Toxic Phytoplankton Blooms in the Sea
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FATE OF DINOFLAGELLATES IN CHESAPEAKE BAY: IS SEDIMENTATION LIKELY?

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ABSTRACT

Dinoflagellate blooms are frequent, aperiodic events in mesohaline Chesapeake Bay with high densities of Prorocentrum, Gymnodinium, Gyrodinium, Katodinium and Heterocapsa. A conceptual model on the fate of bloom carbon and nutrients for Chesapeake Bay suggests the potential importance of sedimentation as a dissipation mechanism for recurrent blooms [1]. Distributions of dinoflagellates as vegetative cells or peridinin-rich particulates in the water column, sediment traps and surficial sediments were estimated during 1985 - 1989. Vegetative cells formed only minor portions (1.5% - 8%) of total phytoplankton carbon in sediments or traps; in addition, < 4% of surface mixed layer autotrophic dinoflagellate biomass appeared in the traps. Sedimentation rates for peridinin gave similar fluxes, < 3% of the phytoplankton community settled as dinoflagellates to the pycnocline or near-bottom depths. However, peridininol, a degradation product of peridinin, formed the largest fraction of total peridinin, at least doubling the flux of dinoflagellates to the pycnocline and below. Only trace amounts of peridinin were found in the sediments, largely because of rapid epoxide rearrangement to form loliolide. These data indicate that only small portions of dinoflagellate production settle through the water column to the sediments even in these shallow environments (< 20 m) and the material that reaches the bottom is rapidly mineralized.

INTRODUCTION

Mesohaline Chesapeake Bay is typified by blooms of several common non-toxic dinoflagellates including Prorocentrum minimum (P. mariae-lebouriae), Gymnodinium nelsoni, G. splendens, Gyrodinium uncatenum, Katodinium rotundatum and Heterocapsa triquetra. These blooms occur year-round, with Gymnodinium and Gyrodinium restricted to the summer, Prorocentrum to the spring-summer and Heterocapsa to the winter-spring. Katodinium blooms can occur throughout the year. As reported previously for this region [1,2], densities, biomass and productivities of these bloom taxa can approach 10^8 cells$\cdot L^{-1}$, 2 mgC$\cdot L^{-1}$ and up to 5 gC$\cdot[m^2\cdot d]^{-1}$.

In an attempt to understand the role of dinoflagellate blooms in estuarine carbon and nutrient cycling, Sellner and Brownlee [1] developed a conceptual model of the fate of bloom production, suggesting a suite of mechanisms potentially important in the seasonal demise of dinoflagellate blooms in Chesapeake Bay. From previously collected summer Chesapeake Bay data for dinoflagellate abundance as well as zooplankton herbivory in blooms, we estimated dinoflagellate loss rates. Except for infrequent periods of Favella dominance, herbivory generally removed < 20% of dinoflagellate standing crop each day [1,2]. In winter Katodinium blooms, the copepod Eurytemora affinis could remove up to 70% of the aggregated dinoflagellate population in the

Patuxent River estuary, a tributary of Chesapeake Bay, facilitating bloom demise in colder periods of the year [3]. However, considering the frequencies of dinoflagellate blooms in the Bay relative to the abundance of Favella and E. affinis, we conclude that zooplankton herbivory is relatively minor in controlling bloom longevity in mesohaline Chesapeake Bay.

With apparent minor losses due to zooplankton herbivory, other mechanisms must be identified that would lead to disappearance and subsequent cycling of dinoflagellate bloom production. In an effort to determine the possible importance of sedimentation in bloom dissipation, vertical distributions and sedimentation rates of vegetative cells and pigments of dinoflagellates were measured during the period 1985 - 1989 in stratified mesohaline Chesapeake Bay. Phytoplankton biomass in the surface mixed-layer (SML) and sub-pycnocline depths has been measured at biweekly to monthly frequencies since August 1984. Phytoplankton biomass in sediment trap-collected particulates (moorings at the pycnocline and 1-2 m above the bottom) and in surficial sediments have also been determined in mid-Chesapeake Bay from mid-1985 to mid-1988. Finally, phytoplankton pigments have been quantified from sediment trap collections of particulates for the period March 1988 - November 1989. These data were combined in order to quantify the fraction of surface dinoflagellate biomass reaching sub-pycnocline depths of the Bay, potentially supporting excessively high water column respiration, sediment oxygen demand and nutrient regeneration rates characteristic of the region [4,5].

