950 to 1990. Long-term changes in the concentrations of surface chlorophyll (B , mg m^{-3}) and integrated water-column chlorophyll (B'_{wc} , mg m^{-2}) are assessed in the context of light and nutrient effects on phytoplankton distributions. Significant long-term increases in B were detected from the 1950s to the 1970s in all regions of the Bay. The seaward, polyhaline Bay showed increases in B of 300 to 500 %, while mesohaline and oligohaline values increased by between 40 and nearly 400 %. Annual means for recent years, 1985–90, showed interannual variations of ca 80 %, but trends of the magnitude observed for 1950–70 were not detected. Frequency distributions of B showed shifts in overall distributions to higher values, particularly in the lower, polyhaline Bay where the frequency of $B < 2 \text{ mg m}^{-3}$ in the 1950s and 1960s was much higher than in 1985–90. B'_{wc} data showed the apparent lack of a winter-spring maximum of contemporary proportions in the 1960s, in contrast to data from the 1970s, early 1980s and 1985–90 that show a well-developed peak in B'_{wc} for most of these years. Nutrient concentrations and ratios have also changed significantly since the 1960s. Concentrations of dissolved inorganic nitrogen (DIN) in the oligohaline Bay have approximately doubled in the past 20 to 30 yr, while orthophosphate (PO_4^{3-}) concentrations have generally declined, producing a change in $\text{DIN}:\text{PO}_4^{3-}$ with ramifications for nutrient limitation in the Bay. These results are discussed in the context of the regulation of interannual variations in the timing, position and magnitude of the winter-spring phytoplankton bloom in the Bay by freshwater flow from the Susquehanna River.

KEY WORDS: Phytoplankton · Chlorophyll · Estuaries · Trends · Chesapeake Bay

INTRODUCTION

Estuaries are characterized by strong gradients in river flow, circulation, tidal mixing, nutrient inputs, sediment loading and temperature. The interplay of these properties produces spatially and temporally heterogeneous conditions for phytoplankton growth. Depending on the relative importance of these properties, annually reiterated sequences of one or several phytoplankton species may develop in individual systems, and distinct assemblages may occupy regions of a given estuary that differ physically or chemically. For example, predictable blooms of diatoms are known to

accompany the spring freshet in several important estuaries in the United States, including San Francisco Bay (Peterson et al. 1975, Festa & Hansen 1976, 1978, Conomos & Peterson 1977, Cloern & Cheng 1981, Cloern et al. 1983), Delaware Bay (Sharp et al. 1982, Pennock 1985, Pennock & Sharp 1986), and the Hudson River estuary (Malone 1977, Malone & Chervin 1979, Malone et al. 1980).

As the largest and historically most productive estuary in the U.S., the Chesapeake Bay has been studied extensively for a period of decades. Much of that research in recent years has focused on the causes and ramifications of eutrophication, particularly the effects of increased nutrient loading from the 64 000 mile² watershed on the abundance and productivity of phytoplankton (U.S. EPA 1983). We know from recent work that an important characteristic of the annual

*Also: Horn Point Environmental Laboratories, Center for Environmental and Estuarine Studies, University of Maryland, Box 775, Cambridge, Maryland 21613, USA

cycle of phytoplankton in the Bay is a transition in the distribution and abundance of phytoplankton in winter-spring when highest biomass densities of diatoms develop (Harding et al. 1986, 1992a, b, 1994, Fisher et al. 1988, Malone et al. 1988, P. M. Glibert et al. unpubl.). The development of this winter-spring bloom appears to be linked to the freshet of the Susquehanna River, the largest source of freshwater to the estuary and a major source of dissolved inorganic nutrients (Harding et al. 1986, 1992a, 1994, Malone et al. 1986, 1988, Fisher et al. 1988, 1992). Phytoplankton uptake of nutrients in spring generates the large biomass that supports high secondary production in the Bay (cf. Boynton et al. 1982, Malone et al. 1986, 1988, Fisher et al. 1988, 1992); this algal biomass is the principal source of organic material whose breakdown is linked to deleterious processes in the estuary, such as the annual formation of subpycnocline anoxia that has become a pervasive environmental problem with severe aesthetic and economic consequences (Officer et al. 1984, Seliger et al. 1985, Tuttle et al. 1987).

A significant transition in the distribution and abundance of phytoplankton also occurs in spring-summer in the Bay. From May to early June, a pronounced floral shift from a high biomass, microplankton community dominated by diatoms to a high productivity, pico-nanoplankton community dominated by a mixed, non-diatom flora has been discussed in the context of the seasonal phase relationship between biomass and productivity (Malone et al. 1988, 1991). The regeneration of nutrients accompanying the breakdown of spring bloom-derived material drives an annual productivity maximum in summer, as reviewed by Malone (1992).

Over a period of decades, it is believed that significant changes have occurred in the phytoplankton dynamics of Chesapeake Bay: (1) elevated nutrient inputs, particularly of nitrogen and phosphorus, have promoted a significant increase in the biomass of phytoplankton since the early 1950s (U.S. EPA 1983); (2) the size structure of Bay phytoplankton has shifted toward a community with abundant picoplankton and nanoplankton (McCarthy et al. 1974, Van Valkenburg & Flemer 1974, Sellner & Kachur 1987, Verity 1988, Malone et al. 1991, Malone 1992); (3) the species composition has changed from an assemblage consisting of immotile, centric diatoms to one predominantly composed of flagellated species (see Wolfe et al. 1926, Cowles 1930, Morse 1947, Patten et al. 1963, Mulford 1972, Marshall & Lacouture 1986). Potential ecological consequences of these changes include: (1) a change in trophic structure from a diatom-zooplankton-fish food chain to a system characterized by a major 'microbial loop' (Verity 1988); (2) an increase in particulate organic material (POM) derived from the eutrophication-

driven increase in algal biomass that supports high rates of microbial decomposition and exacerbates summer oxygen depletion; (3) shading of submerged aquatic vegetation by the reduced clarity of the water caused by increased abundance of phytoplankton in the water column.

Despite years of study and the availability of data spanning several decades, our understanding of long-term changes in phytoplankton dynamics in the Chesapeake Bay lacks synthesis. The problem is that large seasonal and interannual variations in the distribution and abundance of phytoplankton are superimposed on long-term changes that are thought to have occurred over a period of several decades. That is to say, it is difficult to distinguish long-term (decades to centuries) changes in phytoplankton that probably commenced following colonization in the 17th century (cf. Brush & Davis 1982, Cooper & Brush 1991) from short-term (seasonal to interannual) variability we observe in data from recent years (Harding et al. 1994). The goals of this study are: (1) to assimilate historical and recent data on concentrations of chlorophyll and dissolved inorganic nutrients, spanning 1950 to 1990; (2) to quantify long-term trends in these properties and distinguish them from interannual variability that is expressed in more robust data sets from recent monitoring programs; and (3) to use these analyses to provide recent and historical contexts for assessing phytoplankton dynamics in the Chesapeake Bay. I draw on data from the historical data base of the Chesapeake Bay Program (CBP) spanning 1950 to 1983, and cruise data from the Chesapeake Bay Institute from 1982 to 1988 and the CBP Mainstem Water Quality Monitoring Program from 1984 to 1990, to describe the spatial and temporal patterns of phytoplankton abundance in the Bay.

MATERIALS AND METHODS

Data presented in this paper were collected during cruises on the Chesapeake Bay from 1950 to 1990. The major sources of data were the historical archive of the Chesapeake Bay Institute that was deposited with the CBP in Annapolis in the early 1980s, data from cruises conducted as part of individual research projects in 1982–83 and 1984–88, and the data base of the CBP Monitoring Program for 1985–90. The historical (1950–83) data were much more limited in spatial and temporal coverage than recently collected data and have been combined into decadal groupings for analysis. The data from cruises in the early 1980s and 1984–88 were largely from axial transects down the Bay and thus were limited in lateral coverage. CBP Monitoring Program data are collected at 50 stations in

the mainstem Bay and provide good spatial and temporal coverage. The main parameters of interest were chlorophyll, phaeopigments, light attenuation coefficient or Secchi depth, salinity, temperature, dissolved inorganic nutrients, and flow from the Susquehanna River, a major source of freshwater, nutrients and suspended particulate material to the Bay. The data used in these analyses were grouped for 6 regions in the Chesapeake Bay, as shown in Table 1 and Fig. 1.

Concentrations of chlorophyll and phaeopigments were determined with a variety of methods. In retrieving data from different sources in the data base, values determined with similar methods were used whenever possible. Most of the data were derived from measurements made on acetone extracts using fluorometry (Turner model 110 or 111, or Turner Designs model 10) or spectrophotometry (Beckman model DK-2 or equivalent). Prior to 1964, chlorophyll concentrations were determined using the unpublished method of Sargent (Scripps Institute of Oceanography, CA, USA), consisting of filtration of 1 l of sample through a Whatman No. 5 filter, extraction in 80% acetone, and measurements of absorbance at 550, 667 and 750 nm. In the 1960s, fluorometric measurements of chlorophyll concentration were used, with collection of sample on a 0.2 μm membrane filter, methanol extraction, and fluorescence determined on a Turner model 110 or 111 fluorometer calibrated against a dilution series of a standard chlorophyll solution quantified spectrophotometrically. After 1969, the trichromatic method for multiple pigment determination was used (Strickland & Parsons

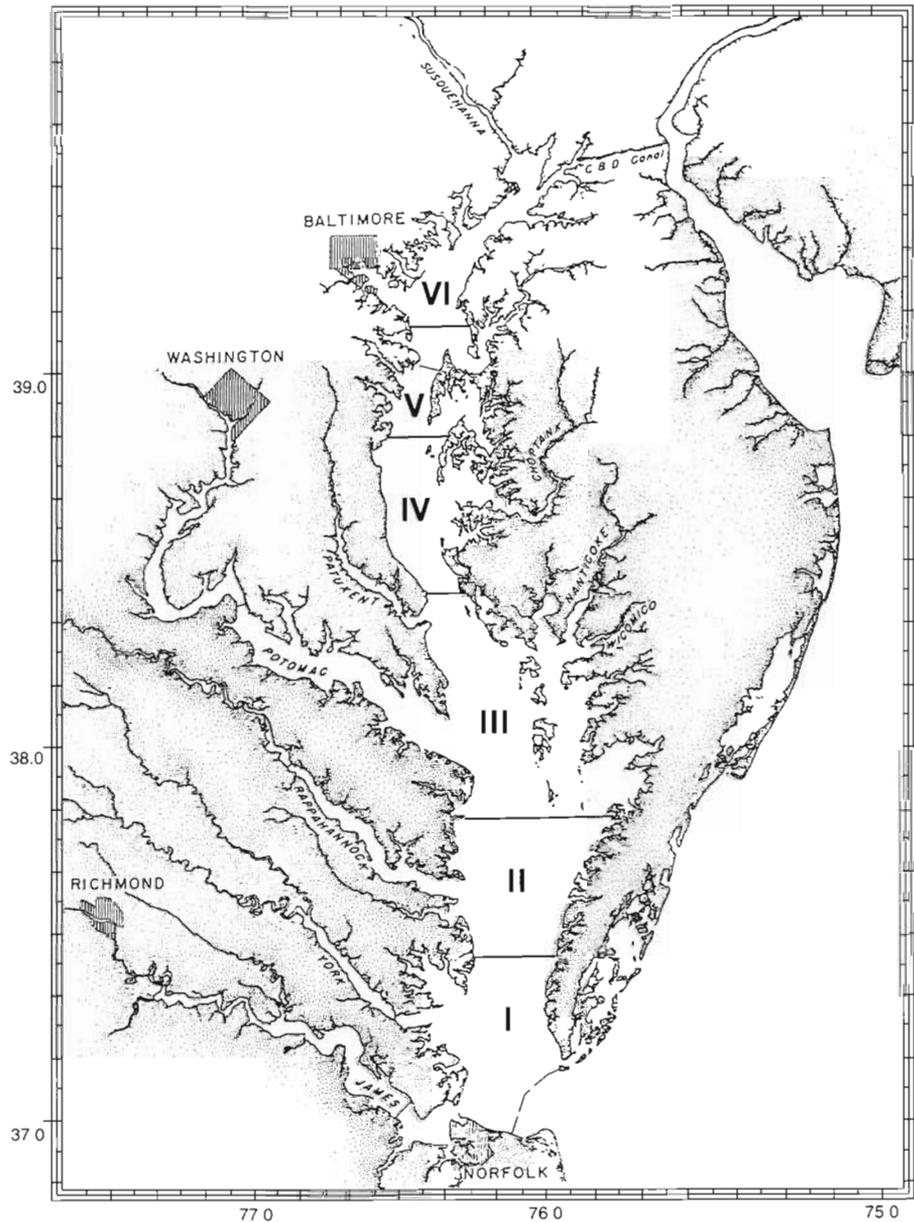


Fig. 1. Chesapeake Bay showing locations of the 6 regions

Table 1. Regions in the Chesapeake Bay by latitude and geographic location

Region	Latitude range	Geographic location
I	36.95 – 37.40° N	Mouth of Bay to Mobjack Bay
II	37.41 – 37.80° N	Mobjack Bay to Rappahannock River
III	37.81 – 38.40° N	Rappahannock River to Patuxent River
IV	38.41 – 38.80° N	Patuxent River to South River/Annapolis
V	38.81 – 39.10° N	South River/Annapolis to Bay Bridge/Magothy River
VI	39.11 – 39.66° N	Bay Bridge/Magothy River to Susquehanna Flats

1968). Most of the data from the 1950s to 1970s were uncorrected for phaeopigments. Based on the historical and recent data for which both uncorrected and corrected values were available, this difference in methods introduced negligible (< 5%) error as an overestimate of chlorophyll for that period. Measurements of pigment concentrations made in recent years (early 1980s and CBP Monitoring Program) determined concentrations of both chlorophyll and phaeopigments using either spectrophotometric or fluorometric methods. The Monitoring Program data presented in this paper are active chlorophyll corrected for phaeopigments. Water column concentrations of chlorophyll were determined by trapezoidal integration on chlorophyll concentrations from vertical profiles.

Temperature and conductivity were measured prior to 1977 with a submersible inductive-conductivity-temperature indicator (ICTI) developed at the Chesapeake Bay Institute (Johns Hopkins University, MD, USA). After 1977, a Plessey-Grundy CTD on a rosette sampler replaced the ICTI. CBP Monitoring cruises measured conductivity and temperature with a Sea-Bird Sealogger CTD or equivalent. Diffuse light attenuation was measured using a Secchi disk calibrated with an underwater quantum meter (Li-Cor model 188B) to determine K_t from vertical optical casts. Based on a large matching data set of Secchi disk readings

and Li-Cor profiles, we found K_t could be estimated as 1.5/Secchi depth (m).

Concentrations of dissolved inorganic nutrients (NO_3^- , NO_2^- , NH_4^+ , PO_4^{3-} , SiO_4^{3-}) were determined with colorimetric methods. Dissolved inorganic PO_4^{3-} (filtered < 0.2 μm) was measured with the ceruleo-molybdate method prior to 1964, using stannous chloride as the reducing agent and measuring the optical density on a Beckman DU spectrophotometer. In 1964–65, an acid digestion method was introduced, and in 1966 high intensity UV digestion replaced the acid method. NO_2^- was measured colorimetrically using a Greiss reaction, and NO_3^- was measured on sample reduced to nitrite using amalgamated cadmium reduction. NH_4^+ determinations used a modified indophenol technique. SiO_4^{3-} was measured using the Technicon Industrial Systems (1977) method. Recent measurements have been made with a Technicon AutoAnalyzer (AA) on Whatman GF/F-filtered water samples using standard wet chemical methods (U.S. EPA 1992). Freshwater flow data were provided by the U.S. Geological Survey gaging station at the Conowingo Dam on the Susquehanna River.

The frequency distributions of chlorophyll and nutrient concentrations were skewed; logarithmic transformations of the data produced normal distributions. Least squares means¹ were computed on the log-transformed data, and back-transformed values for the mean and the upper and lower 95% confidence intervals were determined. The time and space composites of surface and integrated water-column chlorophyll concentrations were generated using gridding algorithms in Surfer v. 4.0 (Golden Software, Inc.); the resulting gridded files were contoured and customized with Transform v. 2.0 (Spyglass, Inc.). Data from the 1950s and early 1980s were not used for decadal time and space composites because of the sparse sampling.

