

Excessive nutrients select for dinoflagellates in the stratified Patapsco River estuary: Margalef reigns

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ABSTRACT: Phytoplankton composition in the mesohaline Patapsco River estuary, a tributary of Chesapeake Bay, is dominated by dinoflagellates throughout the summer. This dominance is attributed to the nutrient-turbulence relationships that have been described by Margalef over the last 30 yr, a field verification of this highly respected theory. The partially stratified estuary is typified by ambient nutrient concentrations higher than those in any other mesohaline area of the northern bay and its tributaries. Mean dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) concentrations in surface waters of the stratified estuary exceed 30 and 0.5 μM , respectively, during the summer, and new and regenerated nutrient loadings ensure maintenance of these high levels through the productive growing season. Turbulence levels are suggested to be low in surface waters of the stratified water column, selecting for motile dinoflagellates throughout the summer. Dinoflagellate dominance in the Patapsco River estuary is further ensured through only minor grazing pressure from low rotifer demand and low standing stocks of ambient herbivorous copepod populations, the latter group being present at levels lower than in any other mesohaline system of the Chesapeake and its tributaries. The resulting high dinoflagellate biomass appears to support a large and active microheterotrophic community (microbial loop), exemplified by abundant rotifers, high oxygen demand, and high nutrient regeneration in the water column and sediments. From these traits, the dinoflagellate-dominated mesohaline Patapsco River estuary and the tidal-fresh cyanobacteria bloom areas of the upper Potomac River appear to be analogous, with salinity defining species composition of the phytoplankton.

KEY WORDS: Dinoflagellates · Nuisance algae · Nutrients · Turbulence · Stratification · Zooplankton · Ctenophores · Food web

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INTRODUCTION

'Nuisance algae' often dominate stratified aquatic systems typified by high nutrient concentrations, with noxious blooms of cyanobacteria (blue-green algae) forming floating scums in many lakes, slow-moving rivers, and farm ponds. In brackish waters, 'nuisance algae' are most often dinoflagellates as low salinities

pose problems for growth of generally halo-intolerant bloom-forming cyanobacteria common to freshwaters by limiting photosynthetic ability and buoyancy regulation (see Sellner et al. 1988). Persistent accumulations of autotrophic dinoflagellates would be expected in nutrient-rich, low-turbulence areas, as described by Margalef (1978).

The Chesapeake Bay and its tributaries are some of the most enriched coastal plain estuaries in North America, resulting in an aggressive multi-State and Federal effort to reduce nutrient loadings and produc-

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tivity in recent decades. By implementing rigorous point-source control strategies and encouraging best management practices in urban and agricultural communities, nutrient loads to many Chesapeake Bay tributaries have been reduced, particularly on the bay's western shore. In some cases, these nutrient reductions have lead to reductions in phytoplankton standing stocks, a first step towards reversing bay eutrophication that has been on-going since European settlement and has accelerated over the last half-century. However, some tributaries have such high loadings that even documented reductions in nutrient inputs still result in high nutrient levels downstream, potentially supporting high phytoplankton production and summer hypoxia/anoxia below the pycnocline in mesohaline areas. Such is the case for the lower Patapsco River estuary in northern Chesapeake Bay, the mesohaline estuary whose watershed includes urban Baltimore and its developed suburbs. Although nutrient loads to the system appear to have declined over an 18 yr monitoring period (1984 to 2001), summer phytoplankton biomass and productivity still remain high, exceeding levels/rates measured in other, similar salinity systems in the watershed. This is probably a result of near optimal growth conditions for the brackishwater dinoflagellates which thrive in this system and are dominated by the motile group because of conditions consistent with the selection processes outlined by Margalef over the last 30 yr.

METHODS

As part of an 18 yr monitoring program (1984 to 2001) in the northern Chesapeake Bay, water quality and lower trophic level collections were made at 1 station in the shipping channel of the lower Patapsco River estuary, a major shipping port, with sampling throughout the productive spring-fall period. Data for 13 yr (1985 to 1997), have been analyzed to assess long-term changes in nutrient stocks and the plankton communities, as well as some components of the benthic recycling community. Water and biological samples were collected every 2 wk at Stn WT5.1 (~15 m; 39° 12' 30" N, 76° 31' 30" W) in the main shipping channel of the estuary (Fig. 1). Routine sampling included biological, chemical, and physical measurements. Vertical distributions of PAR were determined with a LiCor submersible sensor. Using a Beckman RS5-3 salinometer and YSI oxygen meter and, more recently, Scout 2 and Survey 2 Hydrolabs, vertical distributions of temperature, conductivity, salinity, and dissolved oxygen were determined through the water column. Water samples at discrete depths were subsequently collected using a small diaphragm pump, with *in vivo* fluorescence determined at each depth using a Turner Designs Flurometer. Chlorophyll a content at discrete depths was determined according to APHA (1985). For phytoplankton and microzooplankton, samples were combined from 5 depths above then 5 depths below

