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Bacterioplankton and Organic Carbon Dynamics in the Lower Mesohaline Chesapeake Bay†

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The mesohaline portion of the Chesapeake Bay is subject to annual summertime hypoxia and anoxia in waters beneath the pycnocline. This dissolved oxygen deficit is directly related to salinity-based stratification of the water column in combination with high levels of autochthonously produced organic matter and a very high abundance of metabolically active bacteria. Throughout the water column in the lower, mesohaline part of the bay, between the Potomac and Rappahannock rivers, near the southern limit of the mainstem anoxia, bacterial abundance often exceeded 10×10^6 cells per ml and bacterial production exceeded 7×10^9 cells per liter per day during summer. Bacterial biomass averaged 34% (range, 16 to 126%) of the phytoplankton biomass in summer. These values are equal to or greater than those found farther north in the bay, where the oxygen deficit is more severe. Seasonal variations in bacterial abundance and production were correlated with phytoplankton biomass (lag time, 7 to 14 days), particulate organic carbon and nitrogen, and particulate biochemical oxygen demand in spring; but during summer, they were significantly correlated only with dissolved biochemical oxygen demand. During summer, dissolved biochemical oxygen demand can account for 50 to 60% of the total biochemical oxygen demand throughout the water column and 80% in the bottom waters. There is a clear spring-summer seasonal shift in the production of organic matter and in the coupling of bacteria and autochthonous organic matter. The measurement of dissolved, microbially labile organic matter concentrations is crucial in understanding the trophic dynamics of the lower mesohaline part of the bay. The absolute levels of organic matter in the water column and the bacterial-organic carbon relationships suggest that a lower bay source of organic matter fuels the upper mesohaline bay oxygen deficits.

Since about 1980 the environmental problems of the Chesapeake Bay have received increasing attention from scientists, managers, regulatory agencies, and the public. The seasonal, deep-water oxygen deficits which occur annually in the mesohaline portion of the mainstem Chesapeake Bay, from north of the Annapolis Bay Bridge to south of the Rappahannock River, are considered to be among the most serious threats to the integrity and productivity of the Chesapeake Bay (14, 18, 21, 25, 27, 29). In the most general sense, oxygen depletion in the bottom waters of the Chesapeake Bay is linked both to the natural salinity-based stratification of the water column (18, 25) and, anthropogenically, to cultural eutrophication of the bay (14, 25, 29). Although hypoxia and anoxia in the Chesapeake Bay were observed long ago (17, 20), it is generally believed that low oxygen conditions severe enough to threaten the living resources of the bay now occur over a larger geographic area, persist longer in time, and are more severe in the affected portions of the water column than they were in the early decades of the twentieth century (25, 29; D. G. Cargo, J. H. Tuttle, and R. B. Jonas, Spring meeting of the Atlantic Estuarine Research Society, Lewes, Del., 1986).

One main objective of the environmental management community concerned with the problems of the Chesapeake Bay has been to develop strategies for alleviating this oxygen problem. To elucidate the factors that drive oxygen depletion, we conducted a multiyear investigation by synoptically measuring microheterotrophic parameters as well as the more commonly measured physicochemical and phytoplankton parameters. A main hypothesis of the investigation was that bacterioplankton are the biological agents that are responsible for most of the oxygen consumption (25–27) and that assessment of their distributions and activities is necessary to understand oxygen dynamics in the bay.

We focus here on those factors that influenced oxygen consumption during March through August 1987 in a geographical area near the southern limits of anoxia in the Chesapeake Bay. Anoxia in this region occurs only transiently during the summer. We chose this area to determine whether patterns of biological variation and bacteria-organic carbon relationships differed from those of the more northerly portions of the mesohaline part of the bay (hereafter referred to as the upper bay), where anoxia is perceived to be more severe (25, 27). Our specific objectives were to assess the distribution of bacterial abundance and production, biochemical oxygen demand (BOD), and the more commonly monitored bulk water organic components (including chlorophyll and particulate organic carbon and nitrogen) and to determine whether bacterial abundance, production, or both are linked to BOD or to the other more traditionally measured water quality parameters. If the latter are not closely linked with the forcing functions involved directly in oxygen demand, then models based on such parameters are necessarily unrealistic and are unlikely to be reliable predictors of dissolved oxygen responses to various cleanup technologies.

MATERIALS AND METHODS

Sample collection and hydrographic parameters. Samples were collected at six sites located along a transect (GWR)

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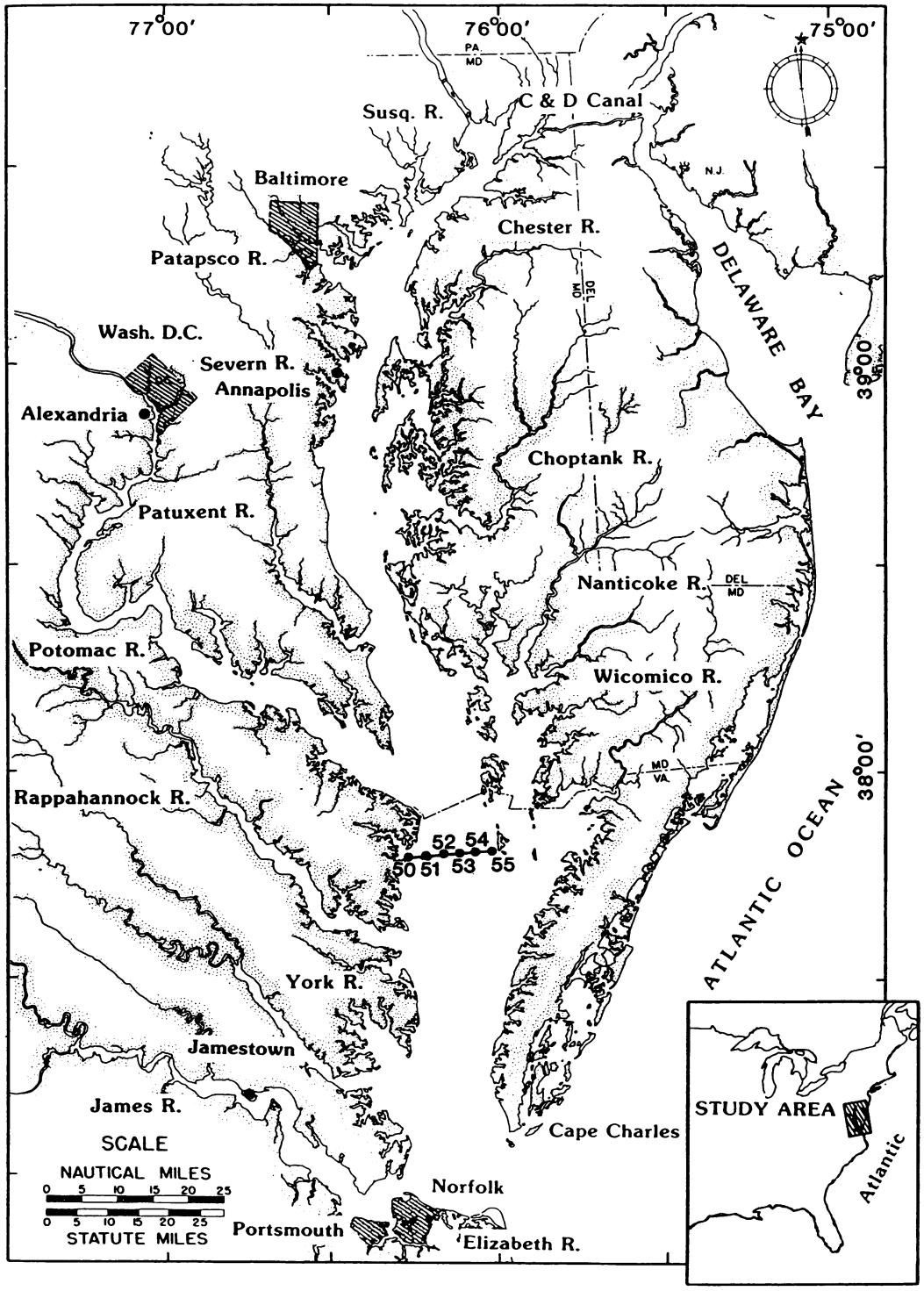