Table 2. Summary statistics on surface chlorophyll concentrations (mg m^{-3}) from historical data for the Chesapeake Bay, 1950–83

Years	Region	n	LS mean	95% LCI	95% UCI
1950–59	I	41	0.79	0.440	1.22
	II	17	1.79	0.960	3.00
	III	109	3.98	3.37	4.69
	IV	11	5.59	3.14	9.50
	V	11	3.35	1.73	5.93
	VI	18	2.88	1.75	4.48
1960–69	I	8	2.03	0.701	4.42
	II	9	3.38	1.57	6.46
	III	28	7.30	5.34	9.86
	IV	58	7.78	6.32	9.54
	V	97	8.42	7.19	9.83
	VI	295	16.1	14.8	17.5
1970–79	I	101	4.83	4.08	5.68
	II	31	7.04	5.23	9.36
	III	100	8.29	7.10	9.66
	IV	194	7.62	6.82	8.51
	V	334	13.3	12.3	14.4
	VI	841	13.6	12.9	14.3
1980–83	I	81	4.78	3.96	5.74
	II	21	8.36	5.83	11.8
	III	81	5.49	4.57	6.57
	IV	62	7.50	6.13	9.13
	V	94	13.5	11.5	15.7
	VI	115	14.7	12.8	16.8

RESULTS

Surface chlorophyll concentrations

Decadal and annual means

Surface chlorophyll (B , mg m^{-3}) in the Chesapeake Bay has increased significantly since the 1950s. Table 2 presents decadal least squares means and 95% confidence intervals of B for the 1950s to the early 1980s for stations within 6 regions of the Bay defined in

¹Least squares mean = adjusted treatment mean; used to correct for the effects of different sample sizes (unbalanced designs) in comparisons (SAS Institute 1990)

Table 1. The largest increases in B occurred from the 1950s to the 1970s in all regions of the Bay. The lower, polyhaline Bay (Regions I & II) showed an increase in the decadal mean of B of between 300 and 500%, while the mesohaline Bay (Regions III & IV) showed a lesser increase, between 36 and 108%. The upper, oligohaline Bay (Regions V & VI) showed increases of nearly 400% from the 1950s to the 1970s.

The annual means of B for 1985–90 showed inter-annual variations of ca 80% (Regions I & II), but trends of the magnitude observed for 1950–1970 were absent except for the northernmost Bay (Region VI) where surface chlorophyll was significantly lower ($p < 0.05$) than in the 1960s and 1970s (Table 3). The mean concentration in the 1960s to the early 1980s was ca 14 to 16 mg m^{-3} and declined to 5 to 8 mg m^{-3} during the 1985–90 period. Other regions had concentrations similar or slightly higher than those observed since the 1970s.

The frequency distributions of B measured in the 1950s to the early 1980s showed shifts in the overall distributions to higher values (Fig. 2). Of particular note were increases in concentrations in the lower, polyhaline Bay (Regions I & II), consistent with the changes noted for the decadal least squares means. This southern portion of the Bay had a high frequency of surface chlorophyll concentrations $< 2 \text{ mg m}^{-3}$ in the 1950s and 1960s, and a shift to higher concentrations by the 1970s was apparent. The frequency distributions for the mesohaline Bay (Regions III & IV) also shifted to high values from the 1950s to the 1970s, but increases in subsequent years were less pronounced. The upper, oligohaline Bay (Regions V & VI) showed a shift to higher values from the 1950s to the 1970s. The frequency distributions of surface chlorophyll concentrations in recent years (1985–90) showed some inter-annual variation, but shifts of the magnitude observed from the 1950s to early 1980s did not occur (Fig. 3).

Seasonal means

Least squares means of B for individual seasons revealed trends that were not apparent in the annual means (Fig. 4a to d). In winter, B in the polyhaline regions (I & II) increased from 2.6 mg m^{-3} in the 1950s to 5–10 mg m^{-3} from 1970–90; data from the most recent 6 yr for these regions indicate that winter B has stabilized at a mean of ca 10 to 13 mg m^{-3} . Increases in winter B have also occurred in the mesohaline (III & IV) and oligohaline (V & VI) regions of the Bay since the 1950s (Fig. 4a). In spring, interannual variability of B was very high and was strongly expressed in the mesohaline to polyhaline Bay (Regions I to IV) (Fig. 4b). The historical trend to higher B that was apparent in the

Table 3. Summary statistics on surface chlorophyll concentrations (mg m^{-3}) from Monitoring Program cruises on the Chesapeake Bay, 1985–90

Year	Region	n	LS mean	95% LCI	95% UCI
1985	I	227	5.17	4.63	5.75
	II	254	5.77	5.22	6.38
	III	149	7.19	6.32	8.17
	IV	142	7.84	6.88	8.92
	V	124	10.5	9.17	12.0
	VI	106	7.17	6.15	8.34
1986	I	240	5.21	4.68	5.78
	II	243	6.79	6.13	7.50
	III	161	7.42	6.56	8.38
	IV	141	7.81	6.85	8.89
	V	143	10.6	9.39	12.1
	VI	118	6.74	5.82	7.78
1987	I	265	8.91	8.12	9.78
	II	249	10.6	9.61	11.6
	III	173	9.86	8.79	11.1
	IV	148	10.5	9.26	11.8
	V	159	12.1	10.8	13.7
	VI	128	7.60	6.62	8.71
1988	I	251	5.05	4.55	5.60
	II	241	8.78	7.95	9.67
	III	160	10.3	9.17	11.6
	IV	124	8.42	7.33	9.66
	V	126	10.9	9.53	12.4
	VI	109	6.04	5.18	7.03
1989	I	243	5.98	5.40	6.62
	II	234	7.51	7.08	7.95
	III	252	8.39	7.62	9.23
	IV	116	8.93	7.74	10.3
	V	230	10.9	9.85	12.0
	VI	223	5.69	5.10	6.33
1990	I	218	6.31	5.67	7.02
	II	234	10.4	9.41	11.4
	III	130	9.90	8.66	11.3
	IV	129	9.49	8.30	10.8
	V	146	10.8	9.53	12.2
	VI	118	4.76	4.08	5.54

data for winter was not as pronounced for spring, although B in the oligohaline Bay (Regions V & VI) has increased from ca 2 mg m^{-3} to 5–15 mg m^{-3} . The most apparent trend in summer B values was for the oligohaline Bay (Region VI) where concentrations have declined from $\geq 20 \text{ mg m}^{-3}$ in the 1950s and 1960s to 7–10 mg m^{-3} in the 1985–90 period (Fig. 4c). A modest increase of B has occurred in the mesohaline (Regions III & IV), but not of the magnitude observed in winter. In fall, B has increased since the 1950s, but recent data reflect variability rather than change. There was some evidence of decreased B in the oligohaline Bay (Region VI) in recent years (Fig. 4d). The mean for the polyhaline regions (I & II) increased in the 1950s to 1960s and remained high, but relatively constant in the 1980s.

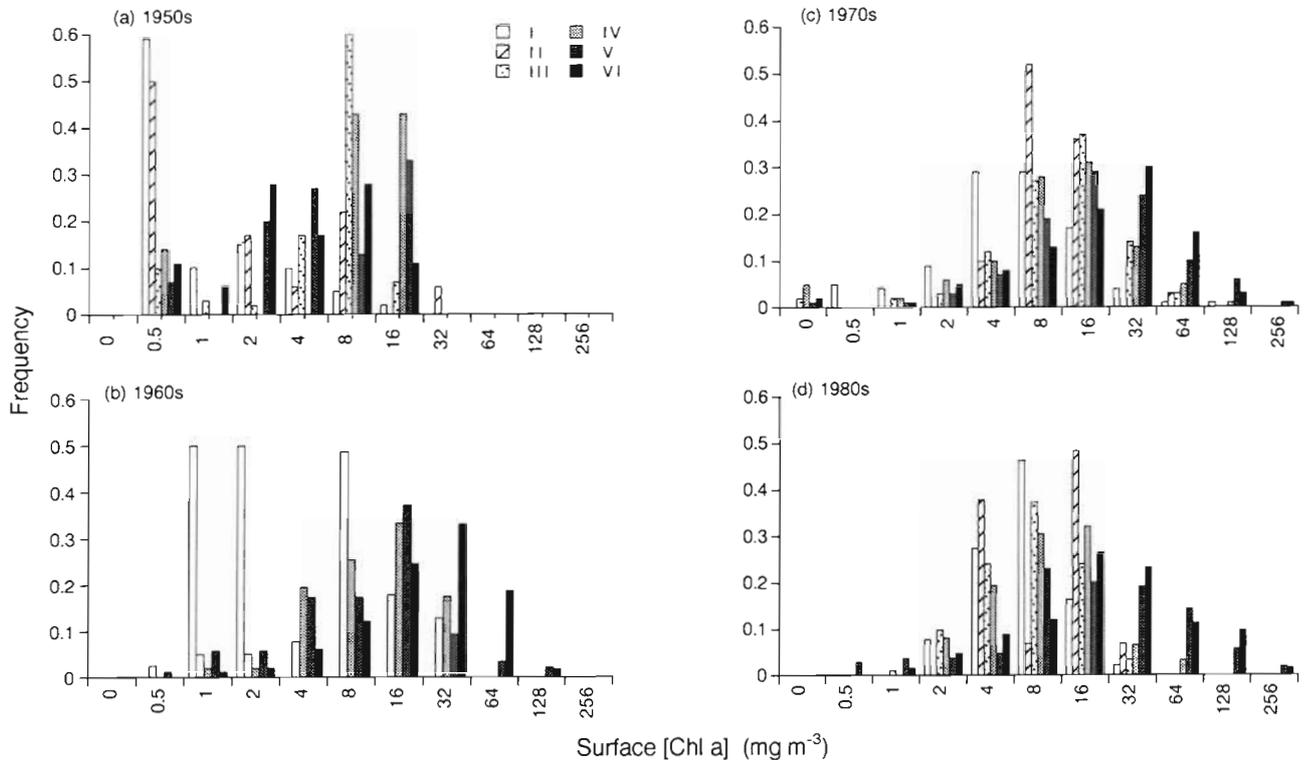


Fig. 2. Frequency distributions of surface chlorophyll concentrations (B) for 1950s to 1980s by region

Time and space composites

Time and space composites of B for the decades of the 1960s and 1970s, and for each year from 1985 to 1990, show the magnitude of interannual variations in the timing, position and magnitude of peaks in phytoplankton abundance (Fig. 5a to h). The data from the 1950s were not amenable to this treatment because of the limited time and space scales of sampling and the small sample size. The data from the 1960s and 1970s were relatively sparse compared to the data for recent years; nonetheless, decadal time-space composites of B provide a historical context for analyzing trends. Data for the 1960s showed relatively low values of B throughout the Bay in winter-spring, with concentrations $\geq 20 \text{ mg m}^{-3}$ occurring in summer-fall in the oligohaline region north of 39.1° N . In the 1970s, the composite shows that B was relatively high by April–May from the polyhaline to the oligohaline region of the Bay, 37.4 to 39.3° N . Concentrations $\geq 25 \text{ mg m}^{-3}$ occurred in March–April near the mouth of the Potomac River, 38.0° N , and by April high concentrations were measured from Mobjack Bay to the Bay Bridge, 37.3 to 39.0° N .

The annual time and space composites of B for 1985–90 provide information on interannual variability in the timing, position and magnitude of the winter-spring bloom in the Bay (Fig. 5c to h):

1985. A pronounced surface chlorophyll maximum occurred in April (Days 90 to 120), with $B \geq 30 \text{ mg m}^{-3}$ observed near the Potomac River mouth (Fig. 5c). Later in April, B was 20 to $> 30 \text{ mg m}^{-3}$ from 38.0 to 39.0° N . By May (Day 120), a discrete peak of ca 40 mg m^{-3} had developed, but was restricted to between 38.8 and 39.3° N , an area of the Bay that experienced a red tide of *Prorocentrum mariae-lebouriae* that year (Coats & Harding 1988, Harding & Coats 1988). Concentrations declined soon thereafter in May and summer values were relatively low ($\leq 20 \text{ mg m}^{-3}$).

1986. B was 10 to 20 mg m^{-3} from the Potomac River mouth to the Bay Bridge, 38.0 to 39.0° N , in April–May (Days 90 to 120), lower than the concentrations observed in 1985 (compare Fig. 5c, d). B declined in the seaward parts of the Bay by early May, and a discrete maximum of ca 30 mg m^{-3} developed in the upper Bay in May that was more localized than the earlier, more seaward peak.

1987. B values $> 30 \text{ mg m}^{-3}$ developed from late March to early April (Days 80 to 140) in this very productive year, with an extensive chlorophyll maximum extending from 37.0 to 38.5° N by mid- to late April, and a seasonal peak of $> 30 \text{ mg m}^{-3}$ persisting until late May (Fig. 5e).

1988. Relatively low $B < 10 \text{ mg m}^{-3}$ prevailed in March (Days 60 to 90), followed by a chlorophyll maximum from 37.5 to 38.5° N in mid-April, and a well-

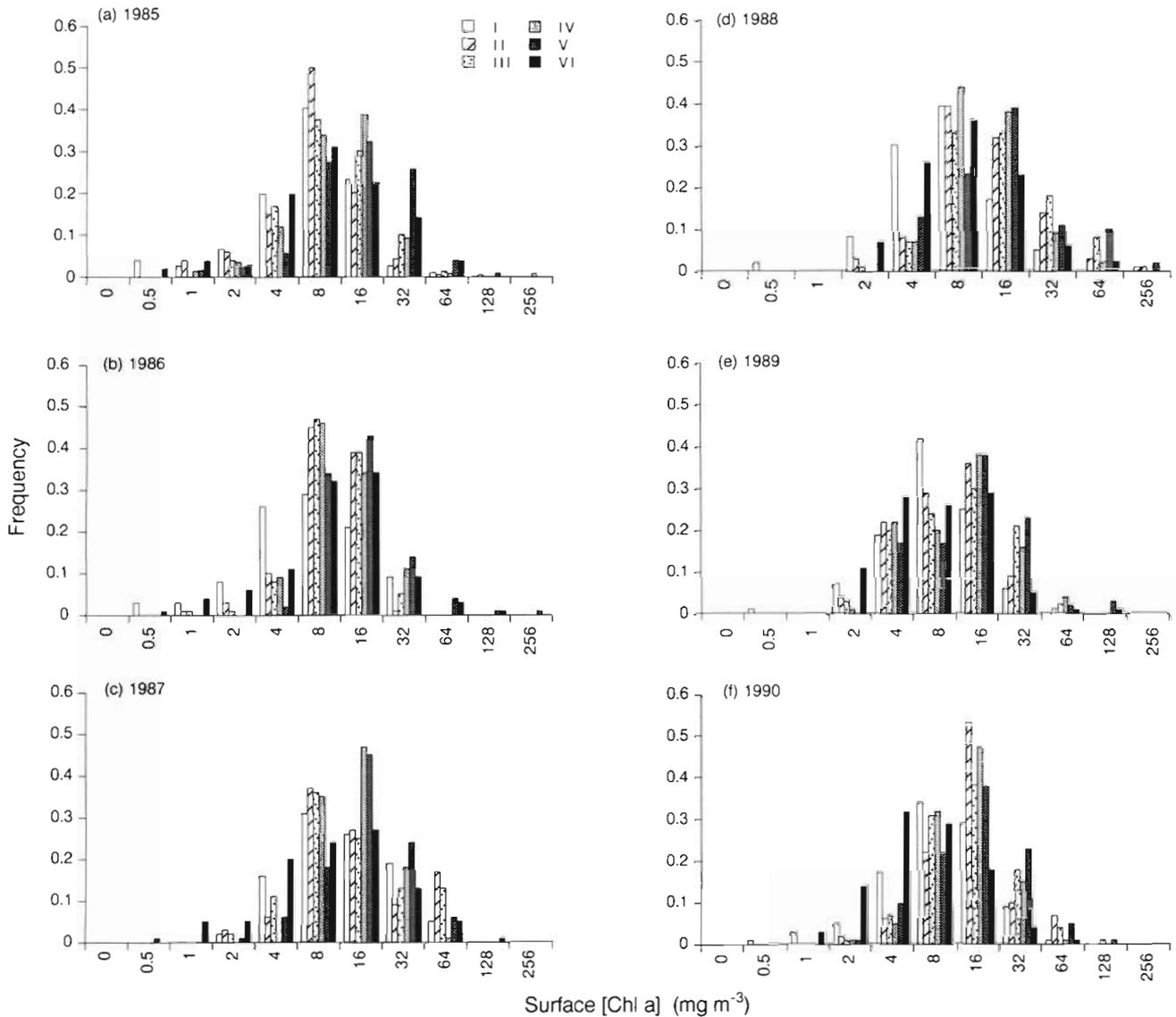


Fig. 3. Frequency distributions of surface chlorophyll concentrations (B) for 1985–90 by region

developed peak in late April to early May in the main Bay from the Rappahannock River to the Patuxent River, 37.5 to 38.3° N, with B reaching 60 mg m^{-3} (Fig. 5f). High values were measured in the upper Bay until late May as the peak in phytoplankton abundance shifted landward, and seaward concentrations declined to ca 10 mg m^{-3} . In summer, B was $\geq 30 \text{ mg m}^{-3}$ in the mesohaline from 38.6 to 39.1° N.

