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## **Modeling the Lower Chesapeake Bay Littoral Zone & Fringing Wetlands: Ecosystem Processes and Habitat Linkages III: Model Scenarios Related to Water Quality and Submersed Vegetation**

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**Modeling the Lower Chesapeake Bay Littoral Zone  
& Fringing Wetlands: Ecosystem Processes and  
Habitat Linkages**

**III. Model Scenarios Related to Water Quality and  
Submersed Vegetation**

by

**Richard L. Wetzel and Christopher P. Buzzelli**

**An Annual Report Submitted to**

**United States Environmental Protection Agency  
Region III  
Chesapeake Bay Program Office  
410 Severn Avenue  
Annapolis, Maryland 21403**

**Special Report No. 342  
in Applied Marine Science and Ocean Engineering**

**School of Marine Science / Virginia Institute of Marine Science  
College of William and Mary  
Gloucester Point, Virginia 23062**

**July 1997**



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## OVERVIEW

The development and testing of ecological, process-oriented simulation models has been undertaken as part of the Chesapeake Bay Program with particular regard to living marine resources. The research and modeling studies accomplished to date as well as those studies proposed for continuing work will enhance our basic understanding of natural processes and anthropogenic influences that control important natural, living resources. In addition, the results bear directly on the development of effective management strategies for the conservation of natural resources and their long-term survival. These ecosystem process modeling efforts also address in ways the larger scale, water quality and hydrodynamic modeling efforts can not: the development of habitat criteria and management strategies for specific living resources. Coupling these efforts with past and continuing efforts in water quality and hydrodynamic modeling will provide both scientist and manager with a powerful suite of tools for estuarine and coastal systems analysis.

Cooperation between the Modeling and Living Resources Subcommittees over the past few years has led to significant advances in the ability of the Chesapeake Bay Program's eutrophication modeling package to resolve and address living resource and habitat questions. Specifically, the enhancements under development include the addition of submerged aquatic vegetation (SAV), benthic algae, benthic macrofauna, and zooplankton. Their inclusion represents successful cooperation between scientists and managers involved in both living resource and water quality issues.

Enhancements of model applications developed under the Living Resources Subcommittee's Ecosystem Process Modeling Program have also benefited from this collaboration. A specific example is the use of temperature and dissolved oxygen output from the hydrodynamic model component for indirect coupling with the fish bioenergetics models (Brandt et al. 1995). In addition to providing stand-alone model solutions to habitat and resource questions, the Ecosystem Process Modeling Program has established a role of testing enhancements (new formulations, additional trophic levels, and biological-physical couplings) on smaller scale models prior to implementation within the eutrophication model package.

In this vein, we have coupled SAV-littoral zone and emergent marsh habitat models with a tidal exchange model in order to explore the interactions of adjacent intertidal and shallow subtidal zones for predicting water quality, system productivity and resource utilization. These modeling activities at the smaller scale of the littoral zone are essential in that they represent boundary conditions for the larger scale modeling efforts. The models in particular provide linkages between traditional water quality models and ecological processes on time and space scales relevant to specific habitats and target species.

Our previous work has focused on the development and simulation analysis of SAV models and hydrodynamically coupled models of littoral zone habitats (i.e. SAV,



subtidal non-vegetated sand bottoms, intertidal mudflats, and intertidal salt marshes). The SAV models have clearly shown the importance of environmental factors (submarine light, temperature) and biological factors (epiphytic fouling, grazing) for controlling SAV growth, distribution, and long-term population survival. The SAV stand-alone model has proved an accurate predictor of water quality-SAV response and habitat criteria for SAV survival. We have over the past three years revised and expanded the modeling effort to include other components of the littoral zone. This effort will make it easier to relate "littoral processes"—which includes the benthos, SAV, and pelagic habitats—to models of hydrodynamics and water quality extant for Chesapeake Bay and its major tributaries.

The focus of the efforts for this latter period has been on the development, calibration, validation, and simulation analysis of ecosystem process models for specific, highly-distributed components of the estuary which emphasize intertidal wetlands, SAV habitat, and other principal components of the littoral zone. We have refined and implemented the conceptual models of the principal habitats of the littoral zone into numerical simulation models. Incorporating spatially-varying information, such as salinity, nutrient concentration, and bathymetry as forcings can suggest how SAV-driven, phytoplankton-driven, and detritus and benthic microflora-driven food webs function along the tributaries and into Chesapeake Bay. One of our goals has been to formulate both spatially- and temporally-varying forcings in ways which will enable the incorporation of biological productivity and biologically-driven elemental cycling (*e.g.*, for carbon, oxygen, and nitrogen) into larger-scale, water quality and hydrodynamic models.

This report describes our efforts over the period of May 1996 to June 1997 to develop, implement and analyze ecosystem process models for littoral zone areas including fringing wetlands of the lower Chesapeake Bay.

## INTRODUCTION

The estuarine littoral zone is a mosaic of different habitat types that are interconnected by the dynamic exchange of primary production, particulate and dissolved substances, and faunal populations (Correll et al., 1992; Childers et al., 1993; Kneib and Wagner, 1994; Rozas, 1995). A number of coastal studies have focused upon subsystem interactions within coastal marsh and shallow nearshore ecosystems (Wolaver et al., 1983; Stevenson et al., 1988; Dame et al., 1991; Correll et al., 1992; Vorosmarty and Loder, 1994). These studies are important because they quantify material production and exchange in fringing habitats that are situated between channel and upland environments. Although biogeochemical processes in the fringing environments are different than those of the adjacent channel, the two estuarine zones are linked on daily, seasonal, and annual time scales (Malone et al., 1986; Kuo and Park, 1995). Watershed factors such as river flow and nutrient run-off can influence the annual patterns of production and nutrient cycling in the estuarine littoral zone (Correll et al., 1992). In order to assess the potential role of the littoral zone in coastal landscape dynamics it is necessary to gain an understanding of the ecosystem processes and habitat patterns that occur within these



fringing estuarine environments and identify which physical, chemical and/or biological factors control ecosystem dynamics.