FIG. 1. Locations of sample stations along the GWR transect in the lower, mesohaline portion of the Chesapeake Bay.

perpendicular to the mainstem of the bay at about 37°50′ N latitude (off the Great Wycomico River [GWR], Virginia) (Fig. 1). A central station (station 53) was located in the deepest (ca. 33 m) portion of the mainstem channel, and the remaining sites were arrayed across the bay to provide representative samples from the entire breadth of the mainstem influenced by salinity stratification. Samples were obtained from each site 12 times during the spring and summer of 1987. All cruises were conducted aboard either the RV *Aqarius* or RV *Orion*. Water samples were collected from various depths with a submersible pump and hose system attached to a metered hydrographic cable. At each station, we established vertical profiles of temperature, salinity, and salinity-corrected dissolved oxygen with a

resolution of 2 m, using a salinometer (model 33; Yellow Springs Instrument Co., Yellow Springs, Ohio) and a digital oxygen meter (model 57; Yellow Springs Instrument Co.). The oxygen meter was calibrated in atmospheric air, and the calibration was checked at each station. Very low oxygen values and anoxia were confirmed either by Winkler titration or by the presence of hydrogen sulfide in the water.

Except where noted, we collected samples 1 m below the surface and 1 m above the bottom at all stations. At station 50, which was only 4 m deep and usually well mixed, samples were taken from only 1 m below the surface. At stations 52 and 54, a third sample was collected from the empirically determined pycnocline depth. At station 53, samples were collected from six additional depths. These were arrayed from the bottom of the upper mixed layer, through the pycnocline, and into the high-salinity deep layer. These intermediate depths were selected in relation to the empirically determined local stratification and light penetration regimes. This design was based on our observation that, in the mesohaline portion of the bay, euphotic zone and pycnocline depths vary significantly over short time scales.

All samples, except those for bacterial production measurements, were collected directly from the pump and hose system in polypropylene bottles which were rinsed three times with sample water. Bacterial production samples were collected in 10-ml, acid-washed, all-polyethylene and polypropylene syringes from a 10-liter polyethylene container which was continuously flushed with water from the pump and hose system. This procedure provided composite samples at ambient dissolved oxygen concentrations (DO) for estimation of in situ bacterial production (9). Samples were either processed aboard the research vessel immediately after collection or preserved for later analysis.

Bacterial analyses. Samples to be used for bacterial abundance determinations were preserved with a final concentration of 2%, particle-free formaldehyde and refrigerated at 4°C in the dark. Bacterial abundance was determined by direct microscopic observation of acridine orange-stained bacteria under epifluorescence illumination (5, 7). Appropriate volumes of preserved samples were mixed with sufficient particle-free bay water to yield a final volume of 2 ml. After staining with particle-free acridine orange, bacteria were collected on 0.2-μm-pore-size black polycarbonate filters (Nuclepore Corp., Pleasanton, Calif.) and observed under ×1,600 total magnification. Five fields, each containing 100 to 200 cells distributed over the surface of the filter, were counted. The mean count was used to calculate total bacterial abundance. If the standard deviation of the five counts exceeded about 10% of the mean, five additional fields were counted and all 10 values were used to calculate the mean.

Bacterial production was estimated by using tritiated methyl thymidine by the method of Jonas et al. (9). For each sample, triplicate, 10-ml live subsamples and one poisoned control, which was treated with 100 μl of 1.2 N H_2SO_4, were inoculated with 50 μl of tritiated methyl thymidine (final concentration, 5 nM; product 24060; ICN Corp.). The syringes were inoculated without introducing air and incubated in the dark at the in situ temperature for 0.5 or 1.0 h, depending on the incorporation rate. Particle-associated radiolabel was collected on 0.2-μm-pore-size filters (GA8-S; Gelman Sciences, Inc., Ann Arbor, Mich.) under vacuum and washed with 4.0 ml of 5%, ice-cold trichloroacetic acid. Cold trichloroacetic acid-insoluble radioactivity was assayed by using a scintillation counter (model 4430 or 4530; Packard Instrument Co., Inc., Rockville, Md.) operated in the DPM mode. There is considerable uncertainty regarding the conversion of thymidine incorporation rates to bacterial production rates (10, 11, 14, 15, 19, 23, 27). For purposes of comparison with previous data, we used a conversion factor of 2×10^{18} cells per mol of thymidine incorporated.

Organic matter measurement. BOD and dissolved (filtered) BOD (FBOD) were determined from changes in oxygen concentration in samples that were incubated in the dark at 20°C for 5 days (6, 8). Samples were aerated by vigorous shaking immediately after collection to achieve approximate oxygen saturation. Subsamples were transferred, in triplicate, to acid-washed, sample-rinsed, 145-ml ground glass-stoppered bottles. Two bottles were stoppered to exclude air bubbles and placed in light-tight stainless steel cylinders which were held in light-tight insulated containers. The third bottle was used for determining initial oxygen concentrations with a stirring dissolved oxygen probe (Yellow Springs Instrument Co.). When ambient water temperatures were less than 12°C, samples were warmed to about 20°C before aeration to avoid outgassing because of oxygen supersaturation. To maximize the accuracy of determining oxygen concentrations, the oxygen probe was calibrated in water-saturated air immediately before samples from each station were processed.

FBOD was determined identically, except that, before aeration, the sample was filtered (ca. 5 in. Hg) through a glass fiber filter (type A/E; Gelman Sciences, Inc.) that was previously rinsed with 100 ml of sample water. Although this procedure likely removed some portion of the microheterotroph community, most bacteria in mesohaline Chesapeake Bay water are free-living and smaller than 0.5 to 1.0 μm (25); and sufficient bacteria remained so that the addition of a microbial inoculum was unnecessary.

We present BOD data derived from the 5-day incubations without conversion to the "ultimate BOD." Although it is standard practice to assume that the 5-day BOD represents about 67% of the ultimate BOD, this assumption has not been verified with Chesapeake Bay samples. Therefore, our BOD values represent minimum estimates of the amount of microbially labile organic matter present in this system. Inorganic oxygen demand from reduced sulfur and nitrogen compounds could influence BOD estimates, but the measured concentrations of these compounds (principally hydrogen sulfide and ammonium) were low and unlikely to influence the BOD estimates significantly.

Chlorophyll *a* (Chl) and phaeopigment concentrations were determined with a fluorometer (Turner Designs). Samples of 50 to 100 ml were filtered through glass filters (5 in. Hg; GF/F; Whatman, Inc., Clifton, N.J.), and the filters were sealed in light-tight aluminum foil packets and frozen at −15°C. Pigments were extracted by grinding the samples in a 3:2 mixture of 90% acetone and dimethyl sulfoxide and by holding them at 4°C in the dark for 24 h. Particulate matter in the extracts was removed by centrifugation, and fluorescence was measured before and after acidification with 1 N HCl.