1989. Uncommonly low B values were observed, with concentrations remaining $\leq 10 \text{ mg m}^{-3}$ until late May and June (Fig. 5g). No discrete chlorophyll maximum developed during spring 1989. Summer concentrations showed some B peaks in the 20 to 30 mg m^{-3} range distributed throughout the Bay.

1990. A broad region with surface concentrations of 15 to 25 mg m^{-3} occurred in March (Fig. 5h). The high-

est values of B developed in the mid- to lower Bay from 37.3 to 38.4° N in April and May (Days 90 to 130), and a pronounced decline of B occurred by early June. Surface concentrations reached values $\geq 40 \text{ mg m}^{-3}$ in the Rappahannock River to Patuxent River area of the mainstem Bay, 37.6 to 38.3° N, in May. Summer concentrations were 10 to 25 mg m^{-3} distributed throughout the Bay.

Water column chlorophyll

Time and space composites

Concentrations of integrated water-column chlorophyll (B'_{wcl} , mg m^{-2}) for the decades of the 1960s and 1970s, and for individual years from 1985–90 are

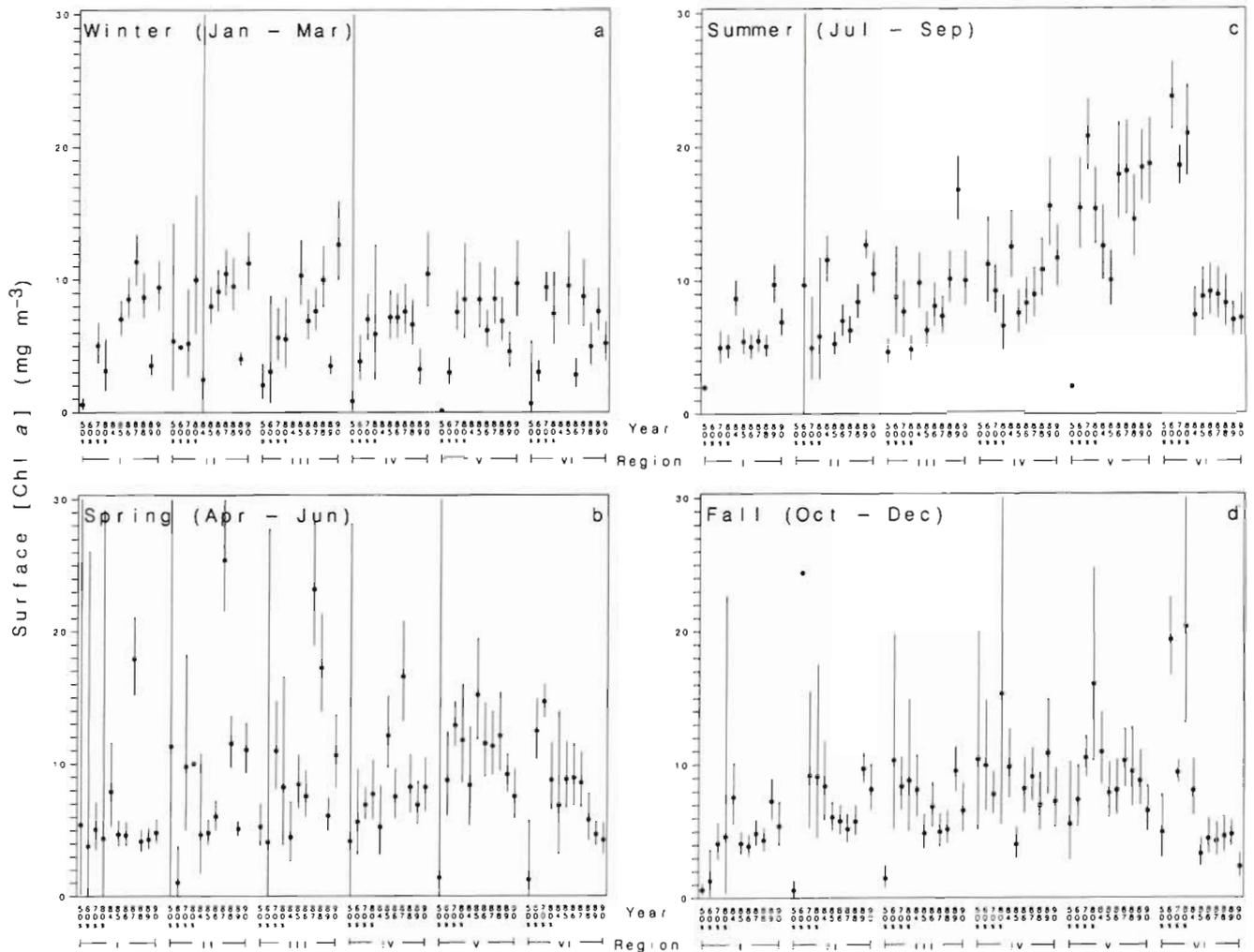


Fig. 4. Least squares means of surface chlorophyll concentrations (B), by season and region, for 1950s, 1960s, 1970s, 1980s and individual years from 1984 to 1990. Error bars are 95% lower and upper confidence intervals

shown as time and space composites to show the biomass distribution (Fig. 6a to h). There was no evidence of a well-developed B'_{wc} maximum in the winter-spring in the 1960s composite (Fig. 6a). In contrast, data from the 1970s show B'_{wc} in the mesohaline to polyhaline regions from 300 to 800 mg m^{-2} encompassing latitudes of 37.3 to 38.3° N (Fig. 6b). The patterns observed in these composites are substantiated by B'_{wc} data from individual spring cruises (Fig. 7a to f). In the 3 yr with most complete spring coverage in the 1960s (1964–66), there were no values $> 300 \text{ mg m}^{-2}$ from March to May. The analogous data from 1978–79 showed elevated B'_{wc} in the mesohaline to polyhaline, with several values $> 1000 \text{ mg m}^{-2}$.

Data for individual years from 1985–90 document high interannual variability in the distribution of B'_{wc} in the Bay:

1985. B'_{wc} values were highest from late winter to early spring (Days 50 to 100), reaching ca 700 mg m^{-2} in late March (Fig. 6c). There was an abrupt decline to $\leq 200 \text{ mg m}^{-2}$ in early to mid-April (Day 110), with low B'_{wc} persisting for the balance of the year. The B'_{wc} peak was spatially widespread, encompassing much of the estuary, and the spring decline commenced earliest in the lower Bay, seaward of the Potomac River mouth at 38.0° N.

1986. $B'_{wc} > 200$ to 300 mg m^{-2} did not occur seaward of 37.8° N, near the Potomac River mouth (Fig. 6d). The decline in B'_{wc} occurred earliest in the seaward part of the estuary, as was observed for 1985, and highest concentrations $\geq 700 \text{ mg m}^{-2}$ were restricted to the mesohaline region of the Bay near 38.3° N.

1987. The distribution of B'_{wc} in 1987 was distinct from both 1985 and 1986, exhibiting a spatially wide-

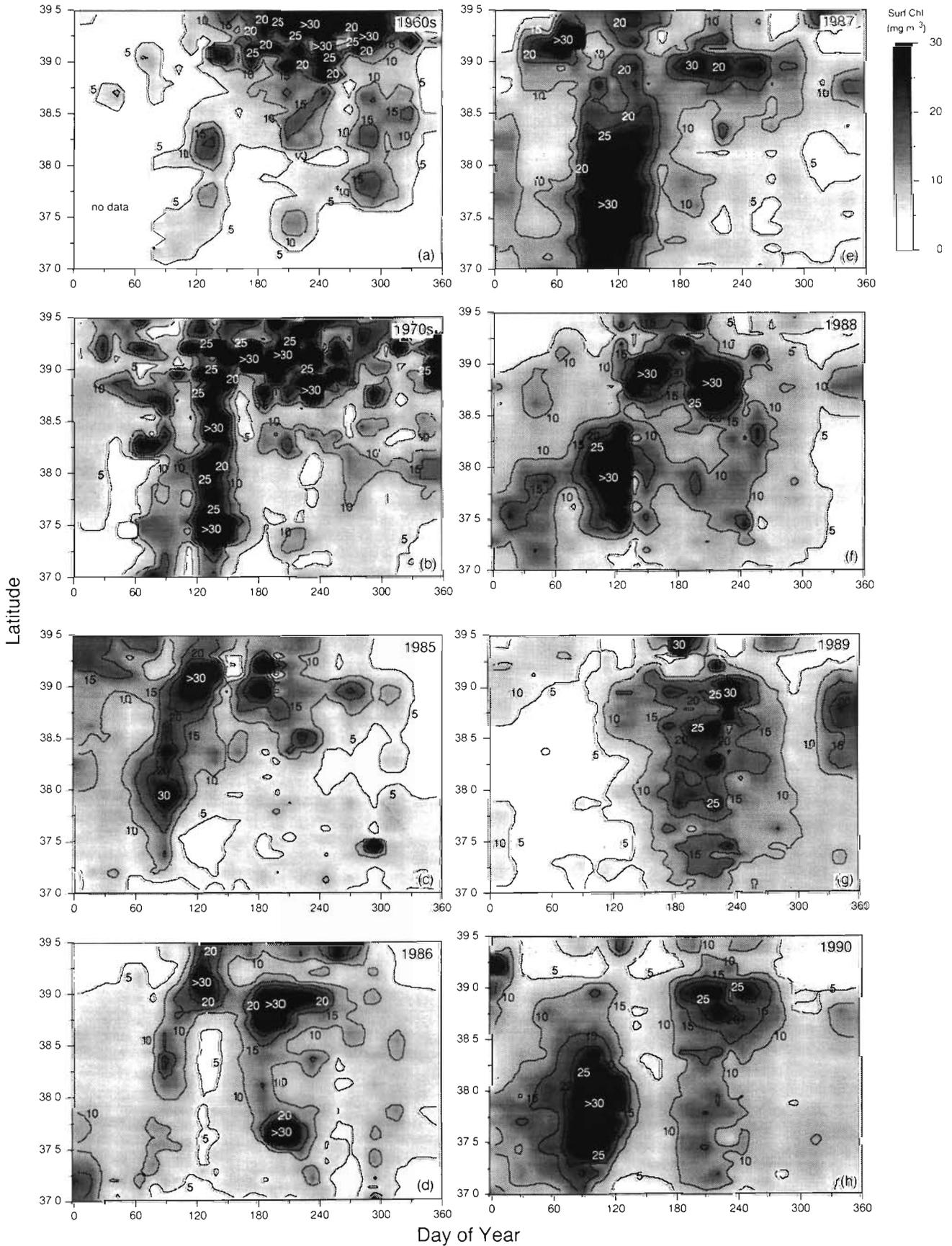


Fig 5. Time-space composites of surface chlorophyll concentrations (B) 1960s, 1970s, and individual years from 1985 to 1990

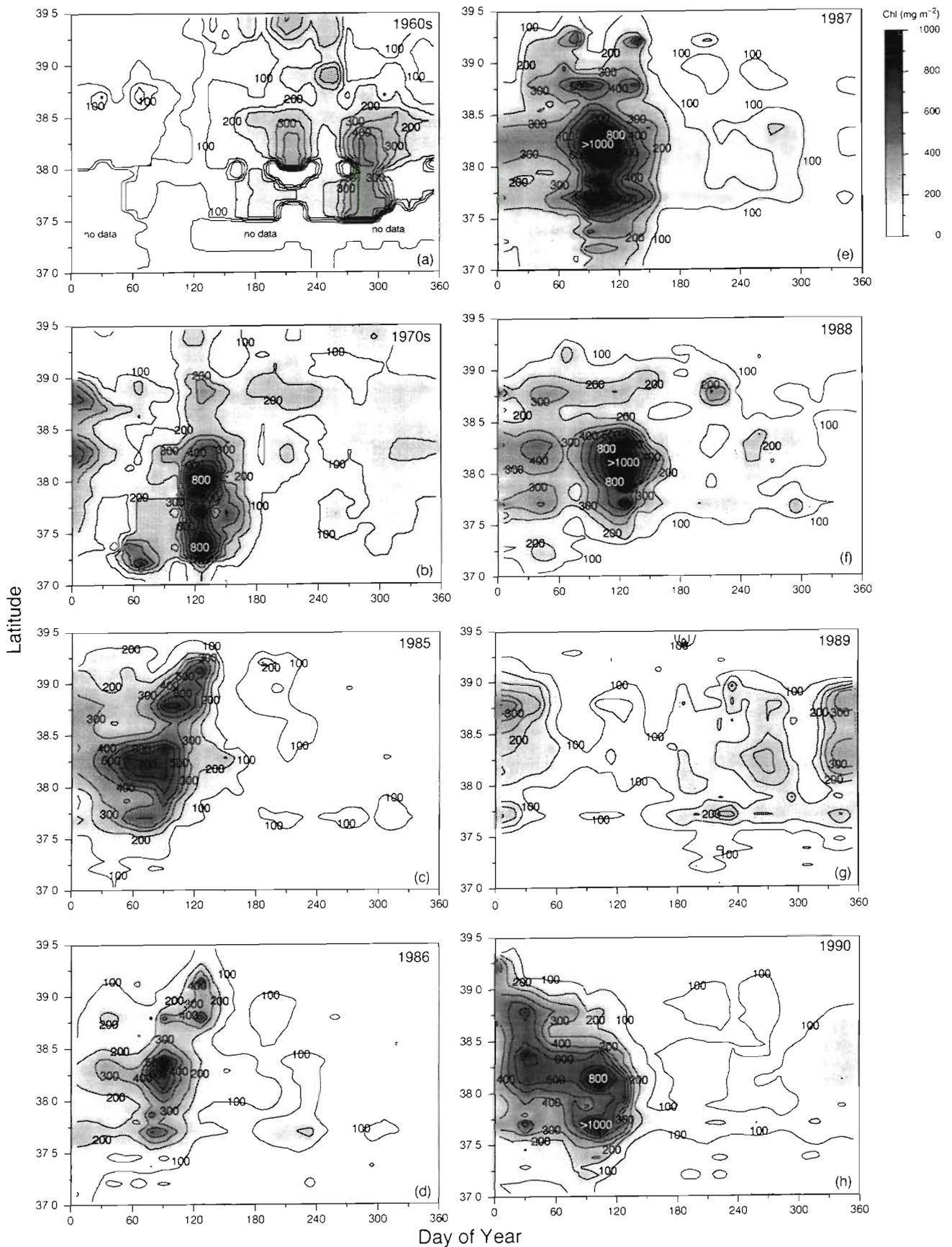


Fig. 6 Time-space composites of water-column chlorophyll concentrations (B'_{wc}) 1960s, 1970s, and individual years from 1985 to 1990