Process oriented simulation modeling of ecosystems offers a unique opportunity to organize available information, identify missing data, and analyze the dynamics of various ecosystem components (Christian and Wetzel, 1991). Dynamic simulation models can be used to integrate ecological processes over various combinations of spatial and temporal scales in order to assess the overall properties of ecosystems (Childers et al., 1993). Simulations performed under different combinations of driving factors can be used in ecosystem hindcasting and/or forecasting (Costanza et al., 1990; Cerco and Cole, 1993; Cerco, 1995). Geographic information systems (GIS) can be coupled with process models both to provide a source of spatially referenced input and as an effective method to visualize model output (Costanza et al., 1990; Lee et al., 1992). Simulation models can be used to link field and geographic research methods in the investigation of coastal landscape dynamics (Lee et al., 1992) and can be used to generate new hypotheses and research objectives (Christian and Wetzel, 1991).

This report is the third in a series on ecosystem process modeling of the lower Chesapeake Bay SAV-Littoral Zone. The first report (Buzzelli et al., 1995) presents a detailed description of model conceptualization, development, parameterization, and initial calibration runs. The second report (Buzzelli and Wetzel, 1996) gives the results of sensitivity analyses, model validation and initial runs that address such ecosystem processes as productivity and material exchange between both littoral zone habitats and the offshore channel boundary. This third and last report specifically addresses water quality issues related to SAV and SAV habitat loss or gain. For consistency among reports, we give a brief overview of the model design and structure. For detailed treatment, the reader should consult Buzzelli et al. (1995) and Buzzelli and Wetzel (1996).

## **MODEL DESCRIPTION**

### ***Reference Site Description***

Data for model development, calibration and verification were taken from the literature and to the extent possible from a single reference site in the lower Bay: the Goodwin Islands National Estuarine Research Reserve (GI NERR). The GI NERR is an 800 hectare (ha) littoral zone ecosystem at the mouth of York River, Virginia, in the lower Chesapeake Bay (37E 12= 46@ N, 76E 23= 46@ W). The islands are owned by the College of William and Mary and are managed by the Chesapeake Bay National Estuarine Research Reserve System in Virginia (CBNERRS-VA) of the National Oceanic and Atmospheric Administration (NOAA). The research reserve includes the islands and a buffer zone that extends seaward to the -2.0 m depth contour (MLW); operationally defined as the littoral zone depth limit and the corresponding lateral boundary condition for the tributary water quality-hydrodynamic model. The GI NERR is an oblong island system with a large subtidal shoal extending between the shoreline and the -2.0 m depth



contour. Between -1.0 and -0.5 m (MLW) is approximately 120 hectares of subtidal SAV, mostly comprised of eelgrass (*Zostera marina* L). There is approximately 100 hectares of nonvegetated intertidal habitats, with fine sands and silty sediments, that surround 90 hectares of intertidal marsh vegetated primarily by smooth cordgrass (*Spartina alterniflora*). Some marsh regions are also vegetated by meadow cordgrass (*Spartina patens*), spikegrass (*Distichlis spicata*) and needlerush (*Juncus roemerianus*). The intertidal marsh grades into a salt bush habitat that includes marsh elder (*Iva frutescens*) and groundselbush (*Baccharis halimifolia*). The largest island has a small amount of maritime forest and upland vegetated by loblolly pine (*Pinus taeda*) and several hardwood species. Intertidal and subtidal habitat patterns vary over time (seasonally, interannually) and space (10's to 100's ha). Historical aerial photography depicts long-term stability in the GI NERR eelgrass meadows, but overall erosion and some horizontal migration for intertidal marshes.

### ***Conceptual Model Structure***

Four, hydrodynamically linked submodels were developed to represent the principal littoral zone habitats: (1) nonvegetated subtidal habitats (NVST) composed primarily of coarse sand; (2) vegetated subtidal habitats (VST) dominated by eelgrass; (3) nonvegetated intertidal (NVIT) typical of sand and mudflats; and (4) vegetated intertidal (VIT) dominated by smooth cordgrass. These four habitats and thus the models were selected based on abiotic and biotic characteristics relative to the depth gradient along which they were located. Figure 1 depicts the conceptual model structures for the four littoral zone habitat models based on the four habitat types. Figure 2 gives a more detailed structure for the SAV habitat model. Table 1 gives a list of the model state variables, their mathematical abbreviation and modeled units.

The global forcing functions were tidally varying water level, solar and submarine irradiance, and water temperature. The subtidal and intertidal nonvegetated models had seven state variables each, including: large and small phytoplankton size classes (diatoms (DIA) and other plankton (OP), respectively); labile and refractory particulate organic carbon (LPOC and RPOC); dissolved organic carbon (DOC); total dissolved inorganic nitrogen (TDIN); and sediment microalgae (SM). In addition to these seven state variables, the vegetated subtidal and intertidal habitat models included additional state variables representing epiphyte carbon (ZepiC), and shoot and root-rhizome carbon and nitrogen for eelgrass (ZSC, ZSN, ZRRC, ZRRN) and smooth cordgrass (SSC, SSN, SRRC, SRRN).

### ***Hydrodynamic Model Design***

The four ecosystem process models were hydrodynamically linked by tidal exchange across the boundaries of a sequence of modeled cells representing the NVST, VST, NVIT, and VIT habitats. The cells filled and drained in sequence relative to the



