Hydrodynamic control on size-structured phytoplankton blooms in a periodically mixed estuary

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ABSTRACT

A plankton ecosystem model was developed to investigate effects of hydrodynamic processes including advection and diffusion on size-structured phytoplankton dynamics in the mesohaline zone of the York River estuarine system, Virginia, USA. The model included 12 state variables representing the distribution of carbon and nutrients in the surface mixed layer. Groupings of autotrophs and heterotrophs were based on cell size and ecological hierarchy. Forcing functions included incident radiation, temperature, wind stress, mean flow and tide which includes advective transport and turbulent mixing. The ecosystem model was developed in FORTRAN using differential equations that were solved using the 4th order Runge-Kutta technique. The model showed that microphytoplankton blooms during winter-spring resulted from a combination of vertical advection and diffusion of phytoplankton cells rather than in-situ production in the lower York River estuary.

INTRODUCITON

Environmental disturbance such as eutrophication can impact aquatic food web structure and fisheries by affecting phytoplankton community since phytoplankton are the main source of carbon and nutrients in a food web. Phytoplankton affect water quality, especially dissolved oxygen by photosynthesis and respiration, and can serve as substrates for microbial decomposition resulting in oxygen depletion when their ungrazed biomass has accumulated (Sundbaeck et al. 1990). In addition, plankton are also light-absorbing particles which can limit their own growth, i.e., self-shading (Kirk 1994), and the depth of light penetration.

Phytoplankton production in aquatic environments may be regulated by bottom-up controls,

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nutrient fluxes associated with physical variability and top-down controls, biotic, trophic interactions (Alpine and Cloern 1992, Kivi et al. 1993). In estuarine environments, these controlling mechanisms interact with phytoplankton in complex ways, mainly because of freshwater and tidal energy inputs into the system (Cloern 1996). Physical processes including advection and diffusion play an important role in estuarine plankton population dynamics (Haas et al. 1981, Delgadillo-Hinojosa et al. 1997, Shen et al. 1999). In this context, understanding of the relationship between physical processes and plankton population dynamics in coastal estuarine systems is important to better understand phytoplankton dynamics and then to better manage water quality in estuarine environments. An ecosystem model was developed and used to explore the relationship between hydrodynamic processes and phytoplankton and nutrient dynamics in the mesohaline zone of the York River estuary, a periodically mixed subestuary of the Chesapeake Bay (U.S.A.).

MODEL DISCRIPTION

The conceptual ecosystem model includes 12 state variables for describing the distribution of carbon and nutrients in the surface mixed-layer of the mesohaline zone in the York River estuary. The state variables consist of autotrophs including pico- (<3 μm), nano- (>3 and <20 μm), and micro-phytoplankton (>20 μm); heterotrophs including bacteria, flagellates+ciliates, microzooplankton (>70 and <202 μm), and mesozooplankton (>202 μm); the nutrients NO2-+ NO_3^-, NH_4^+, and PO_4^{-3}, and non-living organic materials, DOC, and POC. Groupings of autotrophs and heterotrophs are based on cell size and ecological hierarchy; mixotrophy was not considered in the model.

Forcing functions include incident radiation, temperature, tide, wind stress, and mean flow. Incident radiation and temperature were estimated using empirical equations for Gloucester Point, VA. Salinity and wind stress data were collected by the Virginia Institute of Marine Science at Gloucester Point, VA. Daily river discharge rates at the fall line were collected by US Geological Survey. The surface boundary condition is specified by a zero flux condition for all state variables at the atmosphere-water interface. Vertical transport by advection and diffusion, sinking for organisms, and fluxes for nutrients were incorporated into the model as the bottom boundary condition, in which the flux of organisms and nutrients was specified by vertical exchange or sinking rate times biomass and nutrient flux from bottom water respectively. Chlorophyll *a* and nutrients collected from bottom water over an annual cycle and presented in Sin (1998) were used as input data for the bottom boundary condition. The model was developed in Fortran90 (Microsoft® Fortran Power Station) and differential equations were solved using the 4th order Runge-Kutta technique. Mathematical Structure for hydrodynamic, biological and chemical processes was described in Sin and Wetzel (2001).

Field data collected over an annual cycle (Sin 1998) were used as validation data for the three size-structured phytoplankton populations and nutrients. EPA monitoring data collected at the station (WE4.2) nearby the mouth of the York River were used for model validation of micro- and meso-zooplankton. Field data collected at the Virginia Institute of Marine Science, VA were used for the other state variables.