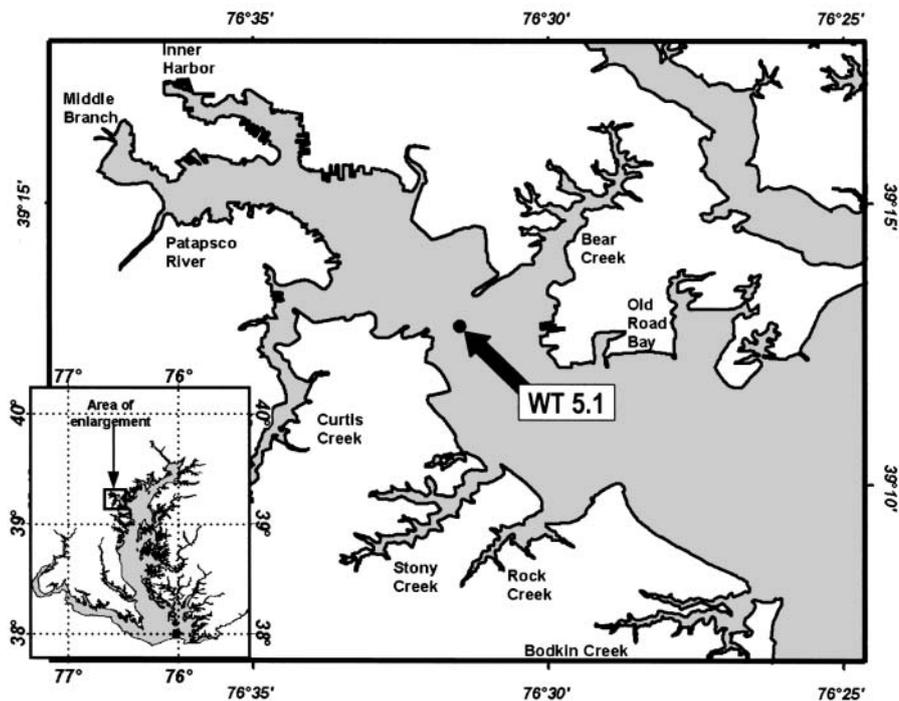


Fig. 1. Station WT5.1 in the Patapsco River estuary, a sub-estuary of Chesapeake Bay

the pycnocline into 2 composite samples above and 2 below the pycnocline. Microzooplankton were concentrated in a submerged 44 μm plankton net, then rinsed into a small jar with 5% buffered formaldehyde. Composite water samples were then gently mixed and water was decanted into 500 ml bottles containing acid Lugol's solution for phytoplankton enumeration with a Leitz Diavert microscope at 312 \times and 500 \times total magnification. A minimum of 250 >2 μm cells were enumerated, and cell volume and cell carbon content were assigned from approximate geometric shapes and the formulas of Strathmann (1967) and Smayda (1978). Microzooplankton were identified at 100 \times and converted to biomass according to Brownlee & Jacobs (1987). Additional subsamples from the surface composite samples were decanted into polycarbonate bottles, enriched with $\text{NaH}^{14}\text{CO}_3$, and incubated for >1 h in a flow-through, water-cooled incubator with $\sim 200 \mu\text{E m}^{-2} \text{s}^{-1}$ from cool-white fluorescent lights. Daily fixation was then estimated according to Keefe et al. (1981). Mesozooplankton were collected using metered, stepped, oblique net (202 μm) hauls through the water column. Ctenophores and medusae were poured off and volume estimated with a graduated cylinder, with the remainder of the plankton samples preserved in a Rose Bengal-5% buffered formaldehyde solution.

Water samples were also retrieved from discrete depths for estimating inorganic and organic nutrient pools. Following filtration through Whatman GF/F filters, dissolved inorganic nitrogen (DIN) was determined as the sum of nitrate, nitrite, and ammonium (EPA 1979); dissolved inorganic phosphorus was also determined according to EPA (1979). Dissolved organic carbon (DOC) was determined following persulfate oxidation (Menzel and Vaccaro 1964). Flows for the Patapsco River and the main tributary to the Chesapeake Bay, the Susquehanna River, were obtained from the United States Geological Survey.

RESULTS

Ambient nutrient concentrations in Baltimore Harbor for the July to September period, 1985 to 1997, were very high. Mean (\pm SE) summer concentrations of DIN and DIP in the surface mixed layer were 32.8 ± 4.4 and $0.5 \pm 0.1 \mu\text{M}$, respectively; for comparison, concentrations of DIN were 3 to 7 times higher than those observed in 4 other mesohaline regions of the study area (Table 1). DIN declined through time in the system, and similarly DIP declined for the first 7 yr, then fluctuated widely (Fig. 2). The high nitrogen concentrations in the estuary resulted in very high summer N/P ratios, exceeding 90 for the 1987 to 1991 period, and then fluctuating between >20 and 60 for the other years (Fig. 2).