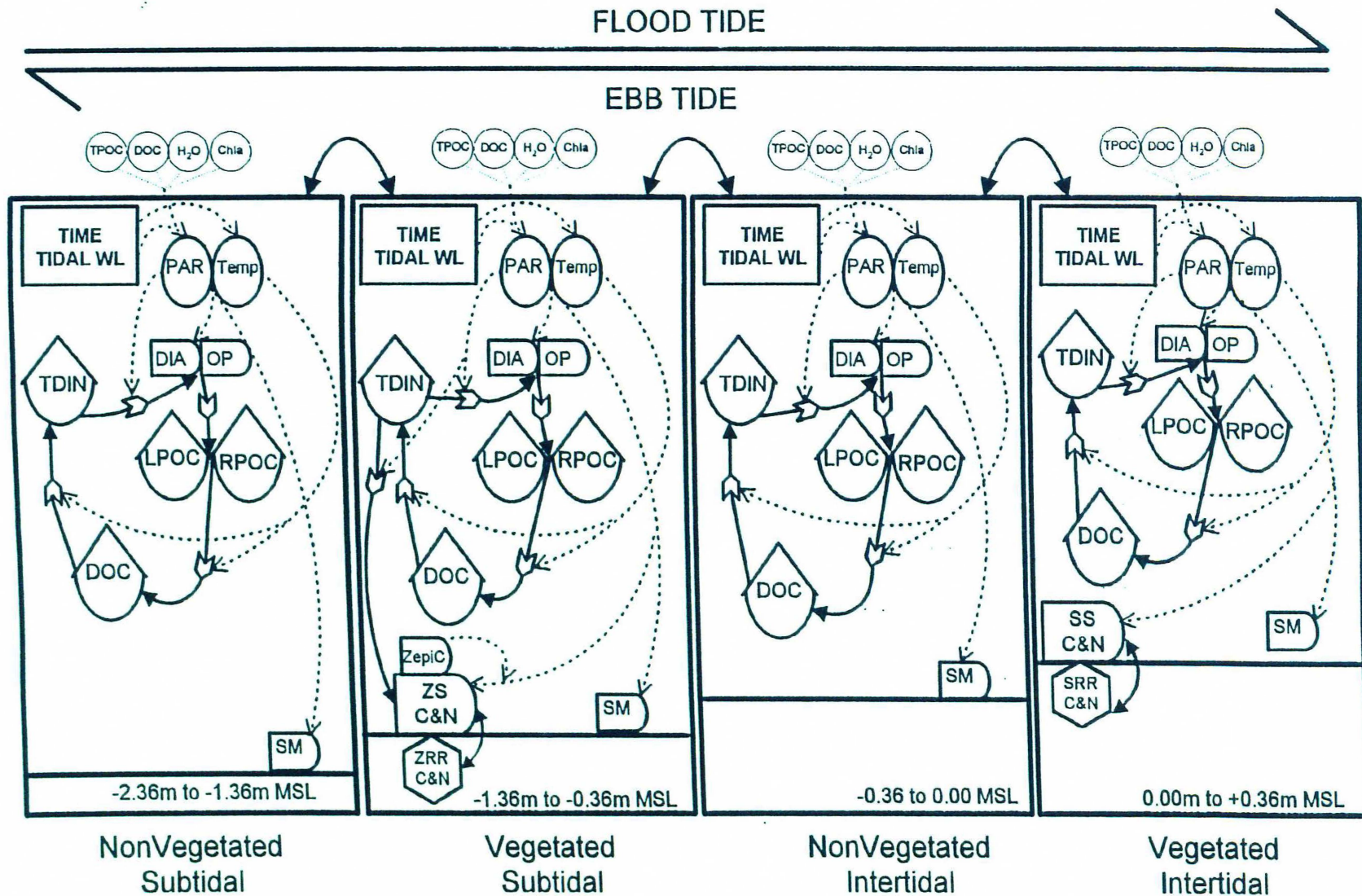


Figure 1. Conceptual SAV-Littoral Zone model for the lower Chesapeake Bay. Transport of dissolved and particulate materials is governed by tidally driven water exchange between the channel boundary and four littoral zone habitats. For a detailed discussion of the conceptual and mathematical structure see Buzzelli, et al. 1995.

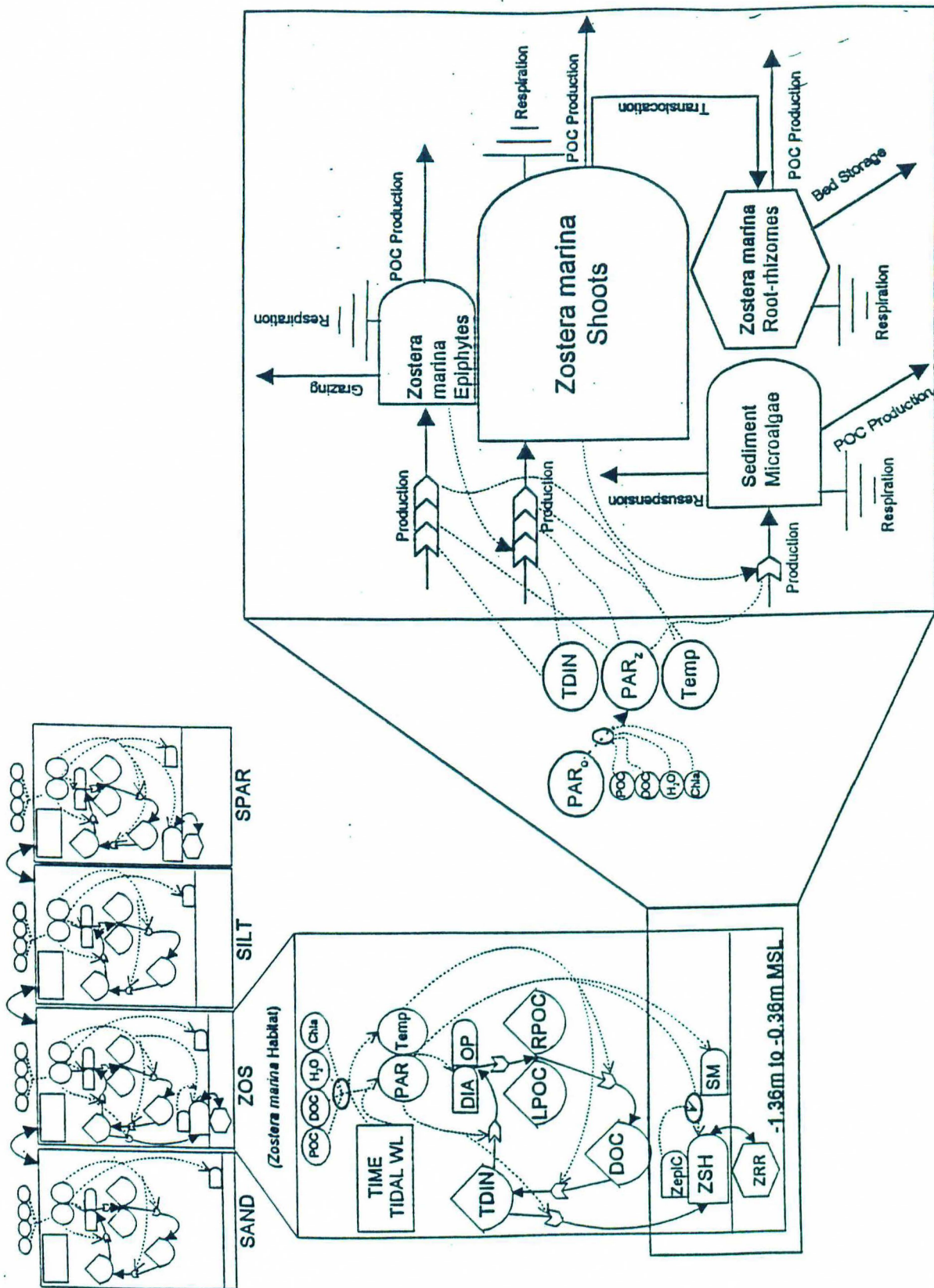


Figure 2. A more detailed illustration of the SAV habitat conceptual model. Dashed lines in the diagram represent information flows (i.e. controls) while solid lines represent material flows.