Samples (50 to 150 ml) to be used for particulate organic carbon (POC) and particulate organic nitrogen (PON) determinations were filtered through glass fiber filters (GF/F; Whatman, Inc.), which were previously combusted at 450°C for 4 h. The filters were stored in combusted aluminum foil packets which were immediately frozen at −15°C. POC and PON on thawed filters were determined by combustion and elemental analysis with an elemental analyzer (model 240B; The Perkin-Elmer Corp., Norwalk, Conn.).

Data presentation. The presentation of seasonal hydrographic and biological data from a cross-bay transect is a

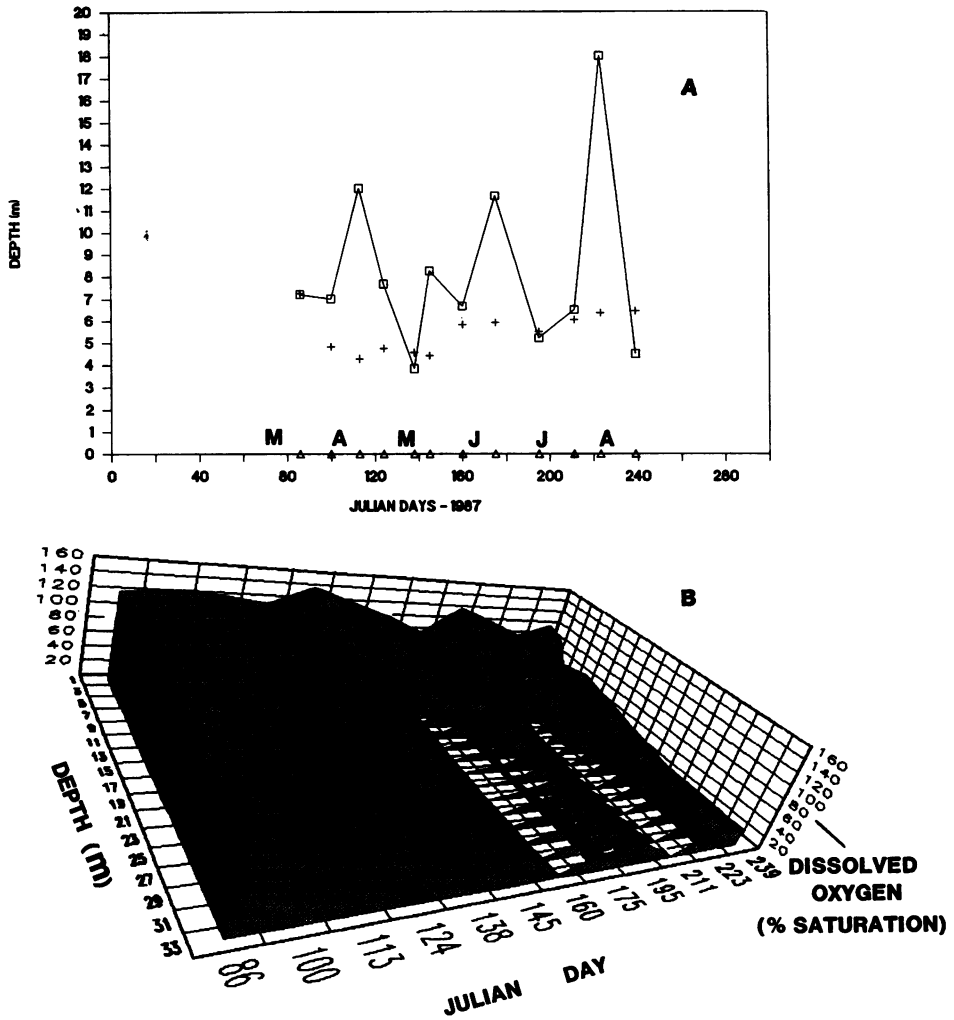

FIG. 2. (A) Seasonal distribution of mean euphotic zone (+) and pycnocline (□) depths at the GWR transect during 1987. Sampling dates are indicated (△). (B) Seasonal variation in the vertical distribution of DO at station 53. Each time point represents a sampling cruise. The time axis is not scaled.

significant challenge because of the importance of depth integration in accurately describing the distributions of the various parameters. Based on the permanent salinity-related density discontinuity in the mesohaline portion of the Chesapeake Bay and the shallow euphotic zone caused by biogenic turbidity, we divided the vertical water column into three depth zones: the euphotic zone (2.7 times the Secchi depth), below the euphotic zone to the bottom of the pycnocline, and below the pycnocline. Each datum point in Fig. 2 through 6 represents the mean of depth-integrated values within a zone for each measured parameter from all six stations. Such depth-integrated transect means were used to more accurately evaluate the associations among pools of organic matter and the potential consumers in the water column.

RESULTS

Hydrographic relationships. The mean euphotic zone depth along the GWR transect had a depth range from about 7 m in early spring to 4 m in late spring and then deepened to about 6 m during the remainder of the summer (Fig. 2A). This pattern reflects spring phytoplankton blooms (see Fig. 5A), which reduced water clarity. In contrast to the relatively stable euphotic zone depth, the mean pycnocline (maximum rate of change in density based primarily on the salinity gradient) depth varied widely with no obvious seasonal pattern (Fig. 2A). The pycnocline was usually below the euphotic zone, but occasionally it was sufficiently shallow to penetrate into it.

During late winter and early spring, in the southern mesohaline region, surface water DO were near saturation but declined slightly beneath the pycnocline (Fig. 2B; note that there is no scale on the time axis). Beneath the pycnocline, the DO began to decline significantly in late April and May, reaching values as low as 20% saturation by mid-May. A slight recovery in deep-water DO in late May was followed by a precipitous decline, leading to a sustained period of very low DO from early June to late August. Bottom-water DO increased in conjunction with several strong wind events which affected the region near the end of August. Anoxia developed in the water column below 13 m in late July (Julian calendar day 211) but did not persist. By mid-August, even the deepest water (33 m) contained substantial (20%

saturation) DO. In contrast, the subpycnoclinal waters at a 20-m-deep station about 50 km to the north remained anoxic and sulfidic from June through mid-August (data not shown).

The association between density stratification and deep-water hypoxia at station 53 was particularly evident during the highly stratified period from June to August. Generally, DO declined with increasing depth beneath the pycnocline, but it was not uncommon to find midwater DO minima (e.g., Fig. 2B; Julian calendar day 175). Such minima may be associated with high rates of respiration in the midwater depths but may also result from northward advection of more highly oxygenated water along the bottom of the bay. During this particular incident, the increased salinity of the subpycnoclinal water (data not shown) near the bottom suggests that advective processes may have caused the DO distribution.

Bacterial distributions. Mean bacterial abundances ranged from about 2×10^6 cells per ml in spring to 16×10^6 cells per ml in summer (Fig. 3A). Bacteria were uniformly distributed with depth during late winter and well into the spring. As late as mid-May there was no significant difference in mean bacterial abundance throughout the water column, despite shifting DO (Fig. 2B) and organic carbon (Fig. 4 through 6) regimes. Abundance increased during early spring and then declined slightly and remained relatively constant until June. During the summer season there were two peaks in bacterial abundance. The first occurred in June, when bacterial abundance throughout the water column increased markedly and subpycnocline bacterial abundances exceeded those in the euphotic zone. Following a precipitous decline in subpycnocline and midwater bacterial abundances, a second peak occurred in late July. The highest abundances occurred in the euphotic zone during this period, but subpycnocline and bottom-water bacterial abundances tracked the surface water bacterial abundances rather closely.