Effects of physical processes including diffusion and advection on phytoplankton and nutrient dynamics were assessed by removing diffusion, longitudinal advection, vertical advection and diffusion + advection processes from the model in the sensitivity analyses. A physical process was considered to be 'sensitive' if removal of the process resulted in ≥ 100 % change in 3 year average concentrations of the state variables relative to the nominal model run. In the model sensitivity analyses, the root mean square deviation (RMS) between the daily values of state variables from nominal model runs and the outputs from sensitivity runs was computed as below and compared with the means of each state variable for the nominal runs.

$$RMS = \sqrt{\frac{1}{n}\sum_{k=1}^{n}(N_k - S_k)}$$

RESULTS AND DISCUSSIONS

Since removal of one or two hydrodynamic processes are not physically realizable scenarios, it is necessary to examine the time series of each term for vertical flux (advection and diffusion) including sinking, longitudinal import/export (advection) and in situ production in order to investigate their relative importance. Figure 1 shows the changes in concentrations of phytoplankton and nutrients due to vertical advection and diffusion vs. longitudinal advection. It is evident that vertical flux serves as a "source" for phytoplankton and nutrients whereas longitudinal transport serves as a "sink" in the model suggesting these two terms are offsetting in the model simulation. The scale or magnitude of the source and sink terms also varies with season, cell size and nutrient species. Seasonality of microphytoplantkon is prominent (Fig. 1C); high during the cold season but low during the warm season. Vertical flux is more important than longitudinal advection for ammonium and orthophosphate pools during the warm season whereas longitudinal advection is more important for nitrite+nirate pools during the cold season (Fig. 1D, 1E, 1F).

The direct effects of the combined hydrodynamic processes were compared with *in situ* production of phytoplankton and nutrients to determine the role of hydrodynamics and biological-chemical processes in water column dynamics of the York River system (Fig. 2). Since vertical advection/ diffusion serves as a source mechanism and longitudinal advection is a sink mechanism in most cases (see Fig. 1), positive values represent vertical flux alone and negative values denote longitudinal export. Changes in pico- and nanophytoplankton biomass due to hydrodynamic processes are small and vary little over time whereas *in situ* production of the small cells is large and fluctuates greatly except for the winter-spring time (Fig. 5A, 5B). However, changes in microphytoplankton biomass due to hydrodynamics are relatively large and fluctuate greatly between "source" and "sink" at the scale of neap-spring tidal cycles during the winter-spring (Fig. 2C). *In situ* production also fluctuates during the winter-spring but is small compared to hydrodynamic processes although the effects of the two are inversely related. The results suggest that *in situ* production is more important than hydrodynamic controls for small cells whereas hydrodynamic processes are more important for large cells.

Hydrodynamics also play a role as a "source" mechanism for ammonium throughout the season, especially summer and fall whereas biochemical processes generally serve as a "sink" mechanism especially during winter season (Fig. 2D). The pattern is reversed for nitrite+nitrate; hydrodynamics serve as a "sink" and biochemical processes serve as a "source" mechanism (Fig. 2E). For orthophosphate, hydrodynamics play a role as a "source" and biochemical processes serve as a "sink" mechanism during summer and fall but the roles are reversed during winter and spring (Fig. 2F).

To further investigate potential influences of physical processes, Figure 3 shows the model outputs for phytoplankton chlorophyll a biomass and nutrients when the processes of advection and diffusion were removed from the model. Chlorophyll *a* concentrations of picophytoplankton did not change greatly but nanophytoplankton chlorophyll *a* concentrations increased slightly. Winter-spring blooms of microphytoplankton completely disappeared when diffusion and advection were removed suggesting that these processes influence the accumulation of large cells during winter-spring in the mesohaline area of the York River estuary. Oscillations in nutrient concentrations observed in the nominal model run during the warm season in 1996 disappeared. 1996's summer peaks of the nutrients also disappeared indicating the importance of physical processes in nutrient dynamics in the study area. Percent changes in concentrations of microphytoplankton, mesozooplankton, and all nutrient pools were greater than 50 % when diffusion and vertical advection were removed from the model (data not shown).

In order to investigate the role of diffusion and vertical advection as a factor influencing phytoplankton and nutrient dynamics, we examined the relationship between upward flows as well as diffusion coefficients (vertical eddy diffusivity, *D*) and model predictions for chlorophyll *a* biomass of phytoplankton and nutrient pools (Fig. 4). Chlorophyll *a* biomass of small cells (pico-, nano-sized) was related negatively to the coefficients and upward flows at the scale of neap-spring tidal cycles (Fig. 4A, 4B). On the other hand, chlorophyll *a* biomass of large cells was related positively (slight) to the coefficients and upward flows (Fig. 4C) suggesting the influence of hydrodynamic processes on phytoplankton dynamics is dependent on size structure and operator at the neap-spring fortnightly time scale. Ammonium showed a positive relationship with vertical eddy diffusivity and upward flow throughout the annual cycle (Fig. 4D). Nitrite+nitrate and orthophosphate showed a positive relationship with the eddy diffusivity during the warm season but was related negatively during the cold season (Fig. 4E, 4F). These results suggest that vertical diffusion (tidal mixing) and advection may play an important role in size-structured phytoplankton and nutrient dynamics in the surface water of the lower York River estuary.