Nutrient concentrations and phytoplankton biomass (as dinoflagellates) were related to open bay flow patterns dominated by the Susquehanna River discharge at the head of the bay. Nutrient concentrations as well

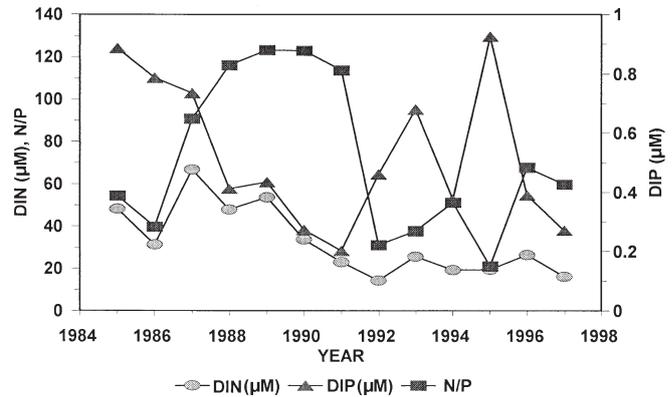


Fig. 2. Summer mean DIN and DIP concentrations (μM) and N/P (at.) in the lower Patapsco River estuary for the period 1985 to 1997

Table 1. Comparison of nutrients and several plankton parameters (means \pm SE) for 5 mesohaline regions of the Chesapeake Bay and its tributaries, July to September, 1985 to 1997. DIN, DIP: dissolved inorganic nitrogen and phosphorus, respectively (μM), for the surface mixed layer. CHL: chlorophyll mean concentration in the surface mixed layer ($\mu\text{g l}^{-1}$); Dino-C: mean surface mixed-layer biomass (C) of dinoflagellates. Biomass data for Dino-C, rotifers, and adult copepods is presented as $\mu\text{g C l}^{-1}$. Ctenophores (Ctenos) data are presented as ml m^{-3} . For the study period, dissolved silicate and dissolved biogenic silicate levels in the surface mixed layer of the Patapsco estuary station were 54.1 ± 3.3 and $9.2 \pm 0.6 \mu\text{M}$, respectively

Region	DIN	DIP	CHL	Dino-C	Rotifers	Copepods	Ctenos
Patapsco	32.8 ± 4.4	0.5 ± 0.1	48.6 ± 8.2	1353 ± 455	45.1 ± 6.3	38.2 ± 6.1	14.5 ± 2.9
Patuxent	6.8 ± 1.1	1.1 ± 0.1	25.3 ± 3.7	596 ± 113	24.9 ± 4.9	76.9 ± 8.6	11.3 ± 5.6
Potomac	5.7 ± 0.6	2.5 ± 0.3	17.5 ± 2.2	763 ± 223	18.5 ± 3.2	43.5 ± 5.7	8.7 ± 3.9
Choptank	9.0 ± 1.2	1.5 ± 0.3	36.2 ± 3.4	231 ± 31	16.5 ± 2.3	89.9 ± 14.5	18.8 ± 7.2
Chesapeake Bay	4.5 ± 1.3	0.7 ± 0.0	8.7 ± 0.7	207 ± 46	3.5 ± 1.1	52.7 ± 10.0	11.5 ± 3.2

^aMesohaline station locations: Patapsco 39° 12' 30" N, 76° 31' 30" W; Patuxent 38° 25' 30" N, 76° 36' 7" W; Potomac 38° 9' 24" N, 76° 35' 48" W; Choptank 38° 34' 48" N, 76° 18' 36" W; open Chesapeake Bay 38° 33' 24" N, 76° 26' 12" W

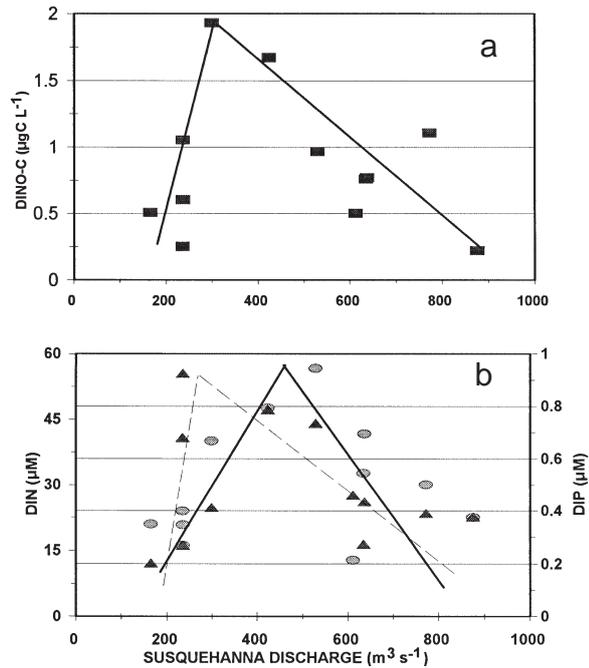


Fig. 3. Relationships between Susquehanna River discharge and (a) mean summer dinoflagellate biomass, and (b) DIN and DIP in the lower Patapsco River estuary, 1986 to 1997 (1985 data excluded due to extremely high dinoflagellate biomass of 7 mgC l^{-1}). Lines have been added to visually assist identifying the increasing and decreasing trends of the 3 parameters

as dinoflagellate biomass increased as Susquehanna discharge increased from approximately <200 to $450 \text{ m}^3 \text{ s}^{-1}$ (Fig. 3). However, at higher flows, DIN, DIP, and dinoflagellate biomass decreased, with DIP and dinoflagellate biomass falling off at lower flows than observed for DIN.