Bacterial production (Fig. 3B) was also uniformly distributed throughout the water column during the late winter and early spring. Production increased slightly from March to May. Euphotic zone and midwater bacterial production continued to increase during May and June, reached a maximum in late June, and then declined and stabilized at about 5×10^9 to 7×10^9 cells per liter per hour.

Although the highest measured bacterial production rates occurred in the euphotic zone, bacterial production in the subpycnoclinal waters exceeded that in the surface and midwaters in June and again in late July. Both subpycnocline bacterial production peaks were associated with increased deep-water bacterial abundance (Fig. 3A), and the June peak coincided with a seasonal maximum in subpycnocline bacterial abundance. In contrast, euphotic zone bacterial production peaks were not closely associated with bacterial abundance peaks.

Bacterial turnover rates (cell-specific growth rates) peaked during early summer. Throughout the water column they were about 0.5 per day in spring and late summer but reached maximum values of 1.0 to 1.6 per day in late June. Among the three depth zones, bacterial turnover and bacterial production were most closely associated in the euphotic zone ($r = 0.85$, $P < 0.05$), intermediately associated in the middle zone ($r = 0.70$, $P < 0.05$), and least associated in the subpycnocline zone ($r = 0.62$, $P < 0.05$).

Organic matter distribution. Mean BOD and FBOD values peaked in late spring (Fig. 4A and B). Generally, however, euphotic zone BOD was similar and FBOD was elevated in summer compared with those values in spring, whereas in

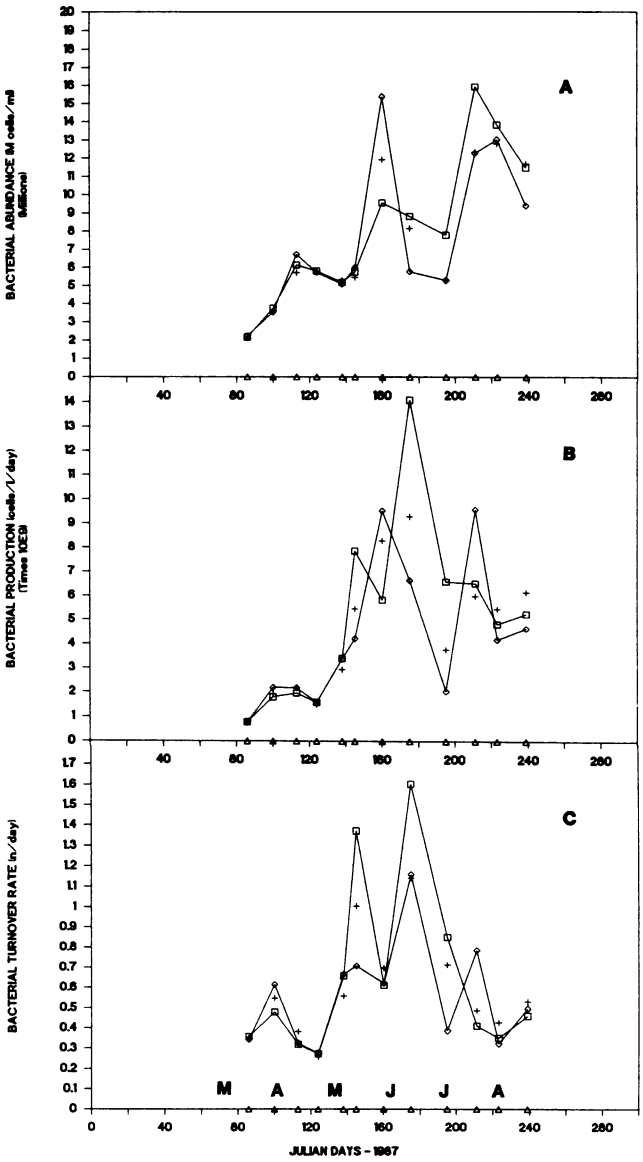

FIG. 3. Depth integrated mean bacterial abundance (A), bacterial production (B), and bacterial turnover rate (C) along the GWR transect during 1987. Symbols: □, euphotic zone; +, between euphotic zone and pycnocline depth; ◇, subpycnocline zone. Sampling dates are also indicated (△).

subpycnoclinal waters, FBOD values were about equal in spring and summer, but BOD values decreased in summer.

Similar to bacterial parameters, BOD was nearly constant throughout the water column in March, but began to diverge among the three depth zones by early April. By late April, bottom-water BOD exceeded surface and midwater values by more than 50%. This rise in bottom-water BOD was not reflected in an increase in FBOD in the deep water. During this interval, FBOD remained uniformly distributed throughout the water column. BOD and FBOD increased at all depths during mid-May and early June and then declined sharply in the mid- and bottom waters. Euphotic zone BOD, while variable, exceeded subpycnocline BOD throughout the late spring and summer. The highest FBOD occurred in late spring in mid- and subpycnoclinal waters rather than in

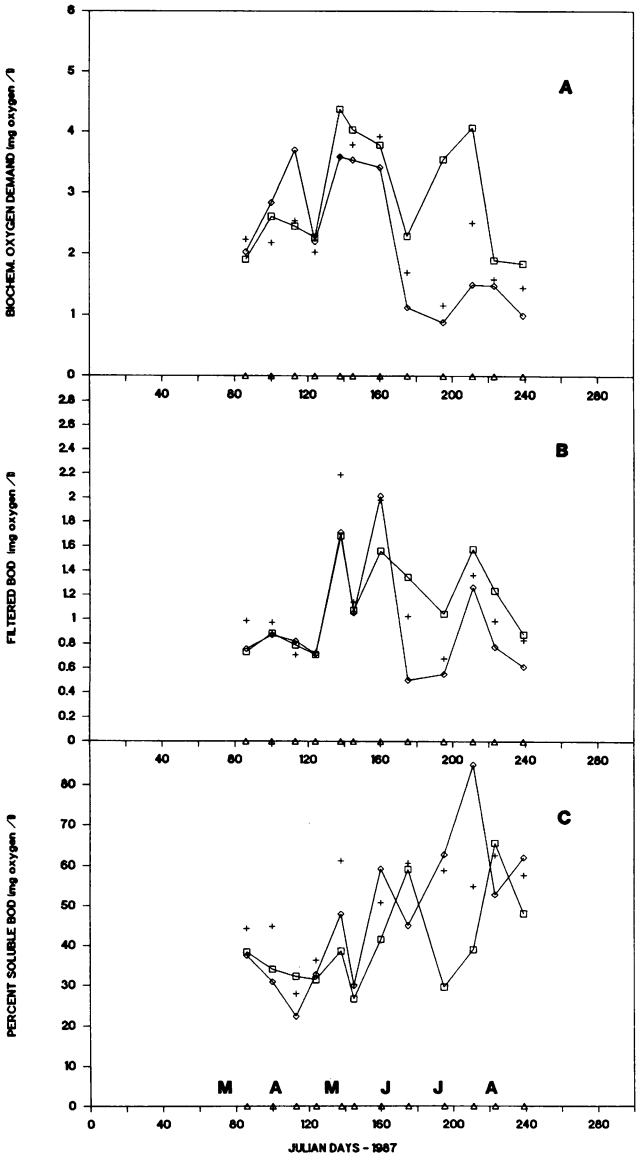

FIG. 4. Depth integrated mean BOD (A), dissolved BOD (B), and percent dissolved BOD (C) along the GWR transect during 1987. Symbols: □, euphotic zone; +, between euphotic zone and pycnocline depth; ◇, subpycnocline zone. Sampling dates are also indicated (△).