In conclusion, I used a tidally-averaged ecosystem model that incorporated physical mechanisms including advection and diffusion with a neap-spring, fortnightly tidal cycle to investigate the relationship between hydrodynamic processes and size-structured phytoplankton and nutrient dynamics in the mesohaline zone of the York River estuary. The simulated high-frequency fluctuations (days) of small cell population densities were phased with the neap-spring tidal cycle (fortnight) indicating that growth of cells over shorter time frames may be controlled by light availability coupled with water column stratification-destratification, and supported by the input of benthic-regenerated nutrients into the surface water through vertical mixing especially during the warm season in the mesohaline zone. Their growth may be limited by light availability during destratification (tidal mixing) because vertical mixing increases the mixed layer depth and decreases light. In contrast to small cells, biomass accumulation (algal blooms) of large cells may be a consequence of vertical and horizontal transport of cells through advection and diffusion from upriver and bottom water rather than in-situ production. This study suggests that it is important to refine the hydrodynamic processes in the ecosystem for better understanding of phytoplankton dynamics and for better management of water quality in coastal estuarine environments.

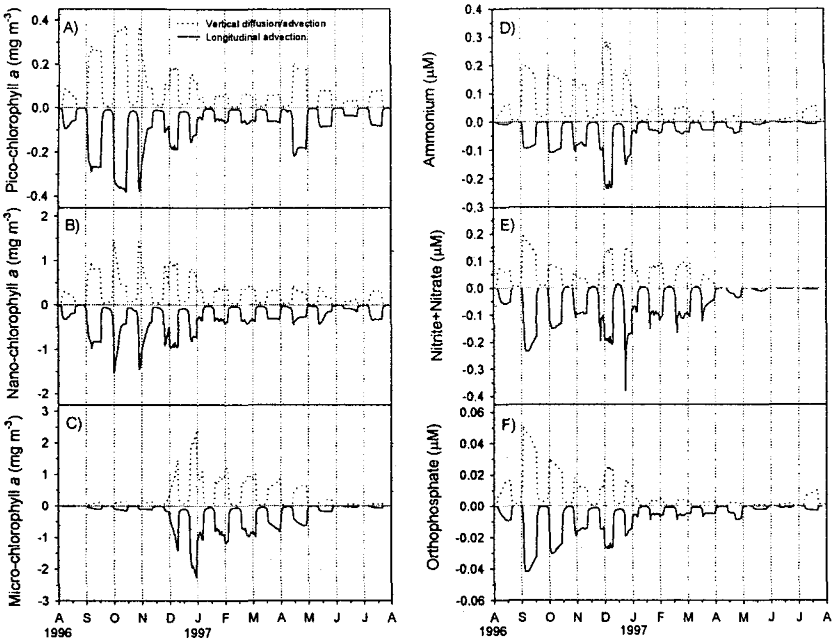

Fig. 1. Temporal distributions of daily changes in concentrations of pico-, nano-, and micro-chlorophyll a (mg m^{-3}) and nutrient (ammonium, nitrite+nitrate, orthophosphate, μM) due to vertical advection/diffusion and longitudinal advection.

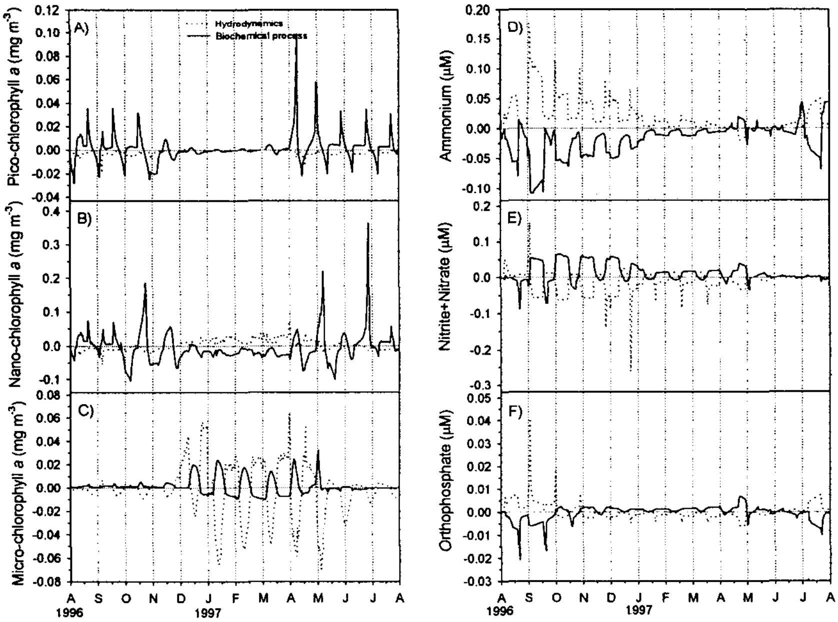

Fig. 2. Temporal distributions of daily changes in concentrations of pico-, nano-, and micro-chlorophyll a (mg m-3) and nutrient (ammonium, nitrite+nitrate, orthophosphate, μM) due to hydrodynamic mechanisms (advection + vertical diffusion) and biochemical processes.