Phytoplankton biomass was high in the estuary over the entire period, ranging from $>7200 \text{ µgC l}^{-1}$ in 1985 to a minimum of 400 µgC l^{-1} in 1993 (Fig. 4). The community was dominated by autotrophic, non-toxic dinoflagellates, with $>85\%$ of the phytoplankton assemblage comprised of dinoflagellates in 1985; the mean contributions of this group to the entire assemblage approximated 61% for the 13 yr period. The primary contributors to the dinoflagellates were *Prorocentrum minimum*, *Gymnodinium* spp., *Heterocapsa rotundata* (= *Katodinium rotundatum*), and *Scrippsiella trochoidea*. Temporal dynamics of the dinoflagellates were not, however, uniquely different from those of other autotrophic eucaryotes in the system, as dinoflagellate and total autotrophic eucaryote biomass followed similar patterns through the study period (Fig. 4).

There were no strong relationships observed between either of the nutrient pools and dinoflagellate

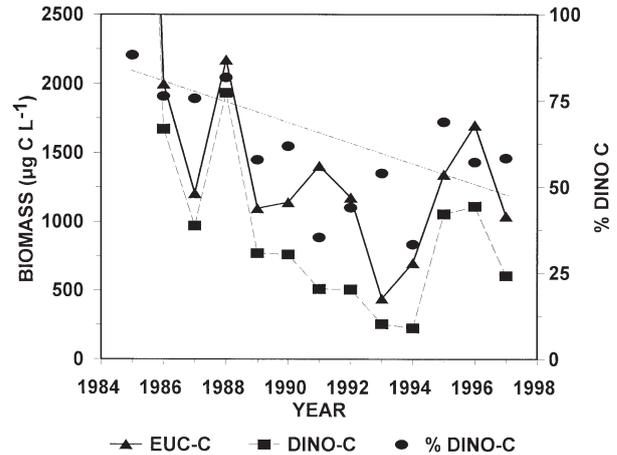


Fig. 4. Temporal distribution of mean summer $>2 \text{ µm}$ eucaryote (▲) and dinoflagellate (■) biomass and the relative contribution of dinoflagellates (% DINO-C, ●). dot-dashed line represents approximate change through time) to the $>2 \text{ µm}$ eucaryote assemblage in the lower Patapsco River estuary, 1985 to 1997

biomass. Of the 3 nutrient parameters (summer DIN, DIP, and N/P) DIN levels were most strongly related to dinoflagellate biomass, but still only weakly ($r^2 = 0.18$, $p < 0.18$), even with the apparent linkage between DIN, dinoflagellates, and Susquehanna flow in Fig. 3. There were no relationships between DIP and dinoflagellate biomass ($r^2 = 0.09$, $p \gg 0.5$) nor N/P to dinoflagellate biomass ($r^2 < 0.001$, $p \gg 0.5$) over the study period.

The high phytoplankton biomass observed in the system supported a large rotifer assemblage, with rotifer biomass higher than that observed in any other mesohaline station in Chesapeake Bay or its tributaries (Table 1). Rotifers in the $>44 \text{ µm}$ fraction, primarily *Synchaeta* spp., were very abundant, resulting in an average summer biomass approximating 45 µgC l^{-1} , levels 2 to 15 times greater than those observed at 4 other mesohaline stations sampled in the program (Fig. 5, Table 1).

The primary planktonic herbivores in Chesapeake Bay in summer, adult and copepodite *Acartia tonsa*, were not well represented in the Patapsco estuary. Mean biomass approximated 38 µgC l^{-1} (~6 adults), the lowest of any mesohaline station in the Chesapeake region (Fig. 5, Table 1), possibly attributed to ctenophore grazing associated with a summer population approximating $14.5 \text{ ml ctenophores m}^{-3}$ on average ($>46 \text{ ml m}^{-3}$ in 1997).

DISCUSSION

A summary of the results leads to the following conclusion, that field conditions of the Patapsco River estu-

ary, specifically high nutrient concentrations and supplies in a stratified water column, low turbulence, and minimal herbivory, select for autotrophic dinoflagellates in this system. This may be the best, or only, field example of Margalef's (1978) theoretical nutrient-turbulence relationship and the selection of dinoflagellates *in situ*.

Justification for this conclusion must cover the components of Margalef's paradigm, and nutrients are addressed first. Unlike the majority of mesohaline reaches in the Chesapeake Bay and its tributaries, inorganic nutrient concentrations in the lower Patapsco River estuary during summer were extremely high. The levels of 32 μM DIN in the estuary were approximately 4 to 5 times the concentrations observed in 4 other mesohaline stations, and far above any levels (0.5 to 1 μM) that could limit nitrogen uptake or growth (see Fisher et al. 1988). Similarly, DIP concentrations of 0.5 μM exceeded limiting concentrations previously reported (Fisher et al. 1988) by about 5-fold. Further, P limitation *in situ* (suggested by the high N/P and previous results in Fisher et al. 1999), would not be manifested as pools, and recycling (see below) probably provides sufficient P for dinoflagellate demands. (Fisher et al.'s results were derived from short-term bioassays at the station, and in 12 of 26 experiments P limitation was detected for the period February 1989 to December 1994. However, P limitation was only observed in non-summer months, consistent with the conclusion above, i.e. that ambient P availability during summer never limits phytoplankton growth.) Therefore the high ambient nutrient levels suggest that nutrient-limited growth in this system would be rarely observed *in situ*.