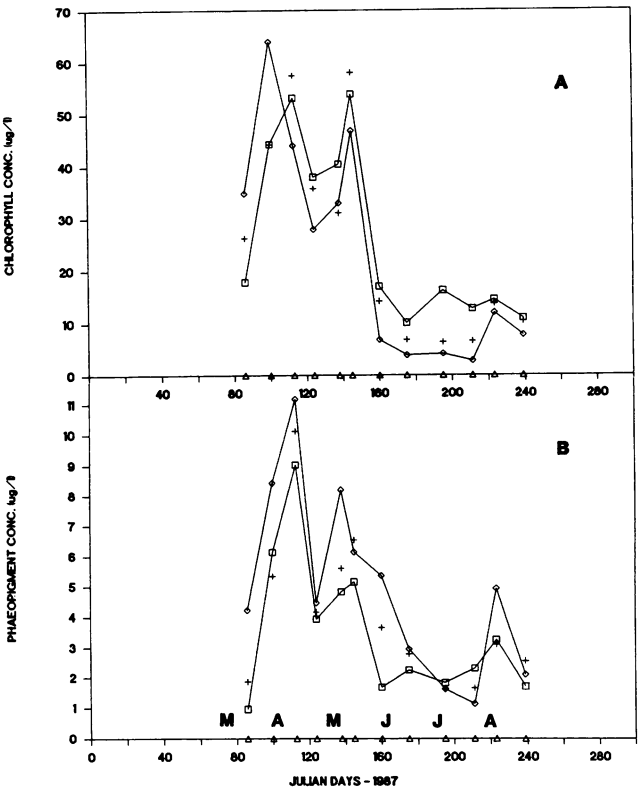

FIG. 5. Depth integrated mean Chl (A) and phaeopigment (B) concentrations along the GWR transect during 1987. Symbols: □, euphotic zone; +, between euphotic zone and pycnocline depth; ◇, subpycnocline zone. Sampling dates are also indicated (△).

the euphotic zone. During summer, subpycnocline and midwater FBOD fell below that of the euphotic zone.

FBOD increased from a mean of about 35% of the total BOD in spring to about 60% in summer (Fig. 4C). During summer, FBOD in the mid- and subpycnoclinal waters was more than 60% of the total, exceeded 85% of the total in July, and at some individual stations (data not shown) made up 95 to 100% of the BOD in the deep water. In the euphotic zone, FBOD represented a slightly smaller proportion of the total, especially in summer. Accumulations of phytoplankton in the bottom water in spring and phytoplankton blooms in surface waters during summer (Fig. 5A) reduced the proportionate importance of the dissolved fraction of BOD, even when the FBOD concentration did not change.

Two blooms dominated the spring distribution of phytoplankton in the lower mesohaline portion of the Chesapeake Bay (Fig. 5A). During the first bloom there was an inversion of Chl in the water column; i.e., bottom-water Chl concentrations exceeded surface concentrations. The highest measured concentration of Chl (>60 μg/liter) occurred in aphotic bottom water during early April. Throughout the water column, spring Chl concentrations exceeded summer values by fourfold. A precipitous decline in Chl in early June marked the transition between spring and summer periods. During summer, Chl concentrations were highest in the euphotic zone and lowest in subpycnoclinal water.

Mean phaeopigment concentrations generally tracked Chl concentrations in terms of seasonal variation (Fig. 5B). The highest concentrations were found in bottom water in spring; two spring peaks occurred, and summer values were lower than spring values. In contrast to Chl, phaeopigments were nearly always highest in the bottom water. Along the GWR transect, phaeopigment concentrations did not exceed Chl concentrations even in the bottom waters.

The highest POC and PON values occurred in spring (Fig. 6A and B). PON tracked POC closely throughout the study. Both POC and PON declined rapidly in May, although that decline was delayed slightly compared with the Chl decline. POC/PON ratios were consistently lower in bottom than in surface waters (Fig. 6C). Springtime surface water POC/PON ratios were about 9 to 10; but in late spring and summer particulate matter was somewhat nitrogen enriched, as indicated by C/N ratios which declined throughout the water column and sometimes reached a ratio of 4 or less in mid- and bottom waters.

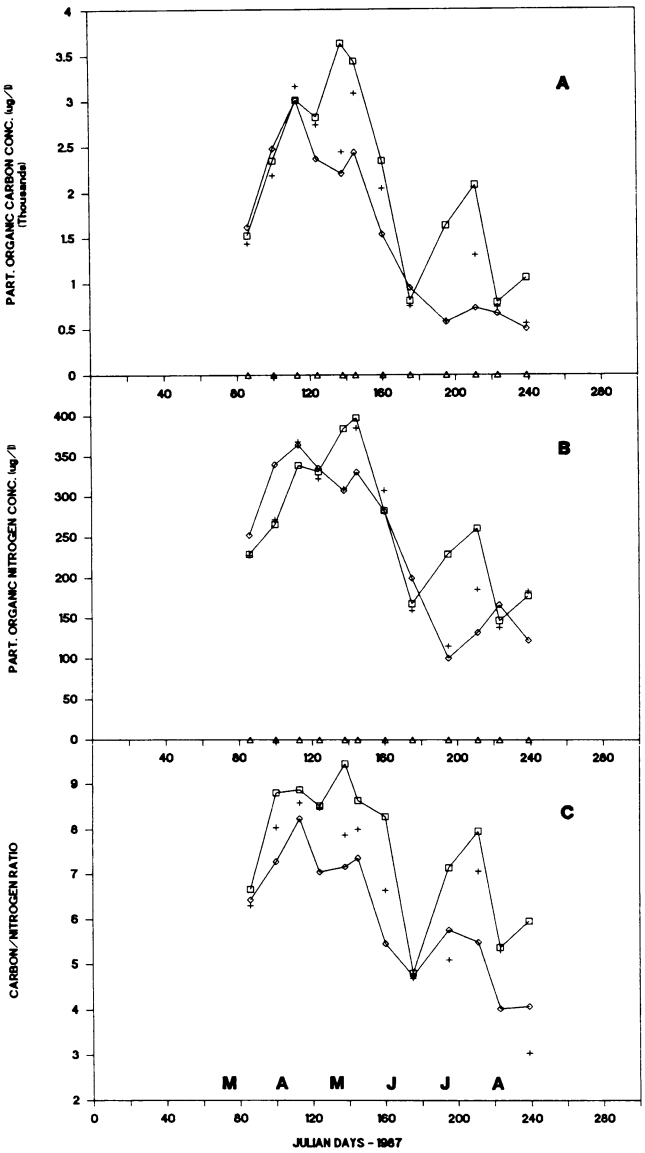

FIG. 6. Depth integrated mean POC (A), PON (B), and particulate carbon to nitrogen ratios (C) along the GWR transect during 1987. Symbols: □, euphotic zone; +, between euphotic zone and pycnocline depth; ◇, subpycnocline zone. Sampling dates are also indicated (△).