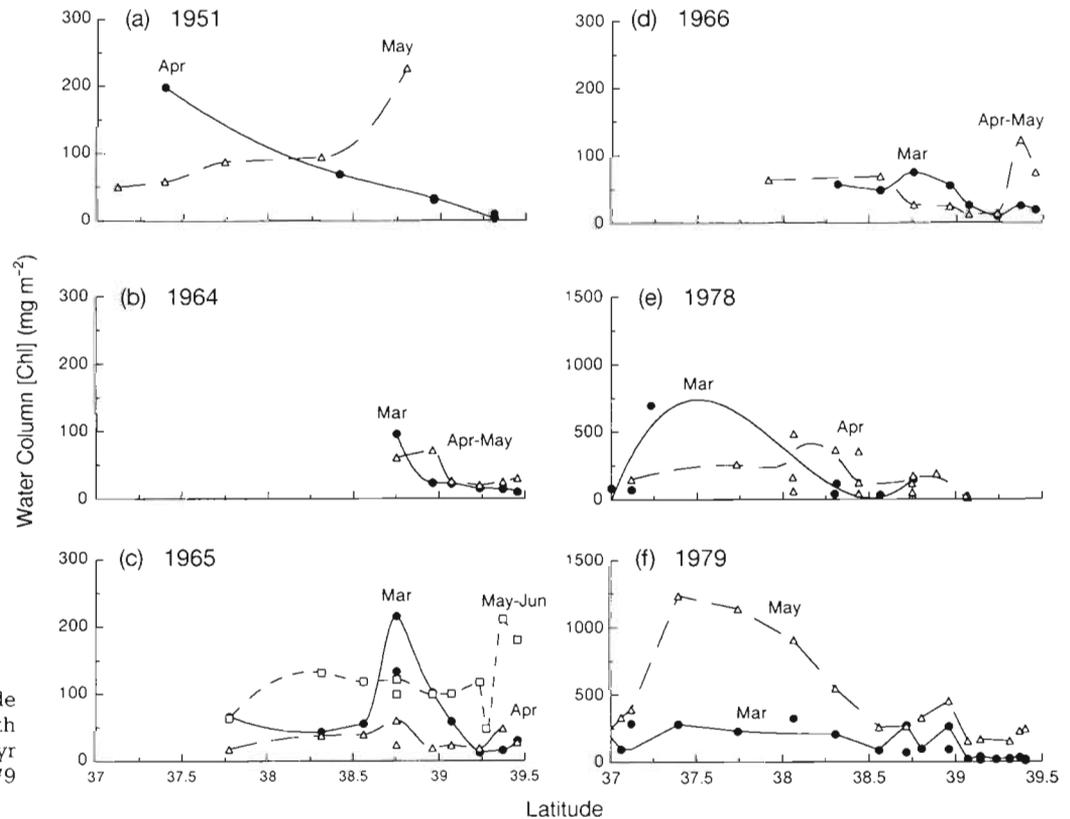


Fig. 7. B'_{wc} vs latitude plots for cruises with spring coverage for 6 yr between 1951 and 1979

spread and long-lived maximum that encompassed much of the estuary from late winter through late spring (Fig. 6e). Highest B'_{wc} values were $> 900 \text{ mg m}^{-2}$ in the mesohaline Bay between the mouth of the Potomac River and the Bay Bridge, 38.0 to 39.0° N . This peak was greatest at the beginning of April (Day 90), but persisted longer than in previous years (to Day 150) in a large part of the mesohaline to oligohaline Bay. A decline to low summer concentrations did not commence until late May to early June (Days 150 to 160) in the Rappahannock River to Patuxent River reach. B'_{wc} was $\geq 500 \text{ mg m}^{-2}$ quite far seaward, however, and was associated with a large diatom bloom that discolored surface waters.

1988. There was also a long-lived B'_{wc} maximum in 1988, although the peak concentrations of 500 to 700 mg m^{-2} were lower than those observed in 1987 (Fig. 6f). Most of the phytoplankton biomass was in the mesohaline to polyhaline regions, with high concentrations from the Rappahannock River to the Patuxent River, 37.7 to 38.3° N . Values declined to $< 300 \text{ mg m}^{-2}$ by mid-June (Days 150 to 170).

1989. The high B'_{wc} values that were observed in winter-spring 1985–88 never developed, i.e. the large accumulation of biomass associated with the winter-spring bloom that was observed in the preceding 4 yr was essentially absent in 1989 (Fig. 6g). A modest

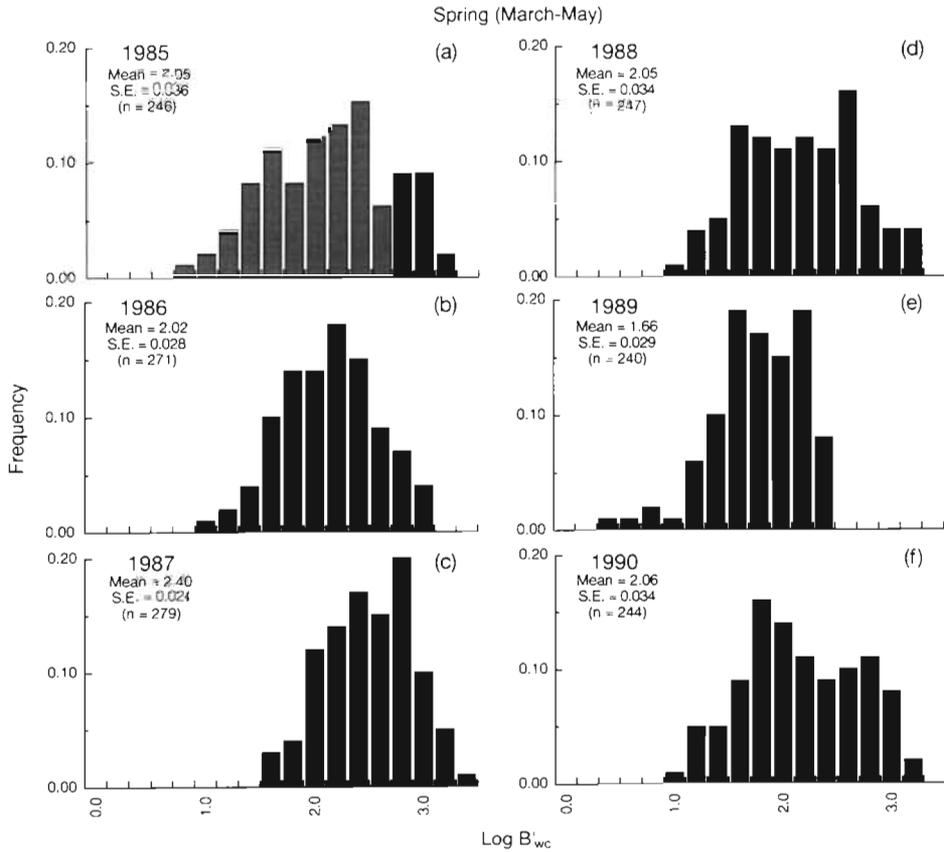
increase in B'_{wc} occurred from late summer to early fall, reaching ca 200 mg m^{-2} in the mesohaline.

1990. B'_{wc} was high from mid-February through March (Days 45 to 90) along much of the salinity gradient of the Bay (Fig. 6h), with values $> 500 \text{ mg m}^{-2}$ observed in mid-March (Days 75 to 80) all the way to the mouth of the Bay. A decline to values $< 100 \text{ mg m}^{-2}$ occurred from late March and early April (Day 90), but $B'_{wc} > 500 \text{ mg m}^{-2}$ occurred again in May (Days 120 to 150) from the Rappahannock River to the Patuxent River mouth. A Bay-wide decline of B'_{wc} to $< 100 \text{ mg m}^{-2}$ occurred after mid-June (Day 180).

The frequency distributions of $\log_{10} B'_{wc}$ for March to May 1985–90 are presented in Fig. 8(a to f) to illustrate the interannual differences in winter-spring biomass, and that these distributions were log-normal, as was the case for B . These data show that the winter-spring bloom was well developed in 1987 and 1990, but only weakly so in 1989, consistent with B'_{wc} data presented in time and space composites (Fig. 6e, g, h).

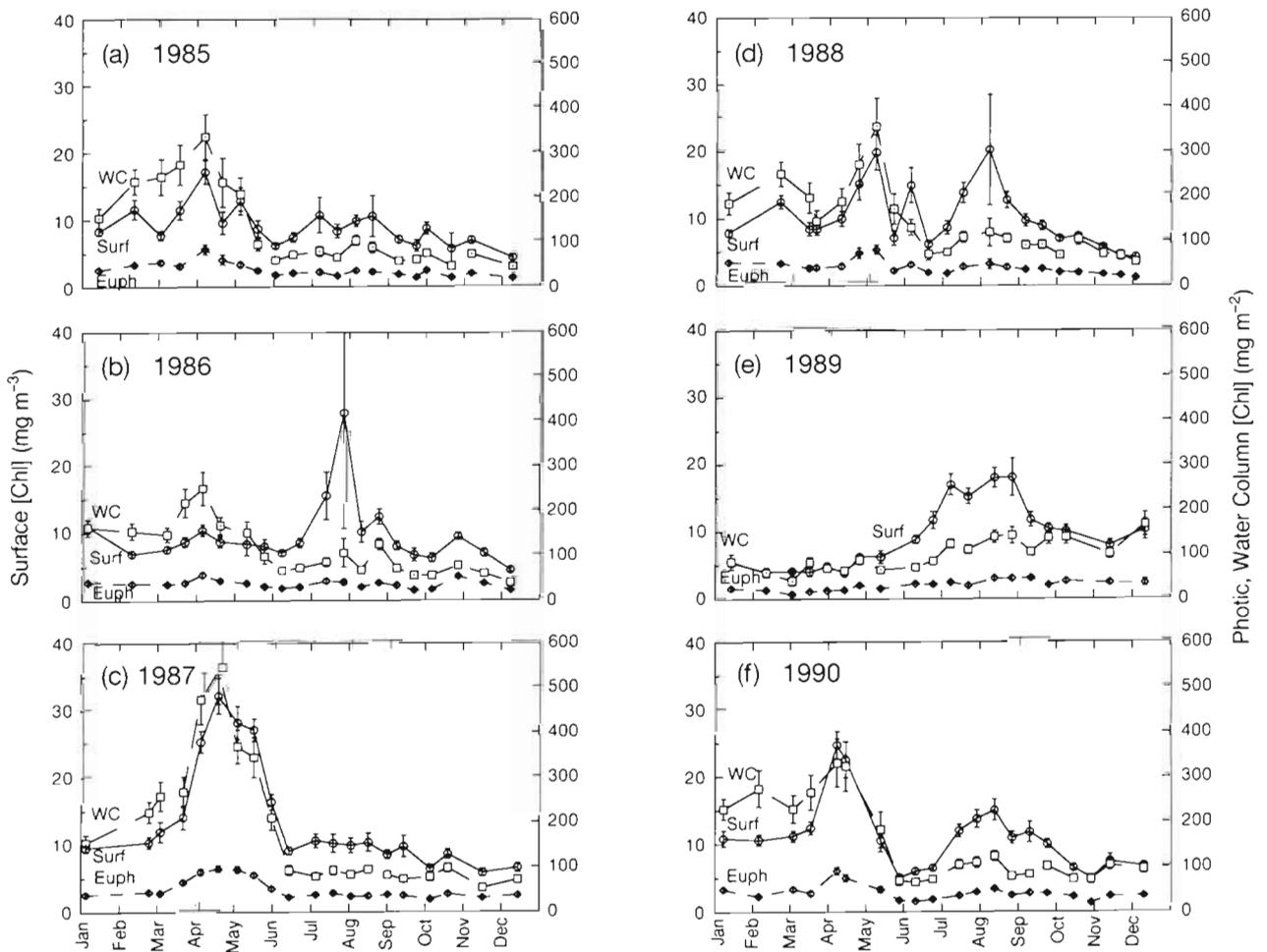
Surface, euphotic layer and water column chlorophyll concentrations

The mean concentrations of surface (B , mg m^{-3}), integrated euphotic layer (B'_{eu} , mg m^{-2}), and integrated water-column (B'_{wc} , mg m^{-2}) chlorophyll for



◀ Fig. 8. Frequency distributions of $\log B_{wc}$, spring 1985-90

Fig. 9. Cruise means of surface, photic layer, and water-column chlorophyll concentrations, 1985-90



each cruise of the CBP Monitoring Program showed several interesting patterns (Fig. 9a to f). First, the peak in B did not always occur in winter-spring; in 1986, 1988 and 1989, the highest mean surface concentration was in summer (Fig. 9b, d, e). Second, the highest B'_{wc} concentrations generally occurred in winter-spring, but there were large interannual variations in the magnitude of that biomass peak. For example, the large bloom in 1987 was reflected in the high means for April to June (Fig. 9c), whereas the absence of a winter-spring bloom in 1989 coincided with the consistently low means observed through the summer (Fig. 9e). Third, the duration of high B and B'_{wc} from winter to spring varied interannually from relatively narrow and shallow peaks, such as were observed in 1986 (Fig. 9b), to broad, pronounced peaks as in 1987 (Fig. 9c). Fourth, B and B'_{wc} tracked one another in winter-spring, but this coupling did not persist in summer when high B values were observed in the absence of high B'_{wc} (e.g. 1986, 1988, 1989 and 1990). Lastly, mean B'_{eu} was less variable than mean B and B'_{wc} and did not show large interannual variability.

Susquehanna River flow

Data on freshwater flow from the Susquehanna River are presented in Figs. 10 to 13. Annual flow for the 40 yr period from 1950–90 identifies relatively wet or dry years (or decades) as compared to the 40 yr mean

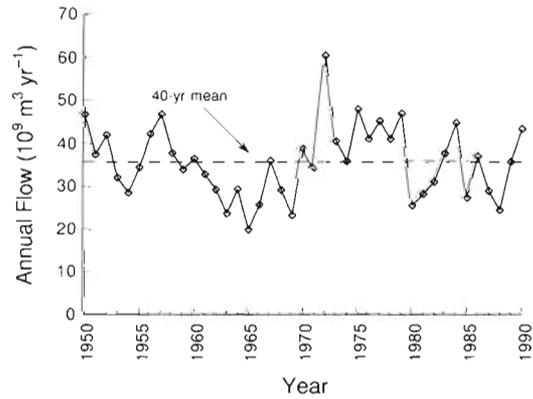


Fig. 10. Annual freshwater flow from the Susquehanna River, 1950–90

annual flow (Fig. 10). Notable features include the high interannual variability in flow, the low flow period of the 1960s, and the high flow period of the 1970s. Interannual variations in the timing and magnitude of freshwater flow for 1950–90 are depicted as the percent difference from the long-term (40 yr) mean, daily flow by season (Fig. 11a to d). The mean, daily flow rates for 1985–90 show the short-term variations in flow for years sampled in the CBP Monitoring Program (Fig. 12a to f). An expanded presentation of the flow data for 1985–90 characterizes flow conditions for successive seasons (Fig. 13).

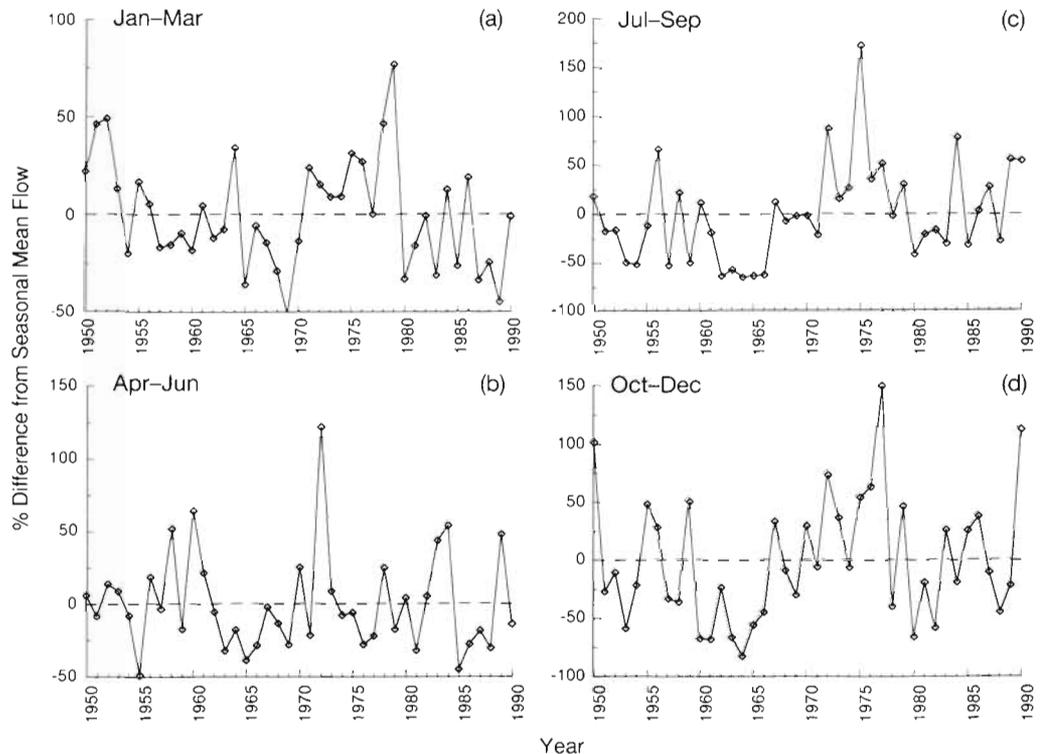


Fig. 11. Seasonal freshwater flow from the Susquehanna River as the percent difference from mean seasonal flow, 1950–90