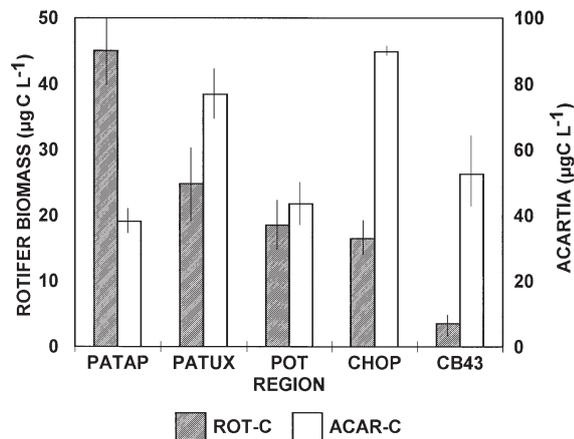


Fig. 5. Mean summer biomass of $>44 \mu\text{m}$ rotifers (ROT-C) and *Acartia tonsa* (ACAR-C) copepodites and adults in the Patapsco River estuary (PATAP) and 4 other mesohaline stations in the Patuxent (PATUX), Potomac (POT), Choptank (CHOP), and main channel of Chesapeake Bay (CB43), 1985 to 1997. Vertical bars represent standard errors

Nutrient concentrations in the Patapsco River estuary were a function of at least 3 mechanisms, with the largest from local inputs from urban Baltimore and its suburbs. Although detailed accounting of loads is not available on an annual basis, total 1996 loads from local watersheds, primarily from industry and sewage treatment plants (79% as point-source inputs), approximated 5.62 and 0.23×10^6 kg N and P, respectively, annually. After correcting for volume of the estuary, this equates to 2.44 and 0.04 μM N and P d^{-1} for the system. Estimates in 1985 were higher still, suggesting elevated nutrient inputs throughout the study period, even with progressive reductions from 1985 to 1996.

Nutrient regeneration also contributes to total nutrient availability in the system, particularly during the high-temperature conditions of the summer season. Weaver et al. (1995a,b) and Boynton et al. (1997) reported summer DIN flux, primarily as ammonium, from the sediments around the harbor, and although no measurements were made directly beneath the plankton station, the mean flux rates for 3 summers was 883 $\mu\text{M m}^{-2} \text{h}^{-1}$ (obtained from averaging maximum and minimum rates). For DIP in the same study, the rate was 54 $\mu\text{M m}^{-2} \text{h}^{-1}$ and, assuming a 24 h day, these fluxes would contribute approximately 1.4 μM DIN and 0.09 μM DIP to the overlying water column each day. These benthic fluxes are 2 to 4 times and 1.8 to 10 times higher, respectively, than for similar salinity stations studied elsewhere (Weaver et al. 1995a,b, Boynton et al. 1997).

Although no bacterial measurements or oxygen fluxes are available for the Patapsco water column, nutrient supply from water column recycling should also be high. As recently argued by del Giorgio et al. (1997), bacterial respiration should approximate 34% of net primary productivity of the lower Patapsco River estuary and, assuming N and P recycling during respiration follows the Redfield ratio, at summer productivities exceeding 2.2 $\text{gC m}^{-2} \text{d}^{-1}$, total N and P remineralization from bacterial catabolism alone would approximate 9.3 and 0.6 $\text{mM m}^{-2} \text{d}^{-1}$, respectively, or approximately 0.62 and 0.04 μM each day—a large and continuous supply of autochthonous nutrient in the 15 m water column.

A slight aside: These high rates emphasize the importance of microheterotrophic metabolism (the microbial loop) in the estuary, further supported by the high biomass of pico- and microplankton-grazing rotifers observed in the system (Table 1). Additionally, hypoxia typified bottom waters from July into September, with occasional anoxia as well, indicating high oxygen consumption and additional support for an active bacterial community. Organic substrates, fueling bacterial metabolism, were also high, approximating $2.9 \pm 0.3 \text{ mg DOC l}^{-1}$ for the period; this is not sur-

prising considering the high overall phytoplankton biomass of the system as well as the large point-source loads from local sewage plants.

The large point-source inputs and high internal recycling rates (the sum of sediment flux and estimated water column recycling) producing 4.5 and 0.17 $\mu\text{M d}^{-1}$ N and P, respectively, probably explain why only modest relationships were observed between ambient DIN levels and dinoflagellates. That is, nutrient loads are so rapid and high that singling out a relationship between primary producers and ambient pools would be difficult. The close correlation between Susquehanna River flow and DIN (and DIP) levels in the Patapsco, particularly evident at flows up to 450 $\text{m}^3 \text{s}^{-1}$ (see Fig. 3), probably reflects the 3-layer flow common to the Patapsco estuary (Olson et al. 1982), whereby low flows from local watersheds are more or less trapped in the estuary by only modest Susquehanna flow at the surface and bottom. This would lead to long residence time and dinoflagellate growth in high ambient nutrient stocks. As the Susquehanna flow increases, resulting in higher flows from the bay into the estuary at the surface and bottom, conservation of mass would force estuarine waters out, leading to a dilution of Patapsco nutrients and accumulated dinoflagellate biomass. This dilution is indicated in the decreasing DIN, DIP, and dinoflagellate biomass during Susquehanna discharges exceeding 450 $\text{m}^3 \text{s}^{-1}$ in Fig. 3.