The importance of dinoflagellates in localized accumulations of phytoplankton carbon are well known for Chesapeake Bay. For example, during the study period, dinoflagellates in spring-early fall surface aggregations resulted in elevated chlorophyll concentrations along the Bay's western shore, routinely exceeding 15 $\mu g \cdot L^{-1}$ and reaching 535 $\mu g \cdot L^{-1}$ in one summer bloom (8 August 1988). Their contribution throughout the year is also substantial. On average, dinoflagellates contributed 23% $\pm$ 2% and 16% $\pm$ 2% of eucaryote biomass in the surface mixed layer and sub-pycnocline depths, respectively, for the period August 1984 - December 1989.

Distributions of autotrophic dinoflagellates varied in space and time within the water column (Figs. 1,2). For each sampling date over the study period, 84% (geometric mean) of the autotrophic dinoflagellate biomass in the SML was below the pycnocline (BP) suggesting little vertical heterogeneity. However, day-to-day meteorological and biological patchiness was partially removed by integrating biomass over each month of the study period. These results suggested that on average 67% (geometric mean) of SML autotrophic dinoflagellate biomass could be found in sub-pycnocline waters.

However, the distributions are in part biased by two distinct seasonal patterns, elevated bottom water dinoflagellates during winter-spring and lower sub-pycnocline biomass during summer-fall stratified periods. In winter-spring, bottom depths were enriched with P. minimum, the autotrophic dinoflagellate that recirculates up-Bay in sub-pycnocline depths during this period [6]. The accumulation of this alga at depth does not represent sedimentation at this site. Autotrophic dinoflagellate biomass was evenly distributed through the water column; within each month from January-June, the ratio of autotrophic dinoflagellate biomass below the pycncline to that in the SML was 1.03 (geometric mean).

In contrast, autotrophic dinoflagellate biomass below the pycnocline from July-December was markedly reduced relative to SML levels. For each sampling date, only 55% (geometric mean) of the SML autotrophic dinoflagellate standing crop was observed below the pycnocline. On a monthly basis, obtained by integrating biomass over each month, levels in sub-pycnocline depths for July-December were only 37% (geometric mean) of the SML standing crop of autotrophic dinoflagellates.

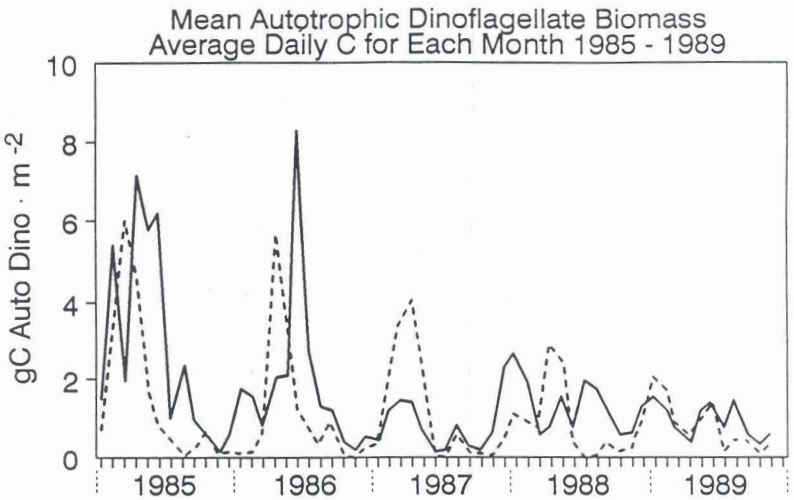

Fig. 1. Average monthly biomass of autotrophic dinoflagellates in the surface mixed layer (——) and below the pycnocline (· · ·) for mesohaline Chesapeake Bay, 1985 - 1989.

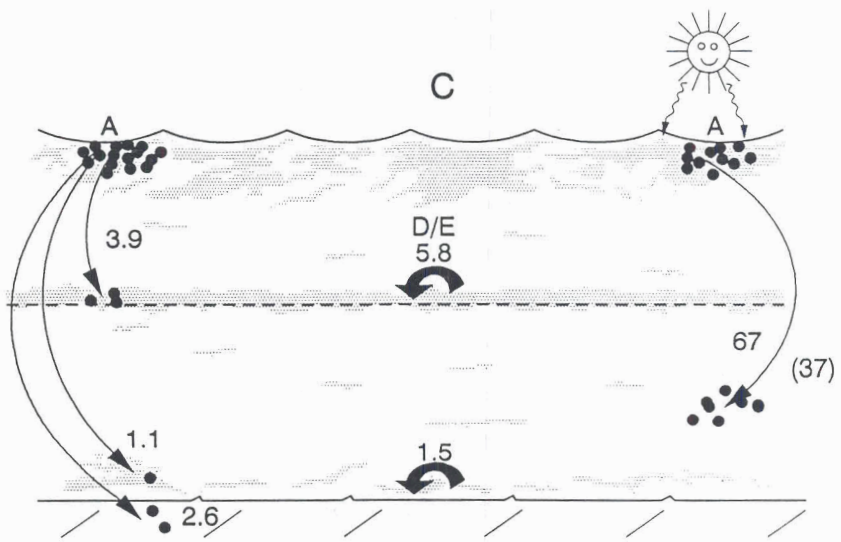

Fig. 2. Distributions of dinoflagellate carbon in mesohaline Chesapeake Bay, derived from cell counts. Numbers associated with long arrows reflect losses (as percentage) of SML biomass. A = autotrophic dinoflagellates and D/E = ratio of dinoflagellate to eucaryote phytoplankton carbon in sediment trap particulates at the pycnocline and above bottom.