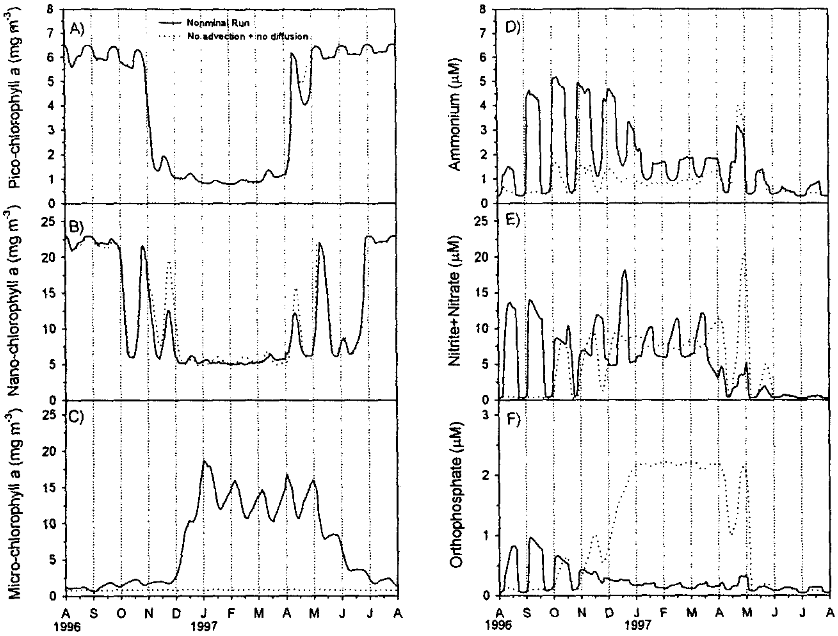

Fig. 3. Results of sensitivity analyses for pico-, nano-, and micro-chlorophyll a (mg m-3) and nutrients (ammonium, nitrite+nitrate, orthophosphate, μM) to examine the effects of advection + vertical diffusion by comparing chlorophyll a and nutrient concentrations between a nominal and sensitivity run when no advection + vertical diffusion were incorporated.

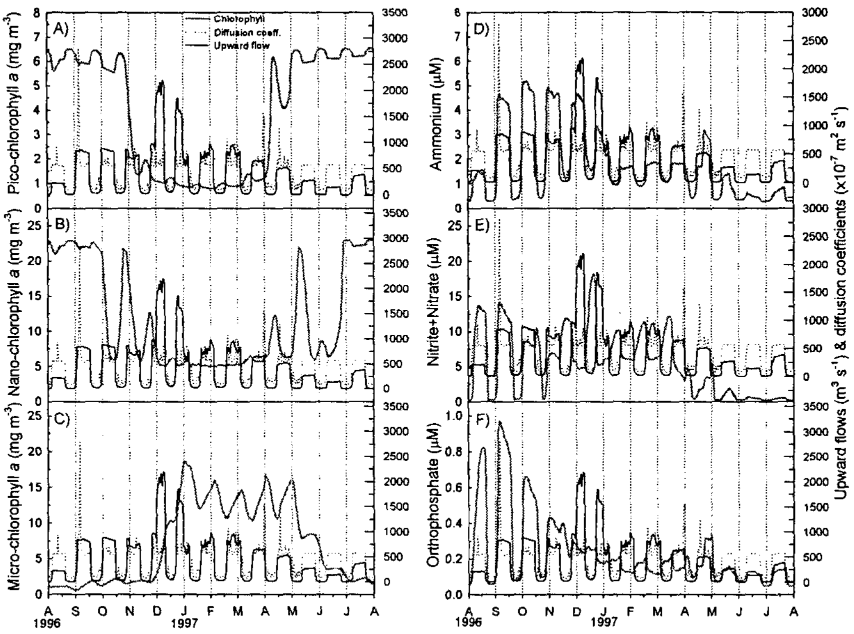

Fig. 4. Temporal distributions of diffusion coefficient, chlorophyll a (pico-, nano-, and micro-sized) and nutrients from the nominal model run of the ecosystem model.

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