The high nutrient concentrations in the stratified Patapsco estuary provide near-optimal growth conditions for motile autotrophic (chlorophyll-rich) dinoflagellates. As outlined by Margalef in a series of papers over the last 30 yr, culminating in his most recent publication (Margalef 1997), the Patapsco nutrient levels coupled with stratification and low turbulence (see below) in the surface mixed layer of the enclosed estuary should have selected for dinoflagellates over diatoms during the 13 yr study. First, motility and positive phototaxis ensure abundant light for the autotrophic dinoflagellates, unlike their water column partners, the non-motile diatoms. Second, the high nutrient stocks and supply rates provide the relatively poorly competing dinoflagellates (high half-saturation constants for uptake and growth) with a better opportunity to compete against other more nutrient-efficient phytoplankton. Third, if required, the presence of high nutrient reservoirs at depth could be readily accessed by diel migrations of the dinoflagellates (e.g., Cullen et al. 1985), ensuring a continuous nutrient supply.

Although not explicitly studied in the present sampling regime, another 'bottom-up' control could conceivably favor dinoflagellate dominance: elevated metal levels which could reduce ambient diatom densities and species. The Patapsco estuary is surrounded by large industries, discharging many toxic metals into

the system, resulting in this system being characterized as a toxic 'hot spot' in the northern Chesapeake Bay. However, demonstrable impacts on the estuarine biota appear to be restricted to fauna associated with the sediment, with little apparent impact on the overlying phytoplankton assemblage. The apparent lack of impact in the water column is likely to be due to metal concentrations that have not been shown to have a demonstrable influence on phytoplankton growth. For example, dissolved copper, cadmium, and arsenic in early summer 1992 were 1.74, 0.054, and 1.17 $\mu\text{g l}^{-1}$, respectively, in the surface water (Riedel et al. 1999), i.e. below levels believed to begin to alter growth and phytoplankton speciation (G. F. Riedel pers. comm.). Field free-ion concentrations for copper were also low, between 0.5 to 8 pM for August (Donat 1994), i.e. below levels previously shown to reduce growth in several coastal phytoplankton species (Brand et al. 1986). In recent experiments at our laboratory, copper levels had to exceed 5 $\mu\text{g l}^{-1}$ for any diatoms to begin to decline in multi-species experiments, mimicking field-enclosure results from CEPEX in western Canada in the 1970s (Harrison et al. 1977, Thomas & Seibert 1977). For arsenic, levels >1.2 $\mu\text{g l}^{-1}$ only begin to alter diatom species when phosphorus concentrations are limiting (S. Rikke & J. G. Sanders unpubl. data) and as the phosphorous concentrations and supply are very high in the Patapsco system (see above), an arsenic effect is unlikely. There have been no demonstrable effects of cadmium on phytoplankton at any levels approaching those levels in the Patapsco. Donat (1994) reported free cadmium ion concentrations in August near the estuary at 0.9 to 20 pM, again below levels that Brand et al. (1986) showed would reduce division rates of coastal phytoplankton populations. So although high industry density around the Patapsco estuary encourages speculation on metal-induced toxicity of the normally dominant diatom assemblages, there are no data supporting selective inhibition of the diatoms for the benefit and accumulation of dinoflagellates.

A fourth reason for dinoflagellate dominance is low grazing pressure (low top-down control) from rotifers, and only modest levels of copepods in the system (Table 1). The net effect would be to reduce mortality of all phytoplankton and, as the dominant populations, the release from grazing pressure would only further the success of the motile dinoflagellates. Rotifers, as several of the largest members of the microzooplankton, feed on small phytoplankton and bacteria. The Patapsco dominant, *Synchaeta* sp., has been observed gorged with the dinoflagellate *Prorocentrum minimum* in several mesocosm samples collected at our laboratory, and feeding on *Gymnodinium pseudopalustre* in the lower Potomac River estuary (Tyler & Heinbokel 1985). For the abundant rotifers of the Patapsco, a diet

consisting of dinoflagellates alone would account for only a trivial amount of ambient dinoflagellate stocks. Using Tyler & Heinbokel's ingestion rates of 2 cells rotifer⁻¹ h⁻¹ for *Synchaeta* sp. in the lower Potomac River estuary in a *G. pseudopalustre* bloom, its total demand would be $<3 \times 10^4$ cells l⁻¹ d⁻¹, far less than 1 % of the ambient concentrations of dinoflagellates present during the summer. There was no correlation between dinoflagellate densities and rotifers for the Patapsco system ($r^2 = 0.02$).