The vertical heterogeneity of dinoflagellates in the water column could be partially explained by quantifying dinoflagellate flux of settling populations from the surface mixed-layer. In order to compute monthly loss rates for the period June 1985 - June 1988, average monthly dinoflagellate biomass in the SML ($mg \cdot m^{-2}$, obtained from cell counts) was compared to average monthly settling rates for dinoflagellates (obtained from cell counts of dinoflagellates in sediment traps deployed at the pycnocline and 1-2 m above the bottom). Each month, only 3.9% $\pm$ 0.7% of the dinoflagellate biomass found in the overlying surface mixed layer settled to the pycnocline (Fig. 2). Even smaller fractions of SML dinoflagellates sank to the sediment traps located 1-2 m above the bottom. On a monthly basis for the period June 1985 - June 1987, only 1.1% $\pm$ 0.3% of SML dinoflagellate biomass appeared in sediment traps immediately above the bottom (Fig. 2). Similar losses of SML dinoflagellate biomass were estimated from densities of vegetative autotrophic dinoflagellates in surficial sediments; autotrophic dinoflagellates in sediments represented only 2.6% $\pm$ 1.4% of SML dinoflagellate biomass on a monthly basis (Fig. 2). These data indicate that little of the surface dinoflagellate assemblage settled through the water column to the aphotic bottom waters or the benthos.

Similar loss terms were estimated from characterizing distributions of phytoplankton pigments. Concentrations of chlorophyll and peridinin, the primary accessory pigment for the Pyrrophyta [7,8], were determined in sediment trap-collected material for the period March 1988 - November 1989. Assuming a peridinin to chlorophyll a ratio of 0.341 [7,8, R. Dawson, unpubl. data], the contributions of dinoflagellates to the total phytoplankton assemblage averaged 8% for pycnocline and above bottom-deployed traps. From estimates of cell carbon in the traps, autotrophic dinoflagellate biomass represented 5.8% of trap-collected eucaryote carbon at the pycnocline and only 1.5% in traps immediately above the bottom (Fig. 2, D/E data).

Peridininol was also found in all traps. The contribution of this compound, derived from heterotrophic degradation of peridinin [9], exceeded peridinin (Fig. 3) and suggests substantial catabolism of surface dinoflagellate production. Repeta and Gagosian [9] suggested that peridininol is a by-product of metazoan herbivory. If this is true for Chesapeake Bay, pelagic grazing would be responsible for > 50% of sedimenting dinoflagellates. Because mid-trap vegetative dinoflagellates comprised 3.9% of the SML dinoflagellate assemblage (see above), we estimate that at least twice this, or > 8%-10% of SML autotrophic dinoflagellate assemblage, might reach the pycnocline and sub-pycnocline depths.

Dinoflagellate chlorophyll settling to the pycnocline and depths immediately above the bottom, estimated from peridinin and peridininol concentrations, was also low (Fig. 4). For the period March 1988 - November 1989, only a trivial fraction of the chlorophyll found in the SML appeared as dinoflagellates in traps. Dinoflagellate chlorophyll collected monthly in mid- and bottom traps approximated only 0.9% $\pm$ 0.1% and 2.9% $\pm$ 0.4% of the chlorophyll found in the overlying surface waters, respectively, minor losses for surface assemblages but similar to estimates made from estimates of cell carbon in the SML and traps (see above).

Only trace concentrations of peridinin were found in sediments of the region due to early diagenetic transformation of this and other 5,6 epoxy carotenoids (fucoxanthin, diadinoxanthin, dinoxanthin) to loliolide [10]. Considering the low numbers of vegetative cells found in the sediments as well as the low dinoflagellate biomass (cell carbon, chlorophyll) collected in the deep sediment traps, it is not surprising that sediment peridinin was small.