DISCUSSION

Our previous work in more northerly portions of the midbay (14, 25, 27), which usually experiences sustained seasonal deep-water anoxia, provided evidence of the key quantitative role played by bacterioplankton as consumers of organic matter and oxygen there. Those data implied that trophic changes in the mesohaline portion of the bay ecosystem occurred, such that a large portion of the primary production is metabolized by bacteria in the water column rather than by organisms higher in the food web (25, 27). In part, our purposes in this study were to assess the geographic extent of these trophic changes in the bay, specifically, in an area considered to have relatively good water quality. A comparison of bacterial and phytoplankton biomass may indicate the importance of bacteria to carbon flow in this southern mesohaline region. Assuming bacterial and phytoplankton carbon contents of 20 fg of C per cell (1, 3, 14) and 70 μg of C per μg of Chl (2, 12, 14), respectively, and considering the entire water column, bacterial carbon averaged only about 3% (range, 2 to 7%) of phytoplankton carbon in March through May, but averaged 34% (range, 16 to 126%) of phytoplankton carbon in June through August. During summer, bacterial carbon averaged 24, 30, and 47% of phytoplankton carbon in the euphotic zone, between the euphotic zone and the pycnocline, and beneath the pycnocline, respectively.

As indicators of organic constituents in the water column which could support this high level of metabolically active bacteria, we considered the Chl concentration, BOD, POC, and PON. The Chl content has been used widely as a measure of the organic carbon available to support oxygen-consuming processes (14, 25, 29). However, based on our repeated observations that nearly all of the water column bacteria in the mesohaline portion of the Chesapeake Bay are free-living rather than particle-associated (27), we suspected that dissolved organic matter derived directly or indirectly from phytoplankton was the immediate energy source for the bacteria. Because total dissolved organic carbon values would likely be dominated by refractory material, we measured total and dissolved BOD to estimate microbially labile organic matter.

Total euphotic zone BOD (Fig. 4B) varied widely throughout the study period, whereas bottom-water BOD peaked in spring and stabilized at lower values during summer. We can estimate a carbon equivalent for these BOD values by assuming a stoichiometry of 1:2 for carbon to oxygen. Thus, 4 mg of O_2 per liter is approximately equivalent to 1.5 mg of C per liter. Average carbon equivalents to BOD were 1.1 mg of C per liter in surface waters, with maximum values of >1.7 mg of C per liter. Bottom-water carbon equivalents averaged about 1.1 mg of C per liter in spring and 0.6 mg of C per liter in summer. The Potomac River, which discharges into the bay about 10 km to the north, may be an important source of plant nutrients that fuel organic matter production in this region of the bay (8).

A large fraction, 30 to 40% in spring and 50 to 60% in summer, of the total BOD was represented by microbially labile material which was functionally dissolved (Fig. 4C). This dissolved organic matter was proportionately more important in water between the euphotic zone and the pycnocline and beneath the pycnocline during summer. Occasionally, more than 80% of the available, microbially labile organic matter was in the dissolved form.

In carbon equivalents, total BOD averaged 43% of POC and 39% of phytoplankton carbon in spring and 76% of POC and 131% of phytoplankton carbon in summer. Dissolved BOD averaged only 16% of POC and 15% of phytoplankton carbon in spring, but 42% of POC and 74% of phytoplankton carbon in summer. In some cases during summer, total BOD carbon was more than 200% and dissolved BOD carbon was more than 100% of phytoplankton carbon.

Atomic ratios of suspended POC to suspended PON ranged from about 3 to 4 in bottom water during summer to >9 in surface water in spring (Fig. 6C). These values are typical of phytoplankton-derived material (24) rather than organic matter of terrestrial origin (16) or from the northern portion of the Chesapeake Bay, where C/N ratios of about 20 were found by Flemer and Biggs (4). Water column POC to Chl ratios averaged 64 during March through May and in late August and averaged 158 during June through mid-August. Assuming typical phytoplankton carbon to Chl ratios of 50 to

TABLE 1. Linear correlations between organic components in the lower mesohaline portion of the Chesapeake Bay during March to August 1987[a]

Organic component	r value											
	Particulate BOD			Dissolved BOD			POC			PON		
	March–August (all)	March–May (spring)	June–August (summer)	March–August (all)	March–May (spring)	June–August (summer)	March–August (all)	March–May (spring)	June–August (summer)	March–August (all)	March–May (spring)	June–August (summer)
Chl	0.66	0.56	0.66	0.09[b]	0.14[b]	0.35[b]	0.85	0.63	0.54	0.85	0.63	0.54
POC	0.85	0.72	0.92	0.19[b]	0.14[b]	0.74						
PON	0.85	0.79	0.85	0.23[b]	0.14[b]	0.77						

[a] Unless otherwise noted, all correlations are significant at $P < 0.05$.
[b] Not significant ($P > 0.10$); t test of Ho:slope = 0.

100 (2, 12, 14), these results suggest that in spring and later summer, particulate organic matter throughout the water column is primarily phytoplankton, whereas in midsummer it is likely nitrogen-enriched phytodetritus.

Especially during summer, neither water column Chl nor POC concentrations provided good estimates of the amount of labile organic matter available to support bacterial metabolism and oxygen consumption. Additionally, although particulate BOD was significantly correlated with Chl in spring and summer (Table 1), dissolved BOD was not. Particulate BOD was also highly correlated with POC and PON during spring and summer, but dissolved BOD was not significantly correlated with either during spring. This suggests that, especially during summer, direct measurements of either BOD or some specific dissolved organic compound(s) in the water are necessary to assess the pools of organic matter that are available to support bacterial growth and metabolism.

In that regard, neither bacterial abundance nor bacterial production was significantly correlated with the Chl concentration, POC, PON, or even particulate BOD during summer at the GWR transect (Table 2). Both bacterial parameters were, however, significantly correlated with dissolved BOD in summer. During spring, however, bacterial abundance and production were significantly correlated with several measures of particulate matter (Table 1). If we incorporated a lag time of 7 to 14 days, spring bacterial abundances were significantly correlated with the Chl concentration ($r = 0.64$, $P < 0.05$), but summer abundances were not.

Caution is necessary in these interpretations, given the sampling intervals that were used. However, those intervals were selected, based on our previous experience (14, 25, 27; unpublished data), to provide appropriate coverage during the periods of most rapid change (e.g., April and May). Both the bacterial and organic carbon data indicate that biological relationships in the March through May period differ significantly from those in the June through August period. One scenario consistent with these observations is that in the southern mesohaline portion of the bay, bacteria, although lagged in time, are rather more closely coupled with phytoplankton during spring than during summer. In summer, dissolved organic matter, which is released either directly from active or scenescent phytoplankton or from phytoplankton consumers, provides the principal link between the primary producers and the bacteria. One of the major tasks of water quality management in the Chesapeake Bay is to predict improvements in the DO regime based on inorganic nutrient removal and consequent phytoplankton reductions. In light of the observations presented here, estimates of the amount of bacterially labile dissolved organic matter would seem essential for the success of that modeling effort.

The patterns of seasonal change for bacterial, phytoplankton, and organic matter parameters at the GWR transect were very similar to those previously observed for the upper bay (25, 27). A key objective of this study was to begin evaluating the importance of down-bay organic carbon pools and metabolic processes on upper-mesohaline bay water quality. For this purpose we compared depth-integrated mean seasonal GWR transect data with measurements made in 1984 and 1985 along the CHOPAX (Choptank-Patuxent rivers) transect (14, 25, 27), which is located about 90 km north (38°34′ N latitude) of GWR (Tables 3 and 4).