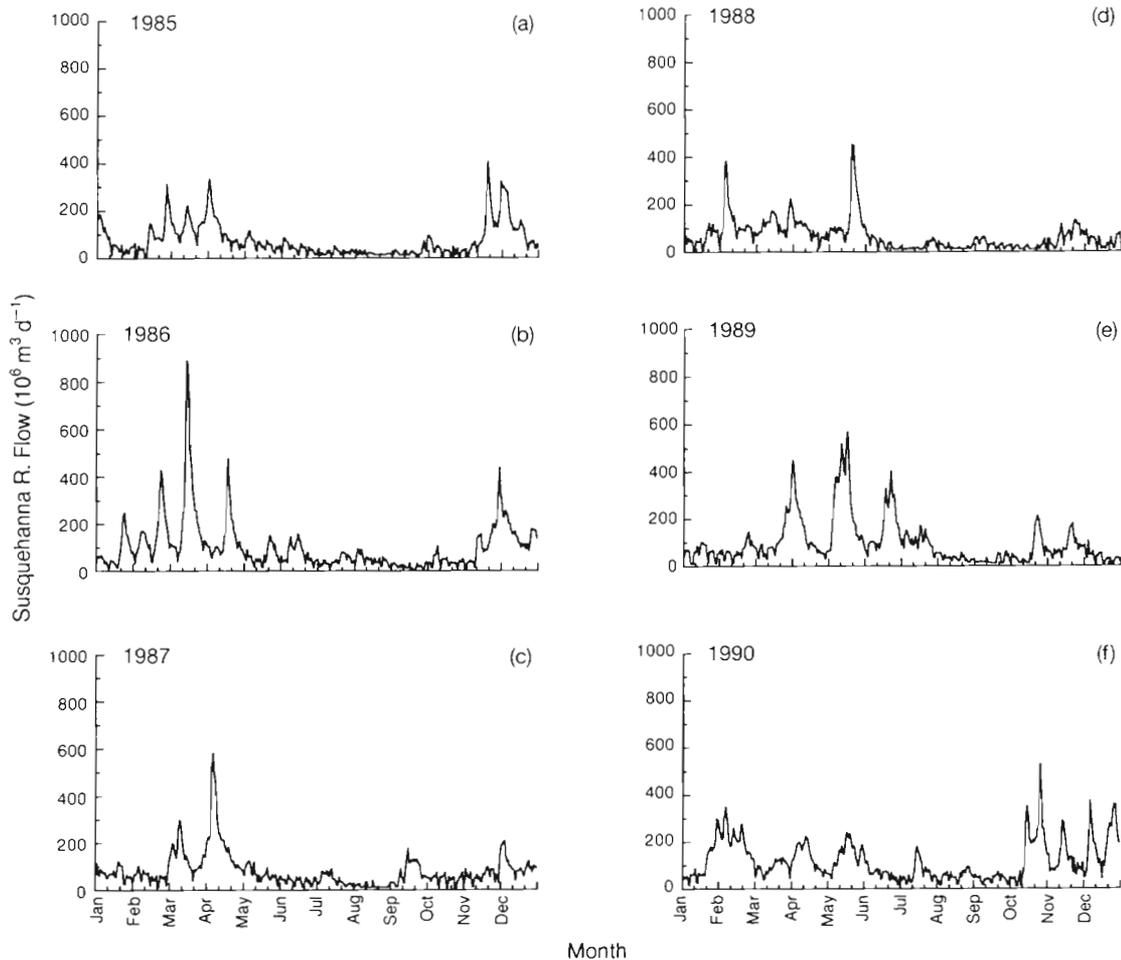


Fig. 12. Daily mean flow from the Susquehanna River, 1985–90

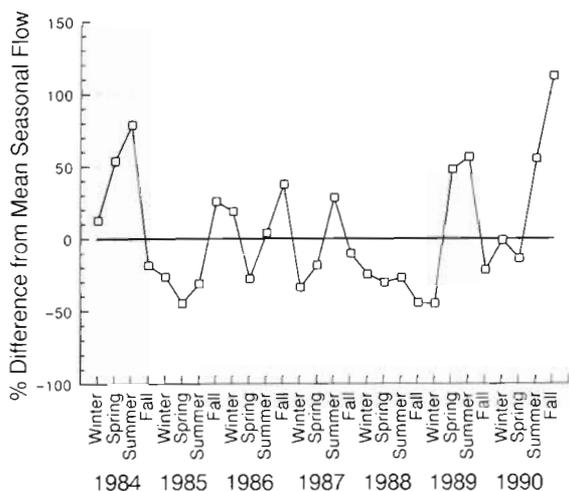


Fig. 13. Expanded view of seasonal freshwater flow from the Susquehanna River as the percent difference from the long-term (1950–90) mean, for the Monitoring Program years, 1984–90

Light attenuation

The historical data do not support an analysis of the distribution of K_t for the 1950s to early 1980s, but recently collected data from the CBP Monitoring Program show that a fairly rapid response to peaks in freshwater flow from the Susquehanna River occurs in the mid- to upper Bay (Fig. 14a to f). In March and April, high flow generally produced very turbid conditions in the oligohaline Bay north of 38.5° N. Diffuse attenuation coefficients declined spatially toward the mouth of the Bay and seasonally as the freshet subsided in late spring. Interannual variability in the distribution of K_t appears to be coupled to differences in flow from the Susquehanna River. For example, K_t in winter 1986 in the upper Bay (> 39.0° N) was relatively low (1.5 to 2.5 m^{-1}), and the seaward movement of the $K_t = 3.0 m^{-1}$ isopleth occurred in late March to early April (Days 90 to 110) (Fig. 14b). This corresponded to high flow in mid-March exceeding $800 \times 10^6 m^3 d^{-1}$. In comparison, low river flow in early 1987 (Fig. 12c) pro-

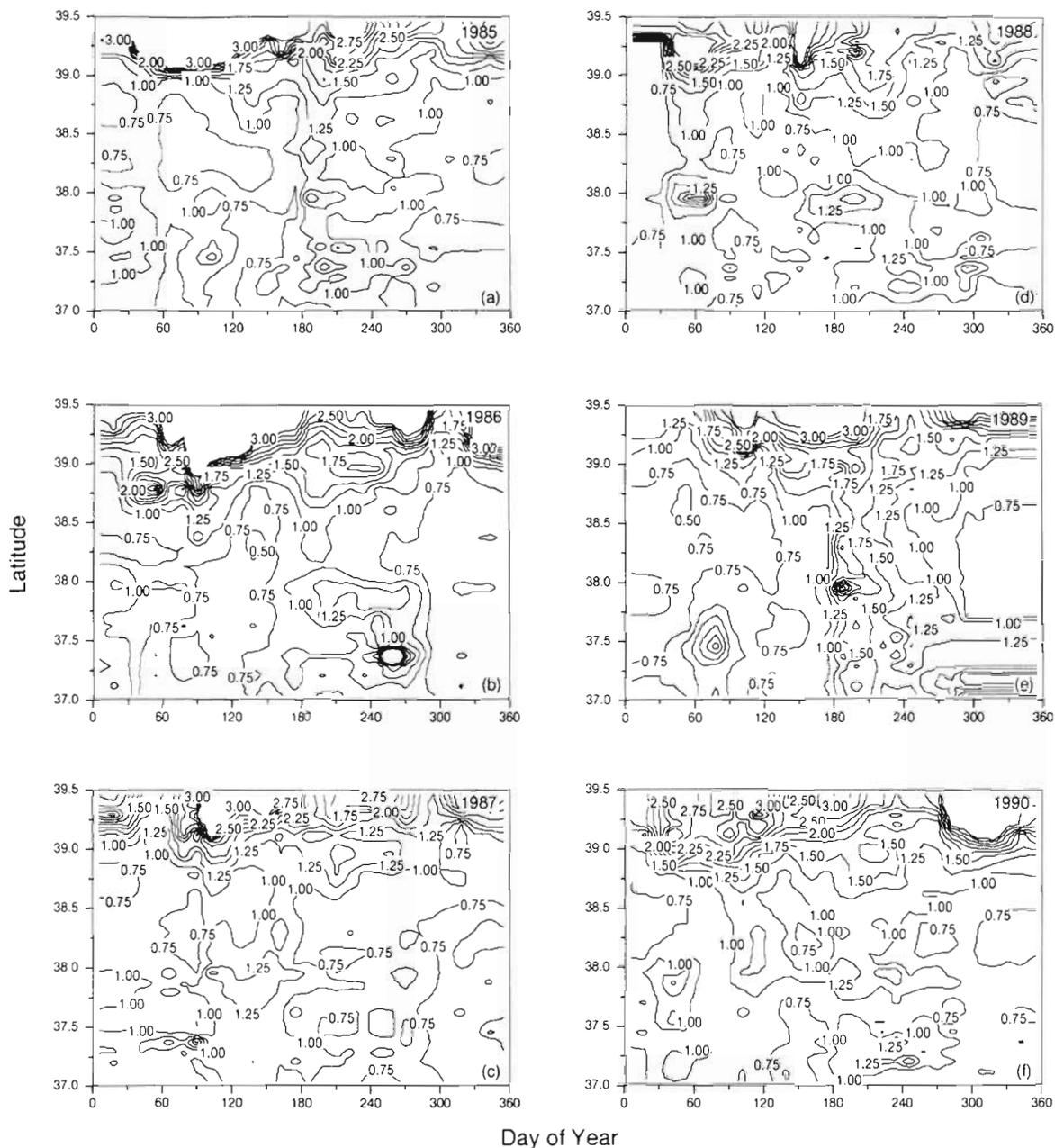


Fig. 14. Distributions of the diffuse attenuation coefficient (K_t) in the Bay, 1985–90

duced relatively low K_t in the upper Bay in winter. The freshet occurred in March and April (2 peaks), and K_t values increased north of 39.0° N. K_t in the mesohaline to polyhaline Bay ranged from 0.75 to 1.0 m^{-1} . In 1989, late peaks in Susquehanna River flow (Fig. 12e) produced high K_t values ($>3.0 m^{-1}$) in the region north of 39.3° N from late May through June (Days 150 to 180). The north-south movement of these isopleths has strong implications for the areal extent of light-limited conditions in the mesohaline to oligohaline Bay (see 'Discussion').

Nutrient concentrations

The frequency distributions of nutrient concentrations (and their ratios, below) were log-normal and sampling was uneven in time and space, as for chlorophyll. The least squares means and confidence intervals of DIN, PO_4^{3-} and SiO_4^{3-} were computed on the logarithms and back-transformed, as for B and B'_{wc} (Figs. 15 to 17). Significant changes in the concentrations of DIN and PO_4^{3-} have occurred in the past 30 yr in the Chesapeake Bay (Figs. 15a to d & 16a to d). The

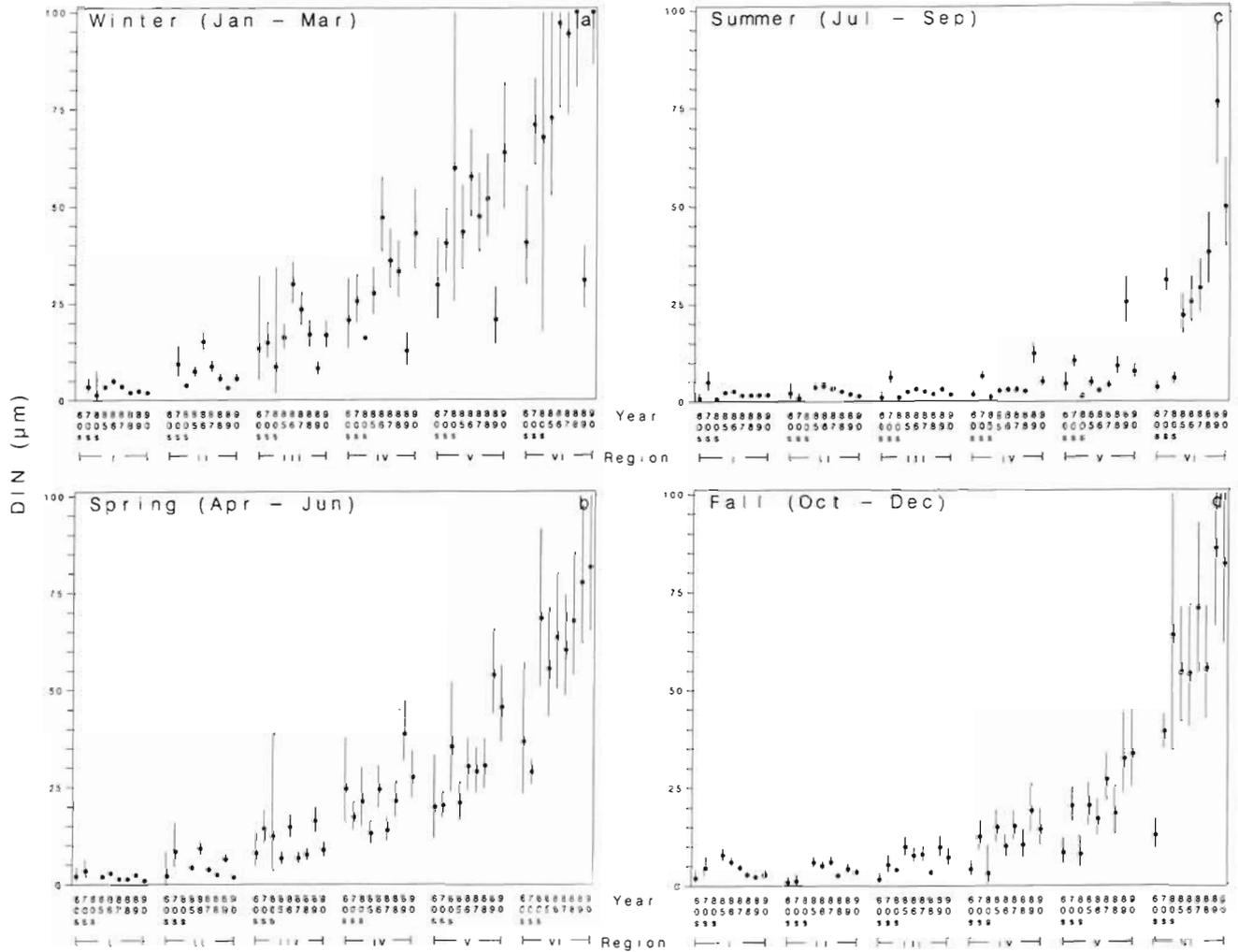


Fig. 15. DIN concentrations by year, season and region for 1960s, 1970s, 1980s and individual years from 1985 to 1990. Error bars are 95% lower and upper confidence intervals

least squares means of DIN concentrations in winter, spring and fall in the oligohaline Bay (Regions V & VI) have increased 25 to 100% since the 1960s; there have been no detectable changes in DIN in the lower, polyhaline Bay (Regions I & II) during this period (Fig. 15a to d). PO_4^{3-} concentrations have declined in the mesohaline and oligohaline Bay (Regions III to VI) since the 1960s for all seasons, and in the polyhaline Bay (Regions I & II) in summer and fall (Fig. 16a to d). In a significant part of the estuary, the least squares mean concentrations of PO_4^{3-} were >100% lower in 1985–90 than from the 1960s through early 1980s; PO_4^{3-} concentrations in the 1960s were not as high as those in the 1970s or early 1980s. Data on SiO_4^{3-} concentrations were available only from recent years and temporal changes were not apparent (Fig. 17a to d).

DIN and SiO_4^{3-} showed strong seasonality in the oligohaline Bay, with highest concentrations occurring

from winter to spring when freshwater flow was highest (Figs. 15a, b & 17a, b). In contrast, PO_4^{3-} concentrations showed no seasonality (Fig. 16a to d). The spatial distributions of DIN and SiO_4^{3-} were strongly influenced by flow from the Susquehanna River, with highest concentrations observed in the upper, oligohaline Bay (Regions V & VI), and lowest concentrations toward the lower, polyhaline Bay (Regions I & II) (Figs. 15a to d & 17a to d). The distribution of PO_4^{3-} did not appear to be strongly linked to flow from the Susquehanna River (Fig. 16a to d).