Table 1. List of state variables for habitat models. Each habitat model includes the first 7 state variables listed. In addition to the basic seven the vegetated subtidal habitat model (VST) includes those related to *Zostera marina* while the vegetated intertidal habitat model (VIT) has those related to *Spartina alterniflora*.

ABBREV.	DESCRIPTION	UNITS
DIA	Diatom Carbon Mass	gC
OP	Other Plankton Carbon Mass	gC
LPOC	Labile Particulate Organic Carbon	gC
RPOC	Refractory Particulate Organic Carbon	gC
DOC	Dissolved Organic Carbon	gC
TDIN	Total Dissolved Inorganic Nitrogen	$\mu\text{M}$
SM	Sediment Microalgae	$\text{gC m}^{-2}$
ZSC	<i>Zostera marina</i> Shoot Carbon	$\text{gC m}^{-2}$
ZSN	<i>Zostera marina</i> Shoot Nitrogen	$\text{gN m}^{-2}$
ZRRC	<i>Zostera marina</i> Root-Rhizome Carbon	$\text{gC m}^{-2}$
ZRRN	<i>Zostera marina</i> Root-Rhizome Nitrogen	$\text{gN m}^{-2}$
ZepiC	<i>Zostera marina</i> Epiphytic Biomass	$\text{gC m}^{-2}$
SSC	<i>Spartina alterniflora</i> Shoot Carbon	$\text{gC m}^{-2}$
SSN	<i>Spartina alterniflora</i> Shoot Nitrogen	$\text{gN m}^{-2}$
SRRC	<i>Spartina alterniflora</i> Root-Rhizome Carbon	$\text{gC m}^{-2}$
SRRN	<i>Spartina alterniflora</i> Root-Rhizome Nitrogen	$\text{gN m}^{-2}$

depth gradient with the output from one cell providing the input for the next in the sequence dependent on tidal stage (i.e. ebb or flood periods). The nonvegetated subtidal habitat was bounded laterally by an infinite source/sink representing the offshore channel. The vegetated marsh was bordered by the upland with no exchange across the marsh-upland boundary. Watershed or upland exchanges were assumed to be zero because the Goodwin Islands had little upland area and are isolated from the mainland. The cell (habitat) volume changed with each model time or integration interval (dt). Tidally driven exchanges for water column constituents (i.e. phytoplankton, DOC, LPOC, RPOC, and TDIN) were derived using finite difference solutions to equations for mass exchanges between a channel and an adjacent control volume in both flood and ebb directions (Kuo and Park 1995). This approach assumes no diffusion, no advection, and that the water within each cell is instantly mixed and homogeneous during each time-step. The change in tidal height with each time step was multiplied by habitat wet area to derive the changes in habitat volumes used in the simulation of water column processes. By definition, subtidal habitat wet areas are constant. Intertidal habitat wet areas vary as a function of tidal inundation and were derived using a hypsometric relationship. Hypsometry was used



because it provided a concise method for representing the cumulative characteristics of basin morphology (Friedrichs and Aubrey 1994; Strahler 1952). The area-height relationship of a hypsometric curve provided a better approximation for habitat inundation regimes than did a linear 2-D profile, because it included the effects of shoreline curvature (Boon and Byrne 1981; Friedrichs and Aubrey, 1994). Also, hypsometric determination of inundation can be useful in the analysis of wetland biogeochemical cycling (Childers et al. 1993; Eiser and Kjerve 1986).

The tidal exchange equation for a constituent (*e.g.*, chlorophyll a) of mass  $M_i$  where the subscript  $I = \{1, \dots, 4\}$  represented each of four habitats is given below.

$$\frac{\Delta M_i}{\Delta t} = (\alpha - m) \bullet M_i + \left[ \frac{C_k \bullet \Delta h}{\Delta t} + b \right] \bullet A_i(t) \begin{cases} \Delta h > 0 (\text{flood}): k = i - 1 \\ \Delta h < 0 (\text{ebb}): k = i \end{cases}$$

Note that  $M_i$  is the total mass of a water borne constituent contained in the cell or habitat volume and can be calculated as  $C_i \bullet h(t) \bullet A(t)$ , where  $C_i$  is the water column concentration,  $h(t)$  is time varying water depth and  $A(t)$  is the time varying wetted area of the habitat.  $A(t)$  was constant for the subtidal habitat, but variable for the intertidal habitats. The tidally varying water height,  $h$ , was referenced to mean sea level, and its change from one model time-step to the next was represented as  $\Delta h$ . Other processes affecting state variable masses were growth or biochemical production (" $\alpha$ "), losses from biological uptake or mortality and/or grazing ( $m$ ); and exchanges with the benthos ( $b$ ) In the present model,  $I=0$  represented the channel boundary condition.

### ***Ecosystem Processes Model Design***

Ecological processes represented in the models for the various habitats included the principal factors controlling the uptake and loss of organic carbon and nitrogen as the primary limiting nutrient in these habitats. Detailed treatment of the mathematical structure, interaction coefficients and data sources for the governing equations are given in Buzzelli et al. (1995) and Buzzelli and Wetzel (1996) and are beyond the scope of this report. Given below is a general description of the ecological processes modeled and the state variables affected.

Primary production ( $\text{gC m}^{-2}$  or  $\text{m}^{-3} \text{d}^{-1}$ ) was modeled using the rates of gross production, respiration, and loss through mortality or grazing. Phytoplankton (diatoms, DIA; and other plankton, OP) were also influenced by exudation, sedimentation, and transport to adjacent habitats. The mathematical representations of the basic metabolic rate processes in diatoms, other plankton, sediment microalgae, and *Spartina alterniflora* were all similar. Gross production was affected by temperature, irradiance, and dissolved inorganic nitrogen. Respiration followed an exponential relationship with temperature (Cercio and Cole 1994). Production and mortality were represented by Gaussian functions



with temperature (Cerco and Cole 1994). Phytoplankton exudation and sedimentation were also modeled according to Cerco and Cole (1994). Sediment microalgae were lost through resuspension and grazing by higher trophic levels. The formulations for carbon productivity by *Zostera marina* and its epiphytes were taken from Wetzel and Neckles (1986) and Wetzel and Meyers (1994). Nitrogen uptake by the shoots and root-rhizomes of *Zostera marina* were modeled using Michaelis-Menten kinetics, limited by feedback functions based on the maximum and minimum nitrogen contents of the tissues. *Zostera marina* shoots and root-rhizomes maintained C:N ratios through the proportional nitrogen loss terms. Nitrogen was translocated only from root-rhizomes to shoots in order to meet shoot nitrogen demand. Nitrogen translocation was also limited by feedback functions based on the maximum and minimum nitrogen contents of the tissues. The formulations for nitrogen state variables of *Spartina alterniflora* were similar to those of *Zostera marina*, except there was no shoot uptake of nitrogen in *Spartina alterniflora*.