TABLE 2. Linear correlations of bacteria with organic constituents in the lower mesohaline portion of the Chesapeake Bay during March to August 1987[a]

Organic component	r value					
	Bacterial abundance			Bacterial production		
	March–August (all)	March–May (spring)	June–August (summer)	March–August (all)	March–May (spring)	June–August (summer)
Chl	0.58[b]	0.38[c]	0.33[c]	0.49[b]	0.50	0.06[c]
BOD	0.00[c]	0.49	0.45[d]	0.10[c]	0.78	0.34[c]
Dissolved BOD	0.37	0.12[c]	0.62	0.42	0.37[c]	0.54
Particulate BOD	NR[e]	0.56	0.27[c]	NR	0.77	0.16[c]
POC	0.42[b]	0.79	0.32[c]	0.36	0.60	0.17[c]
PON	0.38[b]	0.82	0.39[c]	0.29[d]	0.68	0.32[c]

[a] Unless otherwise noted, all correlations are significant at $P < 0.05$.
[b] Negative x coefficient.
[c] Not significant ($P > 0.10$); t test of Ho:slope = 0.
[d] Significant ($P < 0.10$).
[e] NR, Not reported.

TABLE 3. Comparison of summer integrated mean values for phytoplankton, bacterial, and organic matter measurements made at the GWR and CHOPAX transects

Parameter	Transect	Year	Depth zone[a]			
			EZ	BZ/PYC	SUBPYC	WHOLE WC
Bacterial abundance (10^6 cells/ml)	GWR	1987	11.20 ± 2.87	10.40 ± 2.72	10.20 ± 3.73	10.60 ± 3.11
	CHOPAX	1985	10.12 ± 2.86	8.82 ± 3.15	4.78 ± 2.51	7.91 ± 2.84
	CHOPAX	1984	11.88 ± 3.40	9.04 ± 4.50	4.10 ± 1.39	8.34 ± 3.10
Bacterial production (10^9 cells/liter per day)	GWR	1987	7.20 ± 3.16	6.50 ± 1.83	6.11 ± 2.79	6.60 ± 2.59
	CHOPAX	1985	13.00 ± 5.10	10.40 ± 4.65	4.79 ± 3.19	9.37 ± 4.31
	CHOPAX	1984	7.19 ± 2.44	6.29 ± 3.29	3.80 ± 2.68	5.76 ± 2.80
Bacterial turnover (per day)	GWR	1987	0.71 ± 0.43	0.67 ± 0.24	0.63 ± 0.28	0.67 ± 0.32
	CHOPAX	1985	1.28 ± 0.50	1.17 ± 0.53	1.00 ± 0.67	1.15 ± 0.57
	CHOPAX	1984	0.60 ± 0.21	0.70 ± 0.36	0.93 ± 0.65	0.74 ± 0.41
Bacterial carbon (μg of C/liter)	GWR	1987	225 ± 57	207 ± 54	203 ± 75	212 ± 62
	CHOPAX	1985	202 ± 57	176 ± 63	96 ± 50	158 ± 57
	CHOPAX	1984	238 ± 68	181 ± 90	82 ± 28	167 ± 62
Chl (μg/liter)	GWR	1987	13.6 ± 2.6	9.7 ± 3.3	6.2 ± 3.1	9.9 ± 3.0
	CHOPAX	1985	10.6 ± 6.2	7.5 ± 4.8	1.6 ± 0.6	6.6 ± 3.9
	CHOPAX	1984	16.8 ± 31.1	5.6 ± 5.0	1.3 ± 0.7	7.9 ± 12.2
Phytoplankton carbon (mg of C/liter)	GWR	1987	0.95 ± 0.18	0.68 ± 0.23	0.44 ± 0.22	0.69 ± 0.21
	CHOPAX	1985	0.74 ± 0.44	0.53 ± 0.34	0.11 ± 0.04	0.46 ± 0.27
	CHOPAX	1984	1.17 ± 2.17	0.39 ± 0.35	0.09 ± 0.05	0.55 ± 0.86
POC (mg/liter)	GWR	1987	1.45 ± 0.61	1.00 ± 0.53	0.83 ± 0.35	1.09 ± 0.50
	CHOPAX	1985	1.38 ± 0.46	0.85 ± 0.35	0.40 ± 0.11	0.88 ± 0.31
	CHOPAX	1984	1.55 ± 0.80	0.94 ± 0.37	0.76 ± 0.20	1.08 ± 0.46
PON (mg/liter)	GWR	1987	0.21 ± 0.05	0.18 ± 0.06	0.17 ± 0.06	0.19 ± 0.06
	CHOPAX	1985	0.23 ± 0.06	0.16 ± 0.07	0.06 ± 0.03	0.15 ± 0.05
	CHOPAX	1984	0.29 ± 0.15	0.18 ± 0.08	0.13 ± 0.04	0.20 ± 0.09
POC/PON (atomic ratio)	GWR	1987	8.0	6.4	5.8	6.8
	CHOPAX	1985	7.0	6.1	7.9	7.0
	CHOPAX	1984	6.2	5.9	7.0	6.4
BOD (mg of C/liter)	GWR	1987	1.09 ± 0.35	0.77 ± 0.35	0.59 ± 0.32	0.81 ± 0.34
	CHOPAX	1985	0.94 ± 0.22	0.66 ± 0.08	0.35 ± 0.11	0.65 ± 0.14
	CHOPAX	1984	ND[b]	ND	ND	ND
FBOD (mg of C/liter)	GWR	1987	0.48 ± 0.10	0.43 ± 0.16	0.36 ± 0.20	0.42 ± 0.15
	CHOPAX	1985	0.42 ± 0.14	0.35 ± 0.15	0.27 ± 0.08	0.35 ± 0.12
	CHOPAX	1984	ND	ND	ND	ND
FBOD/BOD (%)	GWR	1987	44	56	61	53
	CHOPAX	1985	44	53	77	58
	CHOPAX	1984	ND	ND	ND	ND
PBOD/POC (%)	GWR	1987	42	34	28	35
	CHOPAX	1985	44	28	14	29
	CHOPAX	1984	ND	ND	ND	ND
Bacterial C/POC (%)	GWR	1987	15	21	25	20
	CHOPAX	1985	15	21	24	20
	CHOPAX	1984	15	19	11	15
Phytoplankton C/POC (%)	GWR	1987	66	68	53	62
	CHOPAX	1985	54	62	27	48
	CHOPAX	1984	76	42	12	43
Bacterial C/phytoplankton C (%)	GWR	1987	24	30	47	34
	CHOPAX	1985	27	34	87	49
	CHOPAX	1984	20	46	91	52
Phaeopigments/Chl (%)	GWR	1987	16	26	49	30
	CHOPAX	1985	23	31	74	43
	CHOPAX	1984	32	63	160	85

[a] Values are means ± standard deviations. Abbreviations: EZ, euphotic zone; BZ/PYC, between euphotic zone and pycnocline; SUBPYC, beneath the pycnocline; Whole WC, entire water column.
[b] ND, Not determined.

A potential problem with this comparison is that of interannual variability. However, bacterial, phytoplankton, and organic matter summer integrated means for the CHOPAX transect for these two years were remarkably similar (Table 3), despite large differences in climatic conditions, especially freshwater input into the bay.