Concentrations of dissolved inorganic nutrients during winter-spring in years covered by the CBP Monitoring Program show a repeatable, but variable sequence of SiO_4^{3-} and PO_4^{3-} depletion in the mid- to upper oligohaline and mesohaline Bay, and DIN depletion in the lower, polyhaline Bay. This temporal progression of nutrient distributions in 1985–90 provides

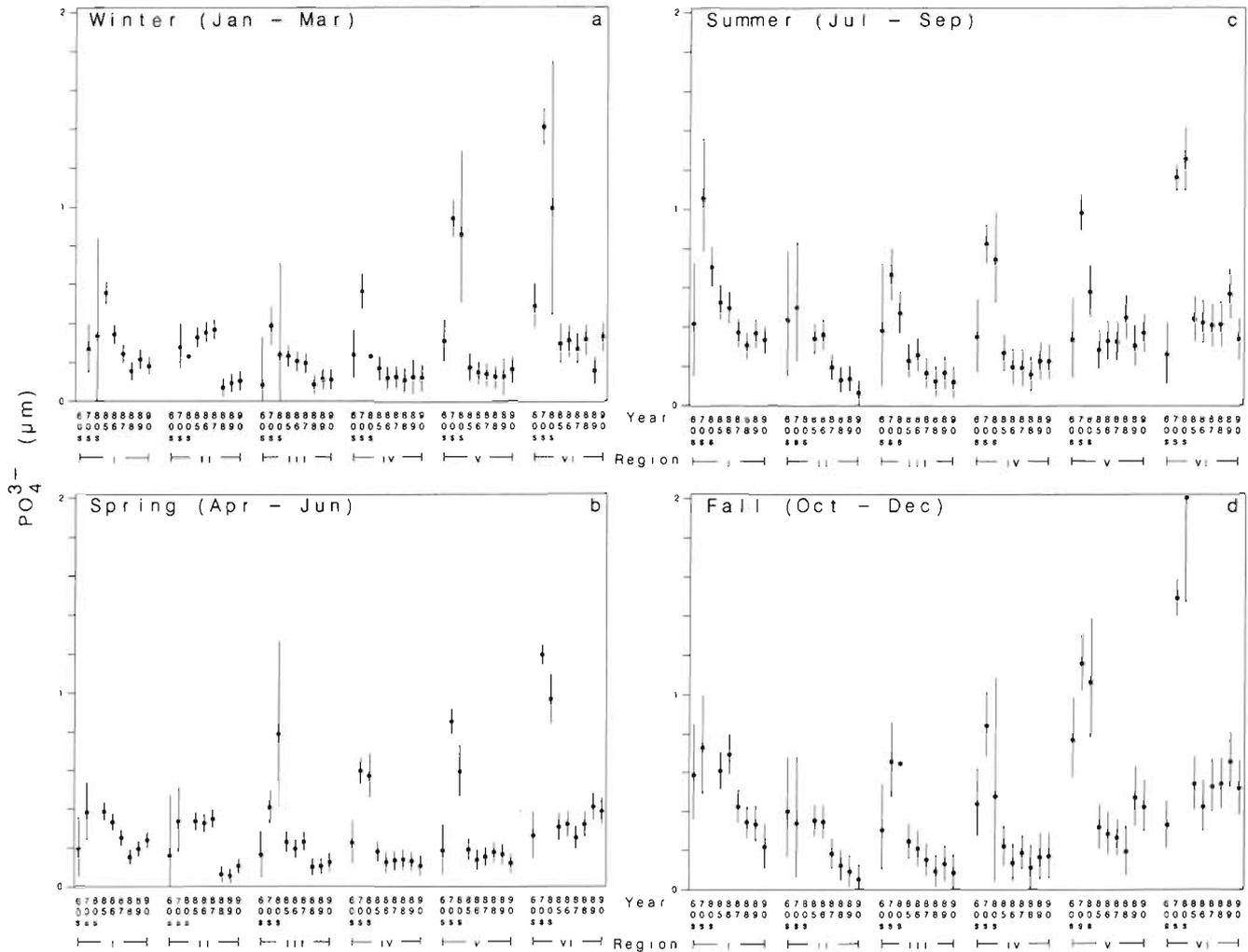


Fig. 16. PO_4^{3-} concentrations by year, season and region for 1960s, 1970s, 1980s and individual years from 1985 to 1990. Error bars are 95% lower and upper confidence intervals

a measure of interannual variations in the roles of individual macronutrients:

1985. SiO_4^{3-} was nearly undetectable by late March seaward of 38.5°N , and PO_4^{3-} was also very low in concentration. A mesohaline decline in NH_4^+ was observed in April, SiO_4^{3-} was unchanged and PO_4^{3-} was low. By late April, SiO_4^{3-} was depleted seaward of 38.8°N . There was some evidence of SiO_4^{3-} replenishment by May in the polyhaline Bay.

1986. The distribution of nutrients was very similar to 1985. In late March, there was abundant DIN, moderate PO_4^{3-} and high SiO_4^{3-} except south of 37.8°N near the Rappahannock River mouth. By early April, a decrease in NH_4^+ was observed in the mesohaline Bay, low PO_4^{3-} prevailed, and SiO_4^{3-} depletion occurred seaward of 38.5°N . By mid- to late April, SiO_4^{3-} depletion in surface waters extended as far north as 38.7°N . SiO_4^{3-} was undetectable seaward of 38.8°N in mid-

May, PO_4^{3-} was low, and there was ample DIN throughout the estuary.

1987. There were relatively low SiO_4^{3-} concentrations along the salinity gradient of the Bay in winter-spring, and depletion of SiO_4^{3-} occurred seaward of 38.6°N by early April. The mesohaline decline in SiO_4^{3-} observed in the previous 2 yr occurred in 1987, and low PO_4^{3-} concentrations were also detected. By late April, SiO_4^{3-} replenishment in surface waters had commenced, suggesting a mixing event had injected newly-sedimented diatom material into the surface mixed layer. NH_4^+ concentrations were high in the mesohaline to oligohaline, consistent with a spring occurrence of vertical mixing between early and mid-April. In early May, PO_4^{3-} was low in most of the Bay, SiO_4^{3-} was present seaward and landward, and mesohaline NH_4^+ was low.

1988. Depletion of SiO_4^{3-} in 1988 occurred early in March seaward of 38.2°N , near the mouth of the

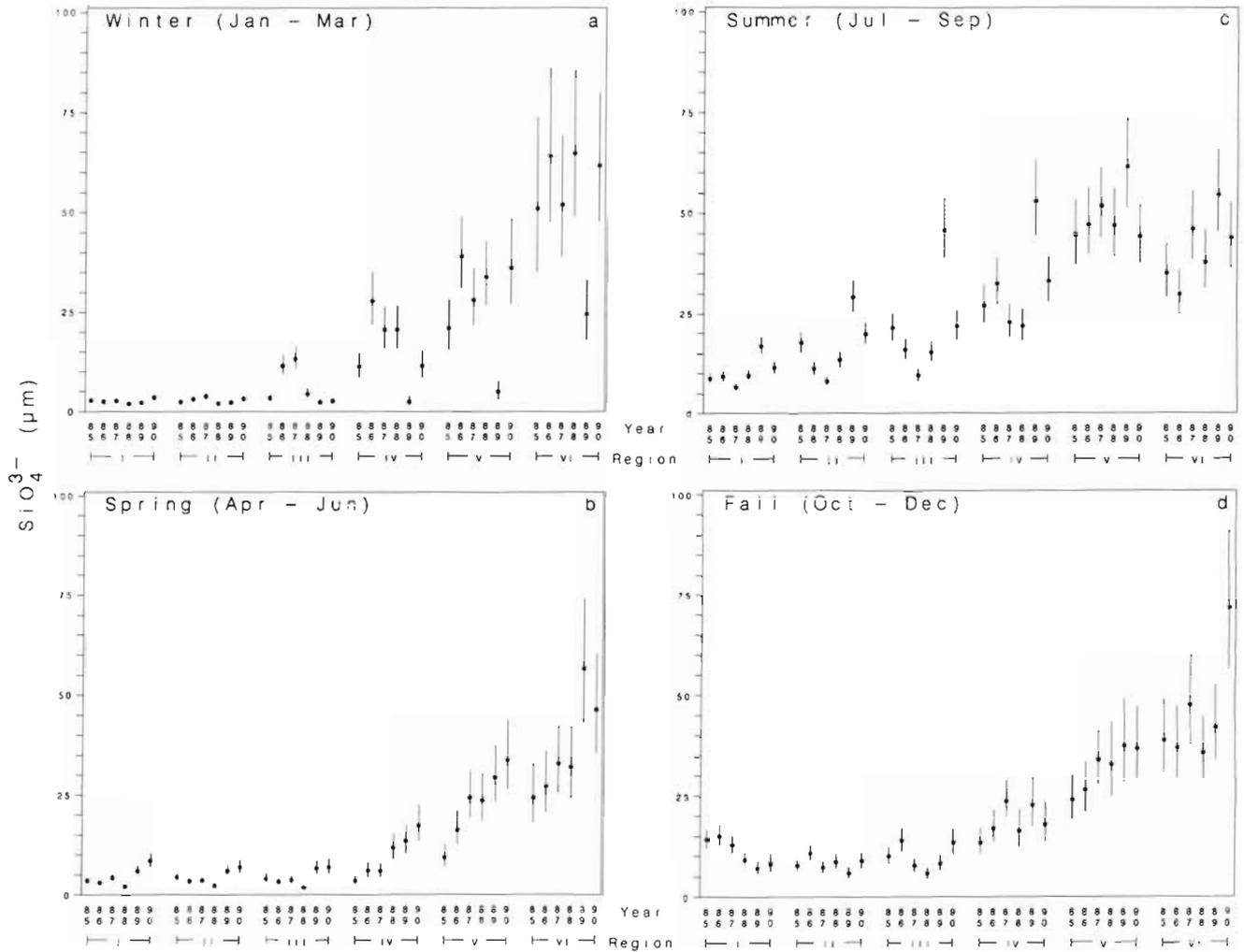


Fig. 17. SiO_4^{3-} concentrations by year, season and region for individual years from 1985 to 1990. Error bars are 95% lower and upper confidence intervals

Patuxent River, and low PO_4^{3-} and ample DIN were measured at that time. By mid-April, DIN was abundant and PO_4^{3-} concentrations were moderate. There were relatively high SiO_4^{3-} concentrations in the upper, oligohaline Bay, but SiO_4^{3-} was undetectable seaward of 38.4°N , between the Choptank and Patuxent Rivers. A mesohaline decline in NH_4^+ was observed by late April, PO_4^{3-} was low, and SiO_4^{3-} was depleted in most of the mesohaline to polyhaline Bay. SiO_4^{3-} was even further depleted by mid-May, NH_4^+ was very low, NO_3^- was abundant, and PO_4^{3-} was low.

1989. The distribution of nutrient concentrations in 1989 was unique as SiO_4^{3-} concentrations in March were lower in the upper Bay than in the previous years, but were still detectable in the lower Bay. This changed significantly in April, but concentrations in much of the mesohaline Bay remained low.

1990. Depletion of SiO_4^{3-} in the mesohaline to polyhaline Bay commenced in March and was spatially extensive by mid-April. PO_4^{3-} was very low in much of the spring throughout the Bay. Ample DIN was detected from March through May.

The molar ratios of macronutrients, DIN, SiO_4^{3-} and PO_4^{3-} , relative to phytoplankton requirements, provide additional data on the spatial and temporal patterns of nutrient limitation in the Bay. The least squares means and confidence intervals of the macronutrient molar ratios were computed on the logarithms and back-transformed (Figs. 18 & 19). There has been a significant long-term increase in $\text{DIN}:\text{PO}_4^{3-}$ ratios since the 1960s in much of the Bay (Regions II to VI). $\text{DIN}:\text{PO}_4^{3-}$ was generally above Redfield's ratio (= 16 by moles) in all regions of the Bay in winter and spring, although the lower, polyhaline Bay (Regions I & II) showed some values near Redfield stoichiometry (Fig. 18). In sum-

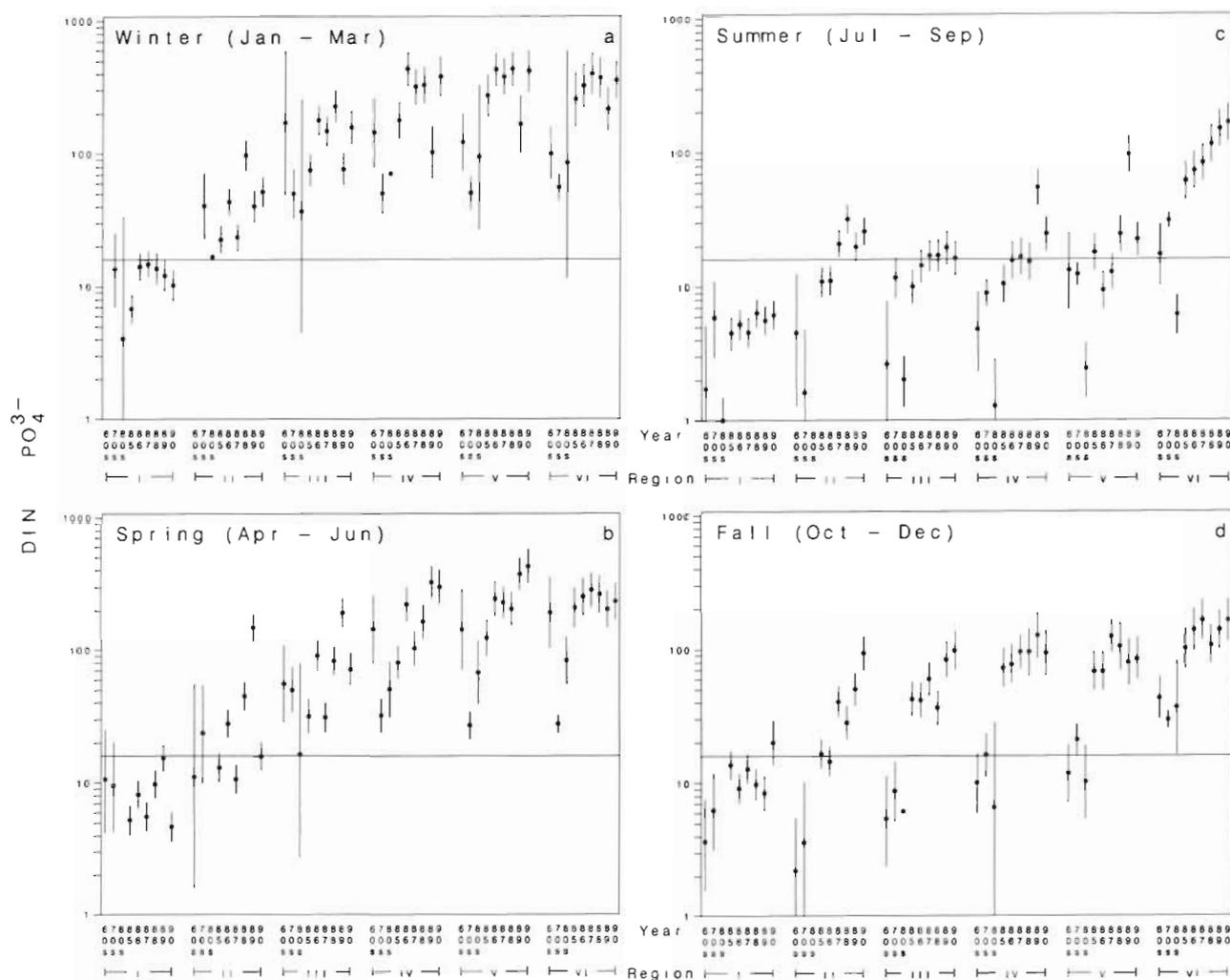


Fig. 18. Molar nutrient ratios of DIN:PO₄³⁻ by year, season and region for 1960s, 1970s, 1980s and individual years from 1985 to 1990. Error bars are 95% lower and upper confidence intervals

mer and fall, DIN:PO₄³⁻ less than Redfield's ratio occurred in much of the Bay, suggesting N limitation (Fisher et al. 1992). The recent data from CBP Monitoring cruises (1985–90) indicated that potentially limiting concentrations of SiO₄³⁻ and PO₄³⁻ often occurred in the mesohaline to polyhaline Bay (Regions I to III) by mid- to late spring. In summer, DIN:PO₄³⁻ ratios were commonly near or below Redfield's ratio in much of the Bay.