Water column particulate organic carbon (POC;  $\text{gC m}^{-3}$ ) was influenced by production, hydrolysis, settling, and exchange between adjacent habitats. POC was produced from phytoplankton and a fractional loss term added to that gained through resuspended sediment microalgae. POC was divided into labile and refractory fractions and rates of hydrolysis were calculated using an exponential relationship with temperature (Cerco and Cole 1994). LPOC and RPOC both settled from the water column and were exchanged laterally. DOC was influenced by production, remineralization, and exchange with adjacent habitats. Hydrolyzed POC provided the DOC production rate and the remineralization rate was controlled by a temperature function and the refractory DOC fraction (Cerco and Cole 1994). Water column TDIN ( $\text{mmoles m}^{-3}$ ) was influenced by production, autotrophic uptake, sediment-water fluxes, and exchange with adjacent habitats. Production was calculated using the DOC remineralization rate and the C:N ratio of dissolved organic matter. TDIN was removed from the water column through uptake by phytoplankton in all habitat models and by *Zostera marina* in the vegetated subtidal habitat model. TDIN was exchanged vertically between the sediment and the overlying water column, based on rates determined from core incubations (Buzzelli 1996).

### ***Model Applications***

For this report, a series of model runs (model scenarios) were undertaken to address water quality and habitat issues related to SAV dynamics. In particular, model runs were made to investigate three specific issues;

1. the effects of changes in water quality relative to nutrients (nitrogen is these cases),
2. the effects of changes in water quality relative to submarine irradiance (i.e. light as photosynthetically active radiation, PAR), and,
3. the overall effects (ecosystem level) of changes in SAV distribution and abundance within the littoral zone.



All model runs were compared to model runs representative of nominal conditions at the Goodwin Islands sites (mouth of the York River). “Nominal” runs reflect water quality conditions in the lower estuary that have not changed demonstrably since 1984 (the beginning of our long term monitoring data base for littoral zone habitats of the York River estuary).

To address altered water quality regimes, the boundary conditions (channel waters) were varied relative to specific water quality parameters. Altered nutrient regimes in the littoral zone were simulated by either halving (0.5X) or doubling (2X) channel TDIN concentrations relative to nominal conditions. Similarly, altered littoral zone submarine light regimes were simulated by changing channel concentrations of chlorophyll, DOC, and POC. Potential combined light-nutrient effects were simulated by changing all channel boundary conditions. Table 2 summarizes changes made in channel boundary water concentrations for the various model scenarios.

Table 2. Channel boundary concentrations used for model simulations to investigate changes in water quality on SAV habitat characteristics.			
Parameter	Nominal Case	0.5X Case	2.0X Case
DIN ( $\mu\text{M}$ )	20	10	40
Chlorophyll ( $\text{mg m}^{-3}$ )	3-20	1.5-10	6-40
POC ( $\text{gC m}^{-3}$ )	5.0	2.5	10.0
DOC ( $\text{gC m}^{-3}$ )	0.70	0.35	1.40

To address changes in SAV coverage (item #3 above), two additional model scenarios were created. Historical aerial photographs depict large variations in the distribution and apparent density of SAV at the Goodwin Islands (C.P. Buzzelli, pers. obs.). There have been times with essentially no SAV present (1937 and 1982) and times when coverage extended to approximately 2m depth (1952 and 1971). Changes in the distribution and abundance of SAV would alter ecosystem carbon and nitrogen cycling characteristics, influence material budgets, and trophic structure (i.e. links to higher food webs). To simulate the range of conditions observed in the long term record, model runs were made where no SAV were present (NO *Zostera* case) and where SAV populated the entire subtidal area (ALL *Zostera* case). The models were run under these two extreme conditions and the output compared to present (nominal) conditions to evaluate the potential changes in total ecosystem production, sediment microalgal production, phytoplankton and nitrogen flux, and nitrogen demand.



## MODELING RESULTS

### *Physical Variables*

The exchange of materials between the channel boundary and the littoral zone habitats is controlled by tidally driven, water movement. Thus both the volume and water depth in a habitat varies constantly. The model equation for tides was derived from the 1993 tidal data base for Gloucester Point, Virginia and includes the largest five amplitudes from the harmonic analysis (Buzzelli, et al., in review). Depending upon the desired resolution, both the spring/neap and semi-diurnal periodicity are apparent in the simulation output (Fig. 3A). Spring tidal height was ca. 0.5 m relative to mean sea level (MSL) in the late February through April (Fig. 3A). Depth in the subtidal sand habitat varied from 1.5 m at spring low to 2.4 m at spring high tide (Fig. 3B). The seagrass habitat was generally less than 1.0 m deep but increased to 1.4 m during March and April spring tides (Fig. 3B). Water temperature was highest in July (30° C) and was lowest in January (2° C; Fig. 3C). Submarine irradiance (PAR) had a bimodal annual distribution with depressed values in June due to increased water column chlorophyll a concentrations (Fig. 3D). Water column PAR ( $PAR_z$ ) approached 1200  $\mu E m^{-2} s^{-1}$  in May and July while the light available to *Zostera marina* leaves ( $PAR_{leaf}$ ) was 1000  $\mu E m^{-2} s^{-1}$  at these same times (Fig. 3D). Light for sediment microalgae ( $PAR_{SM}$ ) was reduced ca. 25% relative to  $PAR_z$  but was similar to  $PAR_{leaf}$  beginning in late August as epiphyte biomass declined (Fig. 3D). Annually, an average of approximately 16.5% of the incident light ( $PAR_o$ ) was attenuated by depth due to the combined effects of chlorophyll a, POC, and DOC; 18.1% was attenuated by epiphyte biomass which resulted in 65.4% of the incident light available to seagrass leaves ( $PAR_{leaf}$ ). An average of 40% of the incident light was available to the sediment microalgae in the seagrass habitat.