Selective grazing of rotifers on other phytoplankton groups might also depress 1 group and allow expression of another, such as dinoflagellates. Dolan & Gallegos (1991, 1992) previously identified an inverse relationship between rotifers and microflagellates in the Rhode River estuary just to the south of the Patapsco system. However, no such pattern was observed in the present study ($r^2 = 0.02$). Further, using Dolan & Gallegos (1991) ingestion rates (approximating 300 cells h⁻¹) and assuming solely microflagellates as prey, Patapsco rotifer populations would remove about one-third of the estimated daily microflagellate production in the system. Considering the diverse assemblage of potential prey in the Patapsco estuary, with enumerated phytoplankton ranging from several to ten million cells per liter, non-enumerated heterotrophic flagellates at 10⁷ ml⁻¹ (e.g., Dolan & Gallegos 1991), <30 µm ciliates at 10⁴⁻⁵ l⁻¹ (Coats & Revelante 1999), and bacteria at 10⁶⁻⁷ ml⁻¹ (e.g., Shiah & Ducklow 1994), it is unlikely that rotifer grazing would selectively remove sufficient autotrophic microflagellates to free dinoflagellates from predation; there is more than enough food, dinoflagellates included, for the ambient rotifer assemblage. More succinctly, dinoflagellate dominance was not likely to have been a result of growth and accumulation as a result of selective predation on other autotrophic members of the phytoplankton.

Copepods, the other primary herbivores, apparently also exerted little pressure on the dinoflagellates. Low copepod biomass (Table 1), equivalent to approximately 6 adults l⁻¹ on average, is likely ensured through top-down control by ctenophores (*Mnemiopsis leidyi* in the Chesapeake Bay system) or alternatively through some other mechanism that might reduce copepod 'success' (e.g., toxicant-reduced fecundity [Sunda et al. 1990] or poor food quality impacts on growth, [Dam et al. 1999]). Ctenophore grazing of *Acartia tonsa* probably removed substantial numbers of this copepod, as ctenophore levels over the study period (14.5 ± 2.9 ml m⁻³, >46 ml m⁻³ in 1997) were the second highest levels observed for 5 mesohaline stations analyzed over the same period (Table 1).

An estimate of carnivory was derived to quantify actual ctenophore demand. As a bulk measurement of ctenophore volume has no individual organism charac-

terization, it is difficult to quantify total ctenophore grazing pressure with any certainty. Therefore, the following assumptions were made. First, 2 extremes in the size distribution of *Mnemiopsis leidyi* were considered, one with all small individuals (5 ctenophores of approximately 3 ml) and a second with 2 large individuals (2 ctenophores of 7 to 8 ml). After converting volume to wet weight (Kremer & Nixon 1976), clearance rates were estimated after Purcell et al. (2001). With these assumptions, ctenophores in the Patapsco estuary would have removed an average of 7 to 10 % d⁻¹ of the ambient copepod stocks over the study period, on the high side of the ctenophore-induced losses reported for mid-Chesapeake Bay in 1988 (Purcell et al. 1994); in 1997, making the same size-distribution assumptions, 22 to 32 % of ambient stocks would have been removed.

Other characteristics of this urban estuary might conceivably further reduce copepod reproductive success. There are some data from the Patapsco estuary suggesting that copepods may experience toxicity from exposure to high toxicant levels of the sediments, and (with fewer observations), from dissolved water-column compounds. In an intensive study of Patapsco estuary sediment toxicities, McGee et al. (1999) reported zinc concentrations of up to 35 nmol g⁻¹ dry wt sediment, overlapping water-column dissolved levels reported to reduce egg-laying and nauplii survival in *Acartia tonsa* (Sunda et al. 1987, 1990). Other components of the sediments might also impact *A. tonsa* as observed for the benthic amphipod *Leptocheirus plumulosus* (McGee et al. 1999); toxic levels of chromium, nickel, lead, copper, zinc, mercury, and selected polyaromatic hydrocarbons recorded for the amphipod might conceivably impact nauplii and adult *A. tonsa* as well, and perhaps reduce egg-hatching success once the eggs sank to the bottom. Using the winter-spring dominant copepod in Chesapeake Bay, *Eurytemora affinis*, Hall et al. (1997) reported that in 4 of 6 exposures to ambient water (October), the mean percent immature stages (nauplii and copepodites) were 0, 0, 0, and 1.6 ± 1.6 % following an 8 d exposure; controls yielded 6.8 ± 2.5 %, suggesting some possibility of toxicity in the system. However, only 1 sample in the estuary exceeded the acute-water quality criteria of the US Environmental Protection Agency for copper, and although the analysis was for total dissolved copper and not cupric ion activity, the results could suggest some toxicity to the ambient copepods from this element. Although mortality was not reported in the Hall et al. study, Sunda et al. (1987) recorded reduced copepod survival (adult and nauplii) when free cupric ion activities exceeded 10⁻¹⁰ to 10⁻¹¹ M. Considering Donat's (1994) report of 0.5 to 8 pM free cupric ion in the water column in August 1992, any toxicity would

be expected to apply to sediments only. Overall, sediment pollutant levels might reduce copepod success through interference with egg-hatching and early life-stage development, while impacts from potentially toxic materials in the overlying waters appear less likely.