DISCUSSION

Historical trends in chlorophyll

The results presented in this paper document significant changes in the distribution of phytoplankton chlorophyll in the Chesapeake Bay during the last 40 yr. Increases in concentrations of surface (*B*) and

integrated water-column (*B'*_{wc}) chlorophyll from the 1950s to the 1970s were evident in the least squares means of *B* for data grouped by region (Table 2, Fig. 4), and in time and space composites of *B* and *B'*_{wc} for the 1960s and 1970s (Figs. 5a, b & 6a, b). The magnitude of these increases has varied with region of the Bay and with season. The apparent lack of a winter-spring bloom of phytoplankton in the 1960s in contrast to the high biomass densities in the 1970s is of particular note, although it should be considered that the time and space scales of sampling were much more limited in those data sets than at present. In recent years (post-1980), the winter-spring bloom has been a common feature of the annual cycle of phytoplankton in the Bay (Figs. 5c to h & 6c to h). Data collected in shipboard monitoring since 1985 documented large interannual variations in the timing, position and magnitude of the winter-spring diatom bloom. I believe that this vari-

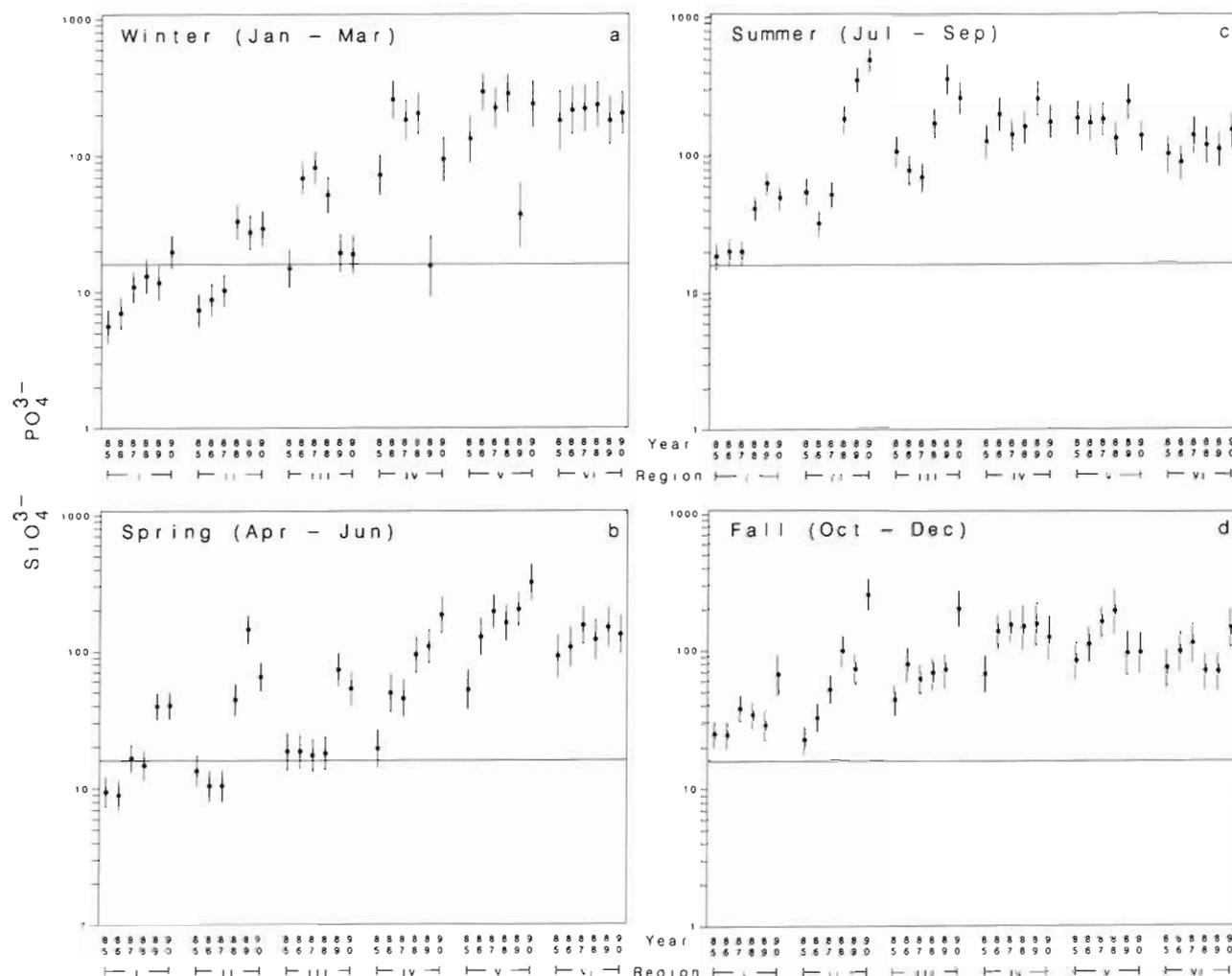


Fig. 19. Molar nutrient ratios of $\text{SiO}_4^{3-}:\text{PO}_4^{3-}$ by year, season and region for individual years from 1985 to 1990. Error bars are 95% lower and upper confidence intervals

ability is linked to freshwater flow from the Susquehanna River and the associated inputs of suspended materials and dissolved inorganic nutrients, that, in turn, regulate the light and nutrient environments of the Bay. This linkage has been suggested previously using data collected along the axis of the mainstem Bay in the early 1980s (Harding et al. 1986, Fisher et al. 1988), in the mesohaline reach in 1985-86 (Malone et al. 1988) and 1984-90 (Malone 1992), and in the mainstem of the Bay from 1989 to 1992 (Harding et al. 1994). Brief descriptions of those data sets and conclusions comprise the following sections.

Axial data, 1982-83

Data from a series of cruises in 1982-83 along the axis of the Bay revealed seasonal shifts in the position

of the chlorophyll maximum as a function of freshwater flow and nutrient input (Harding et al. 1986, Fisher et al. 1988). The Wofsy (1983) model for nutrient-replete systems was applied to these data to show that light-limitation in the oligohaline Bay regulated the location of the peak in surface chlorophyll at the landward end. The number of optical depths in the surface mixed layer in and near the turbidity maximum was >10 when corrected for non-phytoplankton light attenuation; no growth of phytoplankton occurs in such conditions because of severe light limitation although nutrients are abundant. The chlorophyll maxima in 5 cruises on the Bay occurred where there was an average of $5.7 (\pm 1.0)$ optical depths in the surface mixed layer. The geographic location corresponding to these conditions changed seasonally and was commonly in the mesohaline region. At the seaward end of transects, the nutrient-replete criteria of Wofsy's model

(DIN > 2 μM , PO_4^{3-} > 0.15 μM) were not generally met and it was concluded that nutrients regulated the abundance of phytoplankton in the lower, polyhaline Bay. The spatial and temporal resolution on those cruises was very limited, however, particularly in lateral coverage.

Mesohaline studies, 1985–86

Shipboard studies of the mesohaline Bay in 1985–86 obtained higher spatial and temporal resolution for this highly productive area (Malone et al. 1988). Data collected from the Chesapeake Bay Bridge (latitude = 39° N) to the Choptank River and Patuxent River region of the mainstem Bay (38.4° N) were used to show that: (1) the annual cycle of riverine nutrient input is in phase with the development of maximum phytoplankton biomass in spring; (2) it is out of phase with the highest rates of primary production in summer; and that (3) summer phytoplankton productivity is driven primarily by recycled nitrogen derived from the metabolism of particulate organic material produced during the spring bloom (see also Kemp & Boynton 1984, Boynton & Kemp 1985, Fisher et al. 1988). This work documented interannual variations in the distribution and abundance of phytoplankton in the mesohaline Bay in 1985 and 1986, and concluded that differences in freshwater flow from the Susquehanna River, dilution in the mesohaline and delivery of nutrients to the mesohaline and polyhaline Bay generated these variations. Malone et al. (1988) further suggested that the source of highest phytoplankton biomass in the estuary resided in the more seaward regions, outside their study area, as high water column chlorophyll concentrations were dominated by subpycnocline chlorophyll delivered northward in estuarine circulation. This intensive study of the mesohaline Bay gave new insight to phytoplankton dynamics in the Bay by

providing improved spatial and temporal coverage to that obtained in the cruises of the early 1980s, but the sampling was limited in spatial coverage to a relatively small area.

Remote sensing, 1989–present

A combination of remotely sensed and traditional measurements on the Bay in the last several years has provided the spatial and temporal resolution needed to identify the position of high concentrations of surface chlorophyll and biomass in winter-spring. Harding & Itsweire (1991), Harding et al. (1992a, b, 1994) and Itsweire et al. (1991) reported interannual variations in the winter-spring blooms of 1989–92 using the mean concentrations of surface, photic layer and water column chlorophyll, time and space composites of water column chlorophyll derived from aircraft surveys in spring and summer, and full year composites of water column chlorophyll from shipboard measurements. It was concluded that seasonal and interannual variations in flow from the Susquehanna River could explain differences in the pattern of phytoplankton abundance during winter-spring.

Comparative analysis and synthesis

The historical and recent data on B and B'_{wc} synthesized in this paper can be used to extend the reasoning of Harding et al. (1986, 1992a, 1994), Fisher et al. (1988), Malone et al. (1988), and Malone (1992) to additional years, including the decades of the 1960s and 1970s, and individual years from 1985–90, to provide a multi-year context for analyzing the link of freshwater flow to the winter-spring bloom. Table 4 summarizes the timing, position and magnitude of phytoplankton maxima for decadal and annual data

Table 4. Summary of the timing, position and magnitude of surface (B) and integrated water-column (B'_{wc}) chlorophyll maxima and winter-spring freshwater flow (W/S flow) conditions. P: polyhaline; M: mesohaline; O: oligohaline

Year	B			B'_{wc}			W/S flow
	Timing	Position	Magnitude	Timing	Position	Magnitude	
1950s	Summer/fall	M/O	Low/low	–	–	–	> Avg
1960s	Summer	O	High	Summer/fall	M	Low	< Avg
1970s	Spring/summer	P, M, O/O	High/high	Spring	P, M	High	> Avg
1980s	Summer	M, O	Medium	–	–	–	< Avg
1985	Spring/summer	M, O/O	Medium/medium	Spring	P, M, O	High	< Avg
1986	Spring/summer	O/O	Low/medium	Spring	M, O	Medium	> Avg
1987	Spring/summer	P, M, O/O	High/medium	Spring	P, M, O	Very high	< Avg
1988	Spring/summer	P, M/O	High/high	Spring	P, M	High	< Avg
1989	Summer	M, O	Medium	None	–	–	Very low
1990	Spring/summer	P, M/M, O	High/medium	Spring	P/M	High	Avg

groupings and relates these measures to winter-spring flow from the Susquehanna River. As I stated above, time and space composites for the 1960s and 1970s showed that the 2 decades differed significantly in B (Fig. 5a, b) and B'_{wc} (Fig. 6a, b). This may be explained by the low flow during the winter-spring interval prior to the usual formation of the annual phytoplankton maximum in the 1960s as compared to the 1970s (see Fig. 11a, b).

Recent data on phytoplankton abundance documented the absence of a significant winter-spring bloom in 1989; the low B and B'_{wc} that were observed accompanied low nutrient loading associated with persistent drought conditions and below-average Susquehanna River flow for 15 mo prior to spring, and a very late (2 mo) freshet in 1989 that produced exceptionally high light attenuation coefficients in the mesohaline Bay. Malone et al. (1991) concluded that the timing of this freshet did not support a winter-spring bloom as the peaks in freshwater flow from mid-May into June occurred after the usual time of diatom growth and instead affected the summer flora. Moreover, Conley & Malone (1992) and Harding et al. (1992a, 1994) suggested that the unusually low flow prior to spring 1989 restricted the availability of SiO_4^{3-} to support diatom growth, as standing stocks of SiO_4^{3-} can support only 26 to 44 % of total potential diatom production and the balance must be supplied by riverine input.

Winter-spring blooms in other years from 1985 to 1990 were well developed when flow from the Susquehanna River was near or slightly below the long-term average for winter and spring (Table 4, Figs. 5a to h, 6a to h & 11a to d). For example, phytoplankton abundance in 1985 from March to May was high (Figs. 5a & 6a), and followed a freshet that was within 25 % of the long-term seasonal mean (Fig. 13). In 1986 and 1987, the blooms were also well developed; the abundance of phytoplankton in 1987 reached the highest levels since the onset of the CBP Monitoring Program (Figs. 5b, c & 6b, c). 1988 also had high B and B'_{wc} (Figs. 5d & 6d) following near or below average winter and spring flow (Fig. 13). In 1990, freshwater flow from the Susquehanna River was near average prior to winter-spring. The bloom of large, centric diatoms that developed by April–May was spatially extensive and long-lived (Figs. 5h & 6h). Average flow provided sufficient nutrients to support a pronounced bloom, but did not enlarge the area of light-limited conditions beyond the oligohaline Bay (Harding et al. 1992a, 1994).

A separate analysis of the impact of freshwater flow >100 % above the long-term seasonal average in fall 1990 on the distribution of chlorophyll in winter-spring 1991 provides additional insight into interannual variations (Harding et al. 1994). The winter-spring bloom

in 1991 was not well developed and it was concluded that the period of high flow was too early to support a bloom. These findings suggest that the 'memory' of the Bay does not extend to an event >4 mo prior to the usual time of the bloom from March to May, but that multi-year effects of reduced nutrient loading during continued periods of low freshwater flow can significantly influence phytoplankton abundance over a longer time period. This conclusion is consistent with recent findings (Boynton et al. 1991), and has ramifications for ongoing efforts to reduce nutrient loading and phytoplankton biomass in the Chesapeake Bay. If there is little carryover effect of nutrient loading between years, then significant reductions in nutrient inputs from the watershed can be expected to elicit fairly rapid decreases in the abundance of phytoplankton.

Light and nutrients

The interplay of light and nutrients in regulating phytoplankton abundance in the Bay arises from the dominant effect of seasonal and interannual variations in freshwater flow on both particulate and nutrient loadings, as has been discussed extensively in the context of the position of the chlorophyll maximum (cf. Harding et al. 1986, Fisher et al. 1988, Malone et al. 1988, Malone 1992). Subtle interannual variations in phytoplankton abundance, such as were observed between 1985 and 1986, are most likely expressions of this interplay. In both 1985 and 1986, freshwater flow and concomitant nutrient loading were sufficient to generate a bloom of reasonable proportions, but the abundance of phytoplankton in 1985 was significantly higher than in 1986. This was the case even though winter-spring flow in 1985 was both lower than the long-term seasonal average, and lower than winter-spring 1986 flow (Table 4). I suggest that these less pronounced interannual variations result from a balance of the input of suspended particulates and nutrients in the freshet, i.e. lower flow prior to spring 1985 resulted in light conditions more conducive to phytoplankton growth than in 1986, and nutrient concentrations under both flow regimes were sufficient to promote growth in the mesohaline to polyhaline Bay (Figs. 15 to 19). This would be consistent with north-south movement of the landward limit to phytoplankton growth, according to Wofsy's model, at the same time that the seaward limit was regulated by nutrient loading from the identical freshwater source as provides the suspended materials and drives the position of the turbidity maximum.

Superimposed on variations in flow and the attendant effects on light and nutrient conditions are long-

term changes in the concentrations of dissolved inorganic nutrients, such as were evident for DIN, PO_4^{3-} and $\text{DIN}:\text{PO}_4^{3-}$ (Figs. 15, 16 & 18). Clearly, lower concentrations of DIN in the 1960s (Fig. 15), coupled with relatively low freshwater flow from the Susquehanna River (Fig. 10), generated reduced loading of DIN to the estuary in winter and spring. At the same time, PO_4^{3-} was lower in the 1960s than in the 1970s (Fig. 16). $\text{DIN}:\text{PO}_4^{3-}$ in spring indicated that N limitation occurred in the lower, polyhaline Bay, while the mesohaline and oligohaline Bay were probably P limited (Fig. 18). These findings suggest that the region of potential N limitation may have been larger in the 1960s than in the 1970s, and that P limitation was widespread in winter and spring in the balance of the Bay.

Contemporary nutrient data have been discussed elsewhere in the context of seasonal shifts in the nutrient that limits phytoplankton abundance (Fisher et al. 1992, Conley & Malone 1992). It has been argued from the distributions of macronutrients, molar ratios, enrichment studies, and uptake rates that P and Si limit phytoplankton biomass in spring, while N is limiting in summer (Fisher et al. 1992). The data presented here are consistent with those conclusions. DIN was abundant in much of the estuary in winter and spring, with the exception of the lower, polyhaline Bay where concentrations were low (Fig. 15). SiO_4^{3-} was depleted in the mesohaline, with the position of the Si minimum showing interannual variability (Fig. 17). $\text{DIN}:\text{PO}_4^{3-}$ was well above Redfield's ratio from winter through spring in much of the Bay, with the exception of the lower polyhaline (Regions I & II) where N was probably limiting. In contrast, low DIN occurs in much of the Bay in summer (Fig. 15), and $\text{DIN}:\text{PO}_4^{3-}$ is generally below Redfield's ratio (Fig. 18).