### *Water Column Concentrations*

Tides are the principle hydrodynamic force in the model and the spring/neap tidal patterns were evident in the simulated water column variables. Figure 4 gives the simulated annual concentrations of the principal water quality constituents for the three boundary condition scenarios. The submarine light attenuation coefficient ( $k_d$ ) was inversely proportional to habitat depth and directly proportional to water column POC, DOC and chlorophyll concentrations. Light attenuation ranged 0.2-0.4  $m^{-1}$  for most of the year but was 0.6-1.0  $m^{-1}$  during the spring bloom (Fig. 4A). The maximum value of  $k_d$  was reduced to 0.6  $m^{-1}$  with the 0.5X channel concentrations. The range in  $k_d$  increased to 0.3-1.4  $m^{-1}$  when channel concentrations were doubled (Fig. 4A). Nominal water column chlorophyll a was greatest at 9  $mg m^{-3}$  during the phytoplankton spring bloom in May and June (Fig. 4B). Model chlorophyll a concentrations were low around 1  $mg m^{-3}$  for most of the year except for a smaller peak near 3  $mg m^{-3}$  in the fall. Maximum water column chlorophyll a was reduced to 6.0  $mg m^{-3}$  when channel boundary concentrations were halved (0.5X) and increased to 14.0  $mg m^{-3}$  when channel boundary concentrations were doubled (Fig 4B). POC concentrations fluctuated between 0.4 and 1.0  $gC m^{-3}$  in the nominal version and decreased or increased slightly in the 0.5X and 2X scenarios,



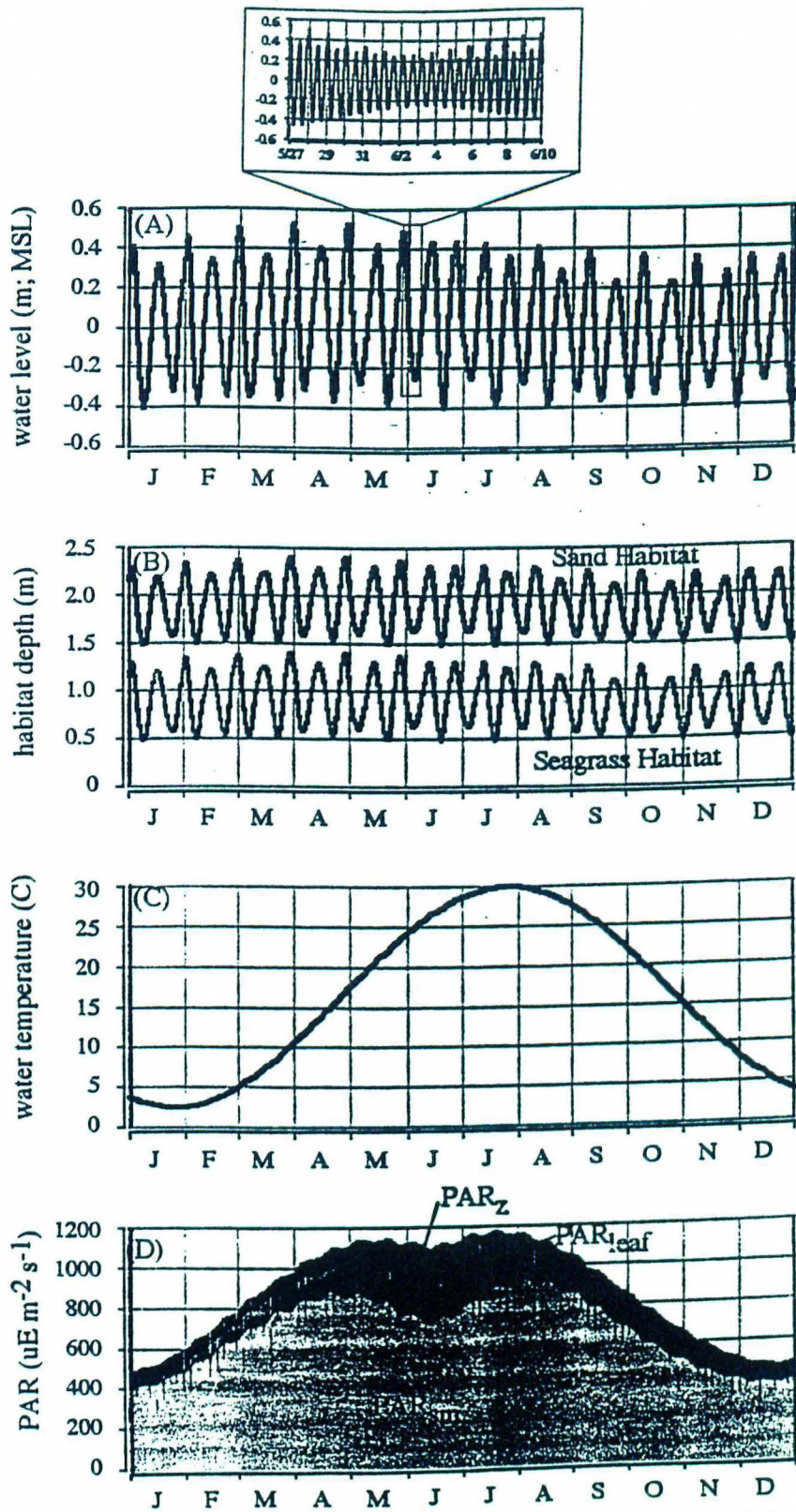


Figure 3. Simulated physical forcing functions for the SAV habitat model. (A) Annual pattern of tidal water levels (m) for an annual cycle with a 14 day lunar cycle shown in the inset to illustrate the diurnal pattern. (B) Annual depth patterns in the subtidal and SAV habitats (m). (C) Annual temperature curve for Gloucester Point, Virginia. (D) Annual light curves at depth ( $\text{PAR}_z$ ), at the seagrass canopy height ( $\text{PAR}_{\text{leaf}}$ ), and the sediment surface available for sediment microalgae ( $\text{PAR}_{\text{sm}}$ ).



respectively (Fig. 4C). DOC were higher than POC concentrations with a distinct peak corresponding to the spring phytoplankton bloom in the nominal version ( $4.5 \text{ gC m}^{-3}$ ; Fig. 4D). The maximum DOC concentration decreased to  $2.8 \text{ gC m}^{-3}$  when channel concentrations were halved and increased to ca.  $7.0 \text{ gC m}^{-3}$  when concentrations were doubled. Nominal DIN concentrations were highest at  $10 \text{ } \mu\text{moles l}^{-1}$  in the winter and summer (Fig. 4E) and exhibited an overall inverse relationship with chlorophyll a. Maximum DIN concentration increased to  $20 \text{ } \mu\text{moles l}^{-1}$  in the 2X treatment. DIN concentrations were reduced to very low levels in May and June for the nominal and 2X scenarios but were maintained at ca.  $2.5 \text{ } \mu\text{moles l}^{-1}$  during the same time span in the 0.5X trial (Fig. 4E).