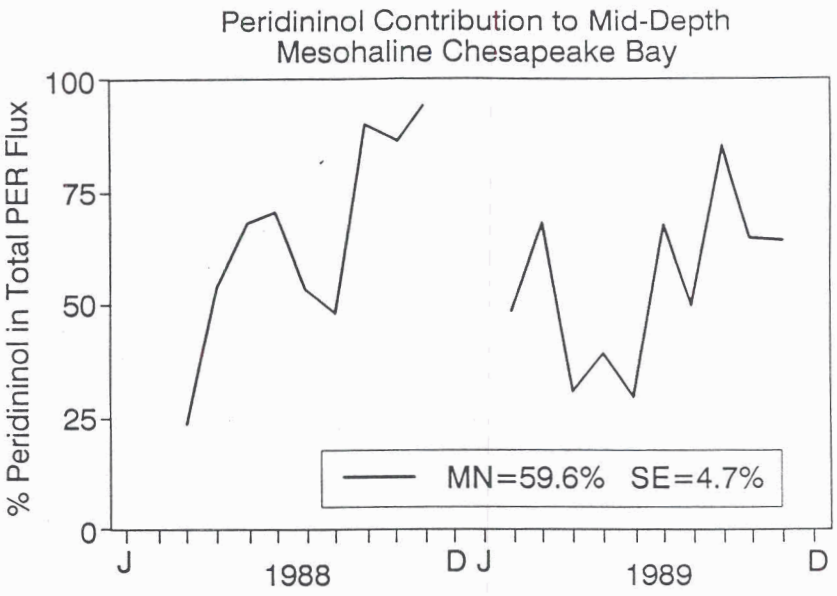

Fig. 3. Peridininol flux as a percentage of peridinin + peridininol flux in mid-depth sediment traps, 1988 - 1989.

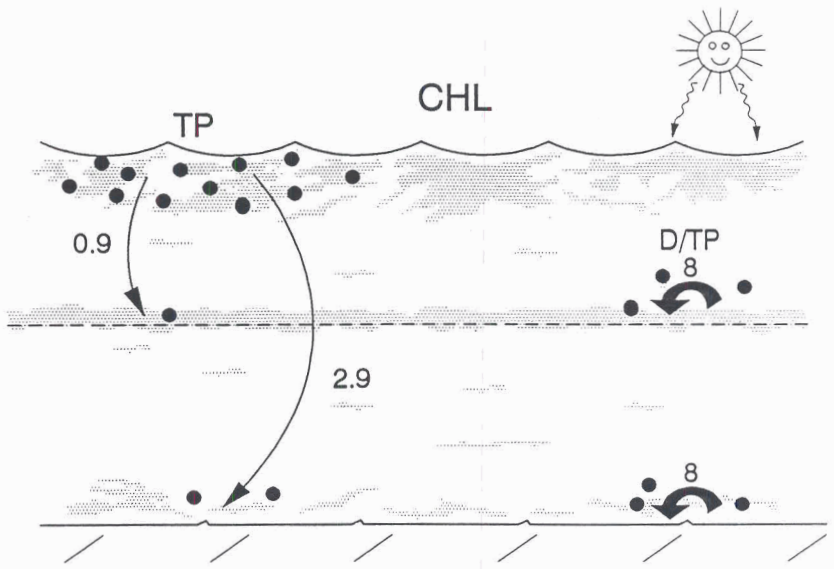

Fig. 4. Dinoflagellate chlorophyll, derived from dinoflagellate peridinin, settling to mid-depth and bottom sediment traps as a percentage of total phytoplankton chlorophyll (TP) in the SML of mesohaline Chesapeake Bay and dinoflagellate chlorophyll as a percentage of total trap chlorophyll (D/TP).

SUMMARY

Vertical distributions of and sedimentation patterns for dinoflagellates generally indicate that sedimentation is not a major loss term for dinoflagellate production in mesohaline Chesapeake Bay. Sellner and Brownlee [1] suggested that sedimentation of vegetative populations to the pycnocline and bottom might be one possible fate for the motile planktors largely because zooplankton grazing is generally low [1,2]. Monthly vertical fluxes estimated from integrating settling rates for dinoflagellate carbon or peridinin-chlorophyll were less than 4% of dinoflagellate and total phytoplankton standing crops in the surface mixed layer. Vertical distributions of vegetative cells indicated a greater enrichment at depth, with approximately 37% of summer surface dinoflagellates found below the pycnocline. Surficial sediments were nearly devoid of vegetative dinoflagellates.

The presence of peridininol in sediment traps suggests that heterotrophic catabolism of dinoflagellates could be substantial. The heterotrophs responsible for peridinin degradation remain to be identified considering previous observations of relatively low copepod, rotifer or tintinnid grazing in regional dinoflagellate blooms [1,2]. Processes producing hydrolyzed peridinin include benthic and pelagic grazing and perhaps encystment. Pigment hydrolysis might also accompany viral-induced autolysis. Future research will focus on quantifying the magnitudes of these processes in the catabolism of dinoflagellate production.

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