High spring freshwater flows, such as those that occurred in 1984, have a detrimental effect on mid-bay water quality, specifically, the increased extent and duration of summer deep-water anoxia (21, 27). In contrast to 1984, 1985 was an abnormally dry year in which anoxia was not observed at the CHOPAX transect (14, 27). Because water flow in 1987 was average (U.S. Geological Survey, Towson, Md.), comparisons of GWR and CHOPAX transect means for these variables across the years 1984 to 1987 seem reasonable.

Two exceptions to the correspondence of parameters obtained in 1984 and 1985 were higher surface water levels of Chl in 1984 but higher bacterial production in 1985 (Table 3).

TABLE 4. Comparison of spring integrated mean values for phytoplankton, bacterial, and organic matter measurements made at the GWR and CHOPAX transects

Parameter	Transect	Year	Depth zone[a]			
			EZ	BZ/PYC	SUBPYC	WHOLE WC
Bacterial abundance (10^6 cells/ml)	GWR	1987	4.79 ± 1.40	4.64 ± 1.34	4.88 ± 1.53	4.77 ± 1.42
	CHOPAX	1985	5.24 ± 1.98	5.15 ± 2.19	4.03 ± 1.32	4.81 ± 1.83
Bacterial production (10^9 cells/liter per day)	GWR	1987	2.89 ± 2.36	2.46 ± 1.50	2.38 ± 1.13	2.58 ± 1.66
	CHOPAX	1985	5.58 ± 4.15	5.30 ± 3.74	2.35 ± 0.86	4.41 ± 2.92
Bacterial turnover (per day)	GWR	1987	0.58 ± 0.38	0.52 ± 0.38	0.49 ± 0.18	0.53 ± 0.27
	CHOPAX	1985	1.07 ± 0.79	1.03 ± 0.73	0.58 ± 0.21	0.89 ± 0.58
Bacterial carbon (μg of C/liter)	GWR	1987	96 ± 28	93 ± 27	98 ± 31	95 ± 28
	CHOPAX	1985	105 ± 40	103 ± 44	81 ± 26	92 ± 61
Chl (μg/liter)	GWR	1987	41.3 ± 12.1	42.1 ± 12.3	41.8 ± 11.9	41.7 ± 12.1
	CHOPAX	1985	17.1 ± 8.6	20.9 ± 14.8	15.0 ± 14.7	17.6 ± 12.7
Phytoplankton carbon (mg of C/liter)	GWR	1987	2.89 ± 0.84	2.95 ± 0.86	2.92 ± 0.83	2.92 ± 0.85
	CHOPAX	1985	1.19 ± 0.61	1.46 ± 1.04	1.05 ± 1.03	1.23 ± 0.89
POC (mg/liter)	GWR	1987	2.80 ± 0.71	2.51 ± 0.59	2.35 ± 0.41	2.55 ± 0.57
	CHOPAX	1985	1.29 ± 0.57	1.30 ± 0.80	1.00 ± 0.67	1.20 ± 0.68
PON (mg/liter)	GWR	1987	0.33 ± 0.06	0.31 ± 0.05	0.32 ± 0.04	0.32 ± 0.05
	CHOPAX	1985	0.18 ± 0.04	0.18 ± 0.09	0.15 ± 0.08	0.17 ± 0.07
POC/PON (atomic ratio)	GWR	1987	10.0	9.3	8.5	9.3
	CHOPAX	1985	8.5	8.3	7.8	8.2
BOD (mg of C/liter)	GWR	1987	1.10 ± 0.35	1.02 ± 0.26	1.12 ± 0.25	1.08 ± 0.29
	CHOPAX	1985	0.76 ± 0.19	0.71 ± 0.28	0.52 ± 0.22	0.66 ± 0.23
FBOD (mg of C/liter)	GWR	1987	0.37 ± 0.13	0.42 ± 0.19	0.37 ± 0.13	0.39 ± 0.15
	CHOPAX	1985	0.27 ± 0.05	0.20 ± 0.05	0.12 ± 0.06	0.20 ± 0.05
FBOD/BOD (%)	GWR	1987	33	41	33	36
	CHOPAX	1985	35	29	24	29
PBOD/POC (%)	GWR	1987	26	24	32	27
	CHOPAX	1985	43	27	18	29
Bacterial C/POC (%)	GWR	1987	3	4	4	4
	CHOPAX	1985	8	8	8	8
Phytoplankton C/POC (%)	GWR	1987	103	118	124	115
	CHOPAX	1985	93	113	104	103
Bacterial C/phytoplankton C (%)	GWR	1987	3	3	3	3
	CHOPAX	1985	9	7	8	8
Phaeopigments/Chl (%)	GWR	1987	12	13	17	14
	CHOPAX	1985	16	19	27	20

[a] Values are means ± standard deviations. Abbreviations: EZ, euphotic zone; BZ/PYC, between euphotic zone and pycnocline; SUBPYC, beneath the pycnocline; whole WC, entire water column.

The former has been attributed to pulsed nutrient inputs and the resultant phytoplankton blooms along the western flank of the bay in 1984 (14). The latter has been explained by potentially higher rates of bacterivory in 1985 compared with those in 1984 (14).

Even though all measures of organic carbon (Chl, POC, PON, BOD, and FBOD) were substantially higher in the spring at GWR than at CHOPAX, bacterial abundance was about the same and bacterial production was about twice as great (except in the bottom water) at the CHOPAX transect (Table 4). At least in the surface water, this may be the result of greater POC lability (higher particulate BOD/POC ratio) at the CHOPAX transect. Whether greater POC lability is a function of a different phytoplankton species composition or physiological state or of differences in zooplankton grazing is unclear.

A key feature of the annual midbay phytoplankton cycle is that peak phytoplankton biomass occurs in the spring, but phytoplankton productivity reaches its annual maximum in July and August (13, 14, 22). Elevated spring biomass levels arise from de novo phytoplankton production in surface waters and the late-winter and early-spring up-bay transport of diatoms and the dinoflagellate, *Prorocentrum* sp., in bottom waters (22, 28). Our findings of approximately equal surface and bottom-water spring Chl concentrations are consistent with this up-bay phytoplankton carbon transport. Furthermore, the decline in particulate BOD/POC ratios with depth at the CHOPAX transect but not the GWR transect and a greater increase in phaeopigment/Chl ratios with depth at CHOPAX indicate that this deep-water particulate organic matter is degraded as it moves north, serving to fuel bacterial oxygen consumption.

Major differences between the GWR and CHOPAX transects in the summer occurred primarily in deep water (Table 3). Deep-water bacterial abundance and production as well as carbon parameters (Chl, POC, PON, BOD, and FBOD) were all subtantially greater at the GWR transect. This indicates that in the summer, as well as in the spring, lower-bay-produced organic matter is transported to the north in the deep water. Observations that deep-water POC is more labile, that phytoplankton is a larger portion of POC, and that phaeopigment/Chl ratios are lower at the GWR transect than at the CHOPAX transect suggest that degradation of that particulate carbon is increased as it moves up the bay. Increased POC/PON ratios, FBOD/BOD ratios, and increased bacterial carbon/phytoplankton carbon ratios in the deep water at the CHOPAX transect also support this hypothesis. The quantitative significance of this up-bay transport cannot be deduced from the data presented here. Synoptic data collected in the same year from multiple

transects ranging from the northern to the southern termini of the mesohaline portion of Chesapeake Bay are required to resolve this question.

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