### ***Rates of Primary Production***

Table 3 summarizes the simulated effects of the 0.5X model scenario on primary production by the various autotrophic groups in the SAV habitat model. Halving the channel boundary DIN concentration from  $20 \text{ } \mu\text{moles l}^{-1}$  to  $10 \text{ } \mu\text{moles l}^{-1}$  decreased the annual rate of phytoplankton production by 2.5% and epiphytes by 1.5% (Table 3). The 0.5X DIN treatment increased the annual production of sediment microalgae by 0.2% and of *Zostera marina* by 0.4%. When channel chlorophyll a, POC, and DOC concentrations were halved, phytoplankton production decreased by 41.9% while the rates for other producers increased 3.9-9.4% (Table 3). A decrease in all channel boundary concentrations resulted in a 44.7% decline in phytoplankton production but enhanced the rates of other producers by 4.2-9.6% (Table 3). The relative differences between model scenarios suggest that the effects of reduced channel chlorophyll a, DOC, and POC (i.e. light effects) had a greater influence on annual rates of primary production than reduced channel DIN concentration (i.e. nutrient effects). *Zostera marina* shoots accounted for 51% of the seagrass habitat annual production in the nominal and 0.5X scenarios while root-rhizomes accounted for 11.5%. Epiphyte production varied 12.6-13.4% among the different 0.5X trials. The sediment microalgal fraction increased by only 0.4% relative to nominal when all of the channel boundary concentrations were decreased. The greatest effect was evident in the phytoplankton component. When all channel boundary concentrations were decreased by 50%, phytoplankton contribution to annual habitat production decreased by 47% (1.55% to 0.83).

Table 4 summarizes the effects of the 2.0X model scenario on primary production by the various autotrophic groups in the SAV habitat model. Doubling the channel boundary DIN concentration from 20 to  $40 \text{ } \mu\text{moles l}^{-1}$  increased annual phytoplankton production by 8.9% and epiphytes by 6.0% (Table 4). Annual production of sediment microalgae and *Zostera marina* decreased by 0.4% and 1.5%, respectively (Table 4). When channel chlorophyll a, POC, and DOC concentrations were doubled, phytoplankton production increased by 61.3%. The same treatment decreased the rates of the other producers in the seagrass habitat by 10.8-17.2% (Table 4). An increase in all channel boundary concentrations resulted in a 69.3% increase in phytoplankton production but decreased the rates of the other producers (Table 4). The relative differences between model scenarios suggests that the effects of increased channel chlorophyll a, DOC, and