A fifth, probably the most important parameter, turbulence in the estuary, is also likely to be of the proper magnitude for dinoflagellate dominance in this system. Margalef (1978) proposed that dinoflagellates would dominate in water columns typified by low turbulence, represented by the coefficient of eddy diffusion K_z , at values of 0.02 to 1 $\text{cm}^2 \text{s}^{-1}$, while diatoms would be favored at K_z levels of 2 to 100 $\text{cm}^2 \text{s}^{-1}$. Another measure, ϵ , turbulent energy dissipation, has also been explored in phytoplankton succession (Peters & Marasé, in Estrada & Berdalet 1998). At values exceeding 0.1 $\text{cm}^2 \text{s}^{-3}$, dinoflagellate growth rates decline whereas growth rates of other phytoplankton remain unaffected. Recent observations in natural systems indicate the importance of turbulence in selection of phytoplankton taxa, specifically dinoflagellates at low turbulence levels. In a study in Lake Kinneret, Berman & Shteinman (1998) attributed the prevalence of *Peridinium gatunense* blooms to very low levels of turbulent kinetic energy (TKE), with bloom intensity inversely related to TKE over a 5 yr period.

Although no direct measurements of turbulence have been obtained for the Patapsco River estuary, it is highly likely that low turbulence typifies surface waters of the stratified system and might be represented by measurements made for other portions of the Chesapeake and its tributaries. Suttles et al. (1999) reported a K_z for turbulent mixing in an open Chesapeake Bay station ranging from 0.001 to $>1 \text{ cm}^2 \text{s}^{-1}$,

with the lowest values in the water column interior and pycnocline and highest values near the surface and bottom. Similarly, ϵ was 0.034 $\text{cm}^2 \text{s}^{-3}$ in surface waters of the Pocomoke River estuary, below the 0.1 $\text{cm}^2 \text{s}^{-3}$ cut-off for inhibition of dinoflagellate growth. Assuming that something close to these rates is applicable to the stratified lower Patapsco, then turbulence is well within the range of minimal levels that select for dinoflagellates when nutrients are excessive (Fig. 6), and this estuary represents one of the few field situations where high nutrients, low turbulence, and minimal top-down grazing pressure are likely to provide near optimal conditions for the overwhelming dominance of bloom-forming dinoflagellate populations. Changing a single parameter, e.g., increasing turbulence in the surface mixed layer, should select for diatoms and not dinoflagellates in the Patapsco estuary, certainly a testable hypothesis for future focused research in the system.

That the Patapsco River estuary is dramatically different from other mesohaline areas of the watershed is not surprising (Table 1) considering the large point-source inputs and regeneration in this system compared to the other areas. The Patapsco receives primarily urban discharge from Baltimore, a city of 1 million with a highly developed local industry around the harbor. In contrast, the other mesohaline reaches are primarily in more rural areas, with little point-source discharge in their immediate vicinity. Additionally, the other areas are open to Chesapeake Bay and meteorological events, so direct bay influence, mixing, and lower nutrient-loading prevents excessive algal accumulation, particularly on-going, persistent dominance by dinoflagellates. Based on the information amassed in this study, it is suggested that minimal turbulence in the enclosed, nutrient-rich Patapsco estuary provides near optimal conditions for dinoflagellate growth.

Finally, there are remarkable similarities between conditions favoring dinoflagellates in the brackish Patapsco River estuary and those associated with cyanobacteria blooms in tidal freshwater of the Potomac River estuary, another Chesapeake Bay tributary. The former represents a phytoplankton response to excessive nutrient loads and availability in a brackish environment, while the latter is characteristic of nutrient-replete, quiescent freshwater systems. Specifically, the tidal freshwater Potomac has very high nutrient levels (Boynton et al. 1995) and the tidal river is large and deep so that it acts as a large lake, permitting buoyant cyanobacteria accumulation at its surface. There is minimal zooplankton herbivory (Sellner et al. 1993), and there is a constant source of nutrients from sewerage plant discharges immediately above the bloom site (Jaworski 1981) as well as phosphorus efflux from local

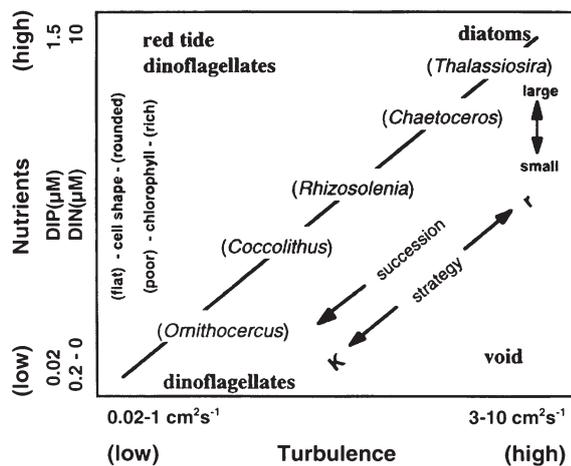


Fig. 6. Phytoplankton succession as a function of turbulence and nutrient concentrations (from Margalef 1978, 1997). High nutrient concentrations, stratification, and low turbulence select for the chlorophyll-rich dinoflagellates noted in the upper left corner of the figure

sediments that increases with bloom-induced elevated pH in the overlying waters (Seitzinger 1991). The differences in 'nuisance algae' between the Patapsco and Potomac systems reflect tolerances to salt. In both cases the excessive biomass of the nuisance taxa selects for microbial-loop-dominated metabolism, diverting energy from harvestable species to water-column oxygen demand, which in turn results in the increasingly frequent and longer-duration hypoxic and anoxic events observed in many of our coastal ecosystems.

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