The distribution of light attenuation coefficients is also directly linked to flow from the Susquehanna River (Schubel 1968, Schubel & Pritchard 1986), and phytoplankton growth in the upper, oligohaline Bay is largely light limited (Harding et al. 1986). Combining data on nutrient availability in the mesohaline to polyhaline Bay with data on light availability in the mesohaline to oligohaline regions should allow us to explain the position of the winter-spring bloom for a given year. For example, the low flow preceding the usual February to May period of the phytoplankton bloom generated light conditions favorable to a landward position of the bloom in 1989. At the same time, nutrient availability was low enough to preclude the development of high phytoplankton biomass. Consequently, a discrete chlorophyll maximum was essentially absent, as is apparent in Figs. 5g & 6g. In contrast, freshwater flow in 1987 was near or slightly below average and the position of high chlorophyll concen-

trations at the landward limit of the bloom met the criteria of Wofsy's model, i.e. highest chlorophyll concentrations occurred throughout the region of the Bay where 4 to 8 optical depths occurred in the surface mixed layer. At the seaward limit, ratios of nutrient concentrations, particularly $\text{SiO}_4^{3-}:\text{PO}_4^{3-}$, approached and fell below Redfield ratios over the course of spring (Figs. 18 & 19), coinciding spatially with the accumulation of phytoplankton biomass (see also D'Elia et al. 1983, 1986, Conley & Malone 1992). In 1991, the landward position of the chlorophyll maximum was regulated by light availability, and the seaward extent of the bloom was limited by nutrient availability, particularly Si (Harding et al. 1993).

Conclusion

The relationship of freshwater flow from the Susquehanna River to the accumulation of phytoplankton biomass in the Chesapeake Bay is complex, and it is difficult to separate variability from trends. Additional research on the timing, position and magnitude of the winter-spring bloom in the Chesapeake Bay needs to focus on the extent to which nutrient inputs in excess of those needed to produce annual biomass maxima in winter-spring accompany specific flow conditions. Improved understanding in this area could make it possible to gauge the extent of improvements in Bay water quality that are likely to occur in the coming decade as reductions in nutrient inputs are realized by management efforts. A further study of the historical and recent data on the distribution and abundance of phytoplankton in the Chesapeake Bay will address this need in hopes of generating a conceptual model of flow, nutrient, light and phytoplankton relations and of specifying trends in phytoplankton abundance from the 1950s to the present.

Acknowledgements. The contributions of L. Bahner, M. Culver, D. Jacobs, J. Macknis, M. Olson, J. Posey and K. Sellner to this work are gratefully acknowledged. I thank D. Conley, C. D'Elia, T. Fisher, D. Jacobs, M. Leffler, G. Mackiernan and T. Malone and 2 anonymous referees for critically reviewing the manuscript. Support was obtained from NSF Grant OCE-8310407, Maryland Sea Grant NA86AA-D-SG006, NA90AA-D-SG063, NOAA Grant NA16RGO362-01 and the NASA Summer Faculty Fellowship Program.

LITERATURE CITED

- Boynton, W. R., Kemp, W. M. (1985). Nutrient regeneration and oxygen consumption by sediments along an estuarine salinity gradient. *Mar. Ecol. Prog. Ser.* 23: 45-55
- Boynton, W., Kemp, M., Barnes, J., Cowan, J., Stammerjohn, S., Matteson, L., Rohland, F. (1991). Long-term character-

- istics and trends of benthic nutrient fluxes in the Maryland portion of the Chesapeake Bay. In: Mihursky, J., Chaney, A. (eds.) *New perspectives in the Chesapeake system: a research and management partnership*. Proc. 2nd Chesapeake Bay Research Conference, Baltimore, Maryland, 4-6 Dec. 1990. Chesapeake Research Consortium Publ. No. 137, Solomons, MD, p. 339-354
- Boynton, W. R., Kemp, W. M., Keefe, C. W. (1982). A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In: Kennedy, V. S. (ed.) *Estuarine comparisons*. Academic Press, New York, p. 69-90
- Brush, G. S., Davis, F. W. (1982). Stratigraphic evidence of human disturbance in an estuary. *Quaternary Res.* 22: 91-108
- Cloern, J. E., Alpine, A. E., Cole, B. E., Wong, R. L. J., Arthur, J. F., Ball, M. D. (1983). River discharge controls phytoplankton dynamics in the northern San Francisco Bay estuary. *Estuar. coast. Shelf Sci.* 16: 415-429
- Cloern, J. E., Cheng, R. T. (1981). Simulation model of *Skeletonema costatum* population dynamics in northern San Francisco Bay, California. *Estuar. coast. Shelf Sci.* 12: 83-100
- Coats, D. W., Harding, L. W. Jr (1988). Effect of light history on the ultrastructure and physiology of *Prorocentrum mariae-lebouriae* (Dinophyceae). *J. Phycol.* 24: 67-77
- Conley, D. J., Malone, T. C. (1992). The annual cycle of dissolved silicate in Chesapeake Bay: implications for the production and fate of phytoplankton biomass. *Mar. Ecol. Prog. Ser.* 81: 121-128
- Conomos, T. J., Peterson, D. H. (1977). Suspended particle transport and circulation in San Francisco Bay: an overview. In: Wiley, M. (ed.) *Estuarine processes*. Academic Press, New York, p. 82-97
- Cooper, W. R., Brush, G. S. (1991). Long-term history of Chesapeake Bay anoxia. *Science* 254: 992-996
- Cowles, R. (1930). A biological study of the offshore waters of Chesapeake Bay. *Bull. Bur. Fish., Wash.* 46: 277-381
- D'Elia, C. F., Nelson, D. M., Boynton, W. R. (1983). Chesapeake Bay nutrient and plankton dynamics. III. The annual cycle of dissolved silicon. *Geochim. Cosmochim. Acta* 47: 1945-1955
- D'Elia, C. F., Sanders, J. G., Boynton, W. R. (1986). Nutrient enrichment studies in a coastal plain estuary: phytoplankton growth in large-scale, continuous cultures. *Can. J. Fish. Aquat. Sci.* 43: 397-406
- Festa, J. F., Hansen, D. V. (1976). A two-dimensional numerical model of estuarine circulation: the effects of altering depth and river discharge. *Estuar. coast. mar. Sci.* 4: 309-323
- Festa, J. F., Hansen, D. V. (1978). Turbidity maxima in partially mixed estuaries. *Estuar. coast. mar. Sci.* 7: 347-359
- Fisher, T. R., Harding, L. W. Jr, Stanley, D. W., Ward, L. G. (1988). Phytoplankton, nutrients and turbidity in the Chesapeake, Delaware and Hudson estuaries. *Estuar. coast. Shelf Sci.* 27: 61-93
- Fisher, T. R., Peele, E. R., Ammerman, J. W., Harding, L. W. Jr (1992). Nutrient limitation of phytoplankton in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 82: 51-63
- Harding, L. W. Jr, Coats, D. W. (1988). Photosynthetic physiology of the dinoflagellate, *Prorocentrum mariae-lebouriae*, during its subpycnocline transport in Chesapeake Bay. *J. Phycol.* 24: 77-89
- Harding, L. W. Jr, Itsweire, E. C. (1991). Synoptic measurements of the distribution of chlorophyll in the Chesapeake Bay using aircraft remote sensing. In: Mihursky, J., Chaney, A. (eds.) *New perspectives in the Chesapeake System: a research and management partnership*. Proc. 2nd Chesapeake Bay Research Conference, Baltimore, Maryland, 4-6 Dec. 1990. Chesapeake Research Consortium Publ. No. 137, Solomons, MD, p. 147-160
- Harding, L. W. Jr, Itsweire, E. C., Esaias, W. E. (1992a). Determination of phytoplankton chlorophyll concentrations in the Chesapeake Bay with aircraft remote sensing. *Remote Sens. Environ.* 40: 79-100
- Harding, L. W. Jr, Itsweire, E. C., Esaias, W. E. (1993). Estimates of phytoplankton biomass in the Chesapeake Bay from aircraft remote sensing of chlorophyll concentrations, 1989-92. *Remote Sens. Environ.* (in press)
- Harding, L. W. Jr, Leffler, M., Mackiernan, G. B. (1992b). Dissolved oxygen in the Chesapeake Bay: a scientific consensus. Maryland Sea Grant College, Publication No. UMSG-TS-92-03
- Harding, L. W. Jr, Meeson, B. W., Fisher, T. R. (1986). Phytoplankton production in two East Coast estuaries: photosynthesis-light functions and patterns of carbon assimilation in Chesapeake and Delaware Bays. *Estuar. coast. Shelf Sci.* 23: 773-806
- Itsweire, E. C., Harding, L. W. Jr, Bahner, L. H. (1991). Comparison of phytoplankton biomass estimates for the Chesapeake Bay using aircraft remote sensing and *in situ* chlorophyll data. In: Mihursky, J., Chaney, A. (eds.) *New perspectives in the Chesapeake system: a research and management partnership*. Proc. 2nd Chesapeake Bay Research Conference, Baltimore, Maryland, 4-6 Dec. 1990. Chesapeake Research Consortium Publ. No. 137, Solomons, MD, p. 161-168
- Kemp, W. M., Boynton, W. R. (1984). Spatial and temporal coupling of nutrient inputs to estuarine production: the role of particulate transport and decomposition. *Bull. mar. Sci.* 35: 242-247
- Malone, T. C. (1977). Environmental regulation of phytoplankton productivity in the lower Hudson estuary. *Estuar. coast. mar. Sci.* 5: 157-171
- Malone, T. C. (1992). Effects of water column processes on dissolved oxygen: nutrients, phytoplankton and zooplankton. In: Smith, D., Leffler, M., Mackiernan, G. (eds.) *Oxygen dynamics in Chesapeake Bay: a synthesis of research*. Maryland Sea Grant, College Park, MD, p. 61-112
- Malone, T. C., Chervin, M. (1979). The production and fate of phytoplankton size fractions in the plume of the Hudson River, New York Bight. *Limnol. Oceanogr.* 24: 683-696
- Malone, T. C., Crocker, L. H., Pike, S. E., Wendler, B. W. (1988). Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. *Mar. Ecol. Prog. Ser.* 48: 235-249
- Malone, T. C., Ducklow, H. W., Peele, E. R., Pike, S. E. (1991). Picoplankton carbon flux in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 78: 11-22
- Malone, T. C., Kemp, W. M., Ducklow, H. W., Boynton, W. R., Tuttle, J. H., Jonas, R. B. (1986). Lateral variation in the production and fate of phytoplankton in a partially stratified estuary. *Mar. Ecol. Prog. Ser.* 32: 149-160
- Malone, T. C., Neale, P. J., Boardman, D. (1980). Influence of estuarine circulation on the distribution and biomass of phytoplankton size fractions. In: Kennedy, V. S. (ed.) *Estuarine perspectives*. Academic Press, New York, p. 249-262
- Marshall, H. G., Lacouture, R. V. (1986). Seasonal patterns of growth and composition of phytoplankton in the lower Chesapeake Bay and vicinity. *Estuar. coast. Shelf Sci.* 23: 115-130
- McCarthy, J. J., Taylor, W. R., Loftus, M. E. (1974). Significance of nanoplankton in the Chesapeake Bay estuary

- and problems associated with the measurement of nanoplankton productivity. *Mar. Biol.* 24: 7–16
- Morse, D. C. (1947). Some observations on seasonal variations in plankton population Patuxent River, Maryland 1943–1945. Chesapeake Biol. Lab., Solomons Island, MD, Publ. No. 65
- Mulford, R. A. (1972). An annual plankton cycle on the Chesapeake Bay in the vicinity of Calvert Cliffs, Maryland June 1969 – May 1970. *Proc. Acad. natl. Sci. Phila.* 124: 17–40
- Officer, C. B., Biggs, R. B., Taft, J. L., Cronin, L. E., Tyler, M. A., Boynton, W. R. (1984). Chesapeake Bay anoxia: origin, development, and significance. *Science* 223: 22–27
- Patten, B. C., Mulford, R. A., Warinner, J. E. (1963). An annual phytoplankton cycle in the lower Chesapeake Bay. *Chesapeake Sci.* 4: 1–20
- Pennock, J. R. (1985). Chlorophyll distributions in the Delaware estuary: regulation by light-limitation. *Estuar. coast. Shelf Sci.* 21: 711–725
- Pennock, J. R., Sharp, J. H. (1986). Phytoplankton production in the Delaware estuary: temporal and spatial variability. *Mar. Ecol. Prog. Ser.* 34: 143–155
- Peterson, D. H., Conomos, T. J., Broenkow, W. W., Doherty, P. C. (1975). Location of the non-tidal current null zone in northern San Francisco Bay. *Estuar. coast. mar. Sci.* 3: 1–11
- SAS Institute, Inc. (1990). SAS/STAT user's guide, Version 6, 4th edn, Vol. 2. Cary, NC
- Schubel, J. R. (1968). Turbidity maximum of the northern Chesapeake Bay. *Science* 161: 1013–1015
- Schubel, J. R., Pritchard, D. W. (1986). Responses of upper Chesapeake Bay to variations in discharge of the Susquehanna River. *Estuaries* 9: 236–249
- Seliger, H. H., Boggs, J. A., Biggley, W. H. (1985). Catastrophic anoxia in the Chesapeake Bay in 1984. *Science* 228: 70–73
- Sellner, K. G., Kachur, M. E. (1987). Phytoplankton: relationships between phytoplankton, nutrients, oxygen flux and secondary producers. In: Heck, K. L. Jr (ed.) *Ecological studies in the middle reach of Chesapeake Bay: Calvert Cliffs. Lecture notes on coastal and estuarine studies.* Springer-Verlag, New York, p. 12–37
- Sharp, J. H., Culberson, C. H., Church, T. M. (1982). The chemistry of the Delaware estuary. General considerations. *Limnol. Oceanogr.* 27: 1015–1028
- Sharp, J. H., Cifuentes, L. A., Coffin, R. B., Pennock, J. R., Wong, K.-C. (1986). The influence of river variability on the circulation, chemistry, and microbiology of the Delaware estuary. *Estuaries* 9: 261–269
- Strickland, J. D. H., Parsons, T. R. (1968). A practical handbook of seawater analysis. *Bull. Fish. Res. Bd Can.* 167: 1–311
- Technicon Industrial Systems (1977). Silicates in water and seawater. Industrial Method No. 186-72W/B. Technicon Industrial Systems, Tarrytown, NY
- Tuttle, J. H., Jonas, R. B., Malone, T. C. (1987). Origin, development and significance of Chesapeake Bay anoxia. In: Majumdar, S. K., Hall, L. W. Jr, Austin, H. M. (eds.) *Contaminant problems and management of living Chesapeake Bay resources.* Pennsylvania Academy of Sciences, Philadelphia, p. 442–472
- U.S. EPA. (1983). Chesapeake Bay: a profile of environmental change. United States Environmental Protection Agency, Washington, DC
- U.S. EPA. (1992). Recommended guidelines for sampling and analyses in the Chesapeake Bay Monitoring Program. United States Environmental Protection Agency, Region III, Chesapeake Bay Program Office, Annapolis, MD (draft, November 1992)
- Van Valkenburg, S. D., Flemer, D. A. (1974). The distribution and productivity of nanoplankton in a temperate estuarine area. *Estuar. coast. mar. Sci.* 2: 311–322
- Verity, P. G. (1988). The trophic structure of pelagic communities: hypotheses and problems. In: Lynch, M. P., Krome, E. C. (eds.) *Understanding the estuary: advances in Chesapeake Bay research.* Chesapeake Research Consortium Publ. No. 129, Baltimore, p. 49–54
- Wofsy, S. C. (1983). A simple model to predict extinction coefficients and phytoplankton biomass in eutrophic waters. *Limnol. Oceanogr.* 28: 1144–1155
- Wolfe, J. J., Cunningham, B., Wilkerson, N. F., Barnes, J. T. (1926). An investigation of the microplankton of Chesapeake Bay. *J. Elisha Mitchell Sci. Soc.* 42: 25–54

This article was presented by D. K. Stoecker, Cambridge, Maryland, USA

Manuscript first received: June 17, 1993

Revised version accepted: November 15, 1993