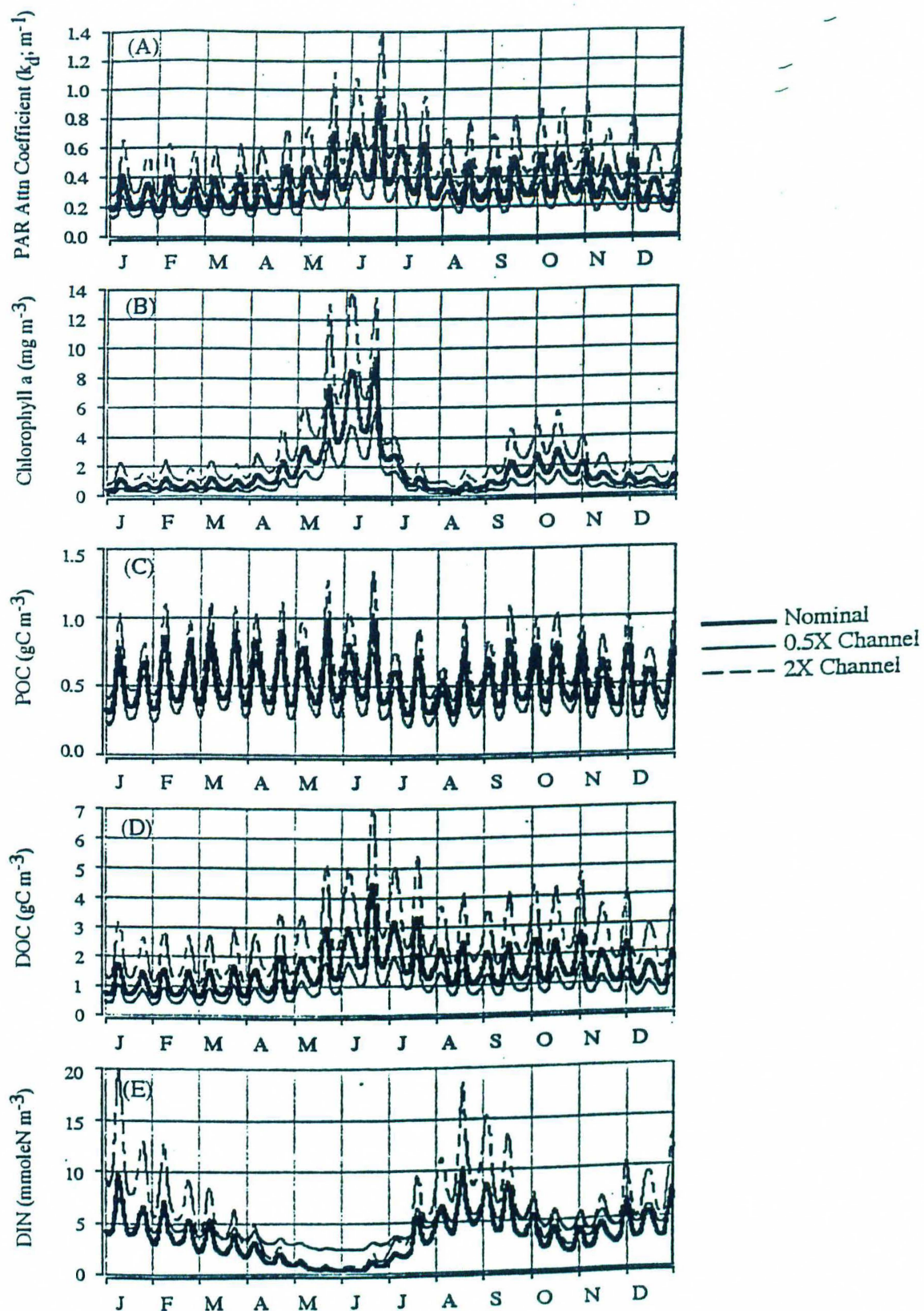


Figure 4. Simulated annual patterns for water quality constituents important in governing SAV habitat dynamics and restoration criteria under different channel boundary conditions: nominal, 0.5X and 2.0X scenarios (see text). (A) PAR attenuation coefficient,  $k_d$  ( $m^{-1}$ ); (B) Chlorophyll ( $mg\ m^{-3}$ ); (C) Particulate organic carbon ( $gC\ m^{-3}$ ); (D) Dissolved organic carbon ( $gC\ m^{-3}$ ); (E) Dissolved inorganic nitrogen ( $\mu M$ ).



POC had a greater influence on annual rates of primary production than increased channel DIN concentration. Epiphyte annual production increased by 6.0% with 2X channel DIN concentrations but decreased by 14% with a 2X increase in the channel constituents that influence light (Table 4). *Zostera marina* shoots accounted for 50-51% and root-rhizomes 11.4% of the annual production in the seagrass habitat in the 2X scenarios. The epiphyte contribution to annual production varied 12.2-13.6% among the 2X scenarios and the response differed depending on treatment. Increased DIN favored epiphyte production while increased POC, DOC and chlorophyll decreased epiphyte production which suggests decreased light availability had a more

Table 3. Effects of halved (0.5X) channel concentrations of DIN, Chlorophyll, POC and DOC on annual productivity ( $\text{gC m}^{-2} \text{yr}^{-1}$ ) by primary producers in the SAV habitat. The percent change ( $\Delta\%$ ) is the annual increase (+) or decrease (-) relative to nominal model simulations. Nutrient (nitrogen) effects were tested by halving the channel boundary DIN concentrations, light effects (indicated in table as 'Light') were tested by halving the principal water column constituents controlling light attenuation (chlorophyll, DOC, and POC), and all variables were halved to test the interactive effects of nutrients and light. All rates are reported in  $\text{gC m}^{-2} \text{yr}^{-1}$

Producer	Nominal	0.5X DIN	$\Delta\%$ DIN	0.5X Light	$\Delta\%$ Light	DIN x Light	$\Delta\%$ All
Phyto-plankton	12.4	12.1	-2.5	7.2	-41.9	6.87	-44.7
Sediment. Microalgae	117.8	118.1	+0.2	128.9	+9.4	129.1	+9.6
Zostera Shoots	247.2	248.3	+0.4	257.0	+3.9	257.6	+4.2
Zostera R/R*	55.6	55.8	+0.4	57.8	+3.9	57.9	+4.2
Zostera Epiphytes	62.2	61.2	-1.5	67.7	+8.9	66.1	+6.4

\*R/R = Eelgrass roots and rhizomes.

pronounced effect than nutrients. The sediment microalgal fraction did not change among the 2X scenarios. The greatest effect was evident in the phytoplankton component. When all channel boundary concentrations were doubled, phytoplankton contribution to annual habitat production increased by 46% (1.55% to 2.86%).

### ***Long-term Zostera marina Response***

The potential impacts of altered water quality included subtle differences in the annual productivity rates of *Zostera marina* that could have cumulative implications over



many years. Ten year model simulations of *Zostera marina* shoot, root-rhizome, and epiphyte biomass were generated using the 0.5X and 2X channel boundary concentration model versions (Fig. 5). When channel boundary concentrations were reduced, *Zostera marina* maximum shoot biomass increased from approximately 95 gC m<sup>-2</sup> to 120 gC m<sup>-2</sup> by the tenth year of simulation (Fig. 5A). Root-rhizome maximum biomass increased each year but epiphyte biomass remained stable at ca. 22 gC m<sup>-2</sup> when channel concentrations were reduced (Fig. 8A). The 12% decrease in *Zostera marina* annual production was evident when channel boundary concentrations were doubled (Fig. 5B). Maximum shoot biomass declined from 85 gC m<sup>-2</sup> to ca. 50 gC m<sup>-2</sup> over the 10 years. Root-rhizome maximum biomass was reduced each year as epiphyte maximum biomass remained stable at ca. 20 gC m<sup>-2</sup> over the 10 year simulation (Fig. 5B).

Table 4. Effects of doubled (2.0X) channel concentrations of DIN, Chlorophyll, POC and DOC on annual productivity (gC m<sup>-2</sup> yr<sup>-1</sup>) by primary producers in the SAV habitat. The percent change ( $\Delta\%$ ) is the annual increase (+) or decrease (-) relative to nominal model simulations. Nutrient (nitrogen) effects were tested by doubling the channel boundary DIN concentrations, light effects (indicated in table as 'Light') were tested by doubling the principal water column constituents controlling light attenuation (chlorophyll, DOC, and POC), and all variables were doubled to test the interactive effects of nutrients and light. All rates are reported in gC m<sup>-2</sup> yr<sup>-1</sup>

Producer	Nominal	2.0X DIN	$\Delta\%$ DIN	2.0X Light	$\Delta\%$ Light	DIN x Light	$\Delta\%$ All
Phyto- plankton	12.4	13.5	+8.9	20.0	+61.3	21.0	+69.3
Sediment. Microalgae	117.8	117.3	-0.4	97.6	-17.2	97.1	-17.6
Zostera Shoots	247.2	243.6	-1.5	220.5	-10.8	217.9	-11.9
Zostera R/R*	55.6	54.8	-1.5	49.5	-10.9	49.0	-12.0
Zostera Epiphytes	62.2	65.9	+6.0	53.2	-14.3	55.1	-11.3

\*R/R = Eelgrass roots and rhizomes.

### SAV Coverage Scenarios

Table 5 summarizes the results of model runs where large scale changes in the distribution and abundance of *Zostera* were simulated. Three scenarios are presented in the table; the nominal (current) case; removal (or loss) of all SAV from the habitat, and the case where the habitat was completely populated with SAV.

There was a 45% increase in net annual ecosystem carbon production ( $3.05 \times 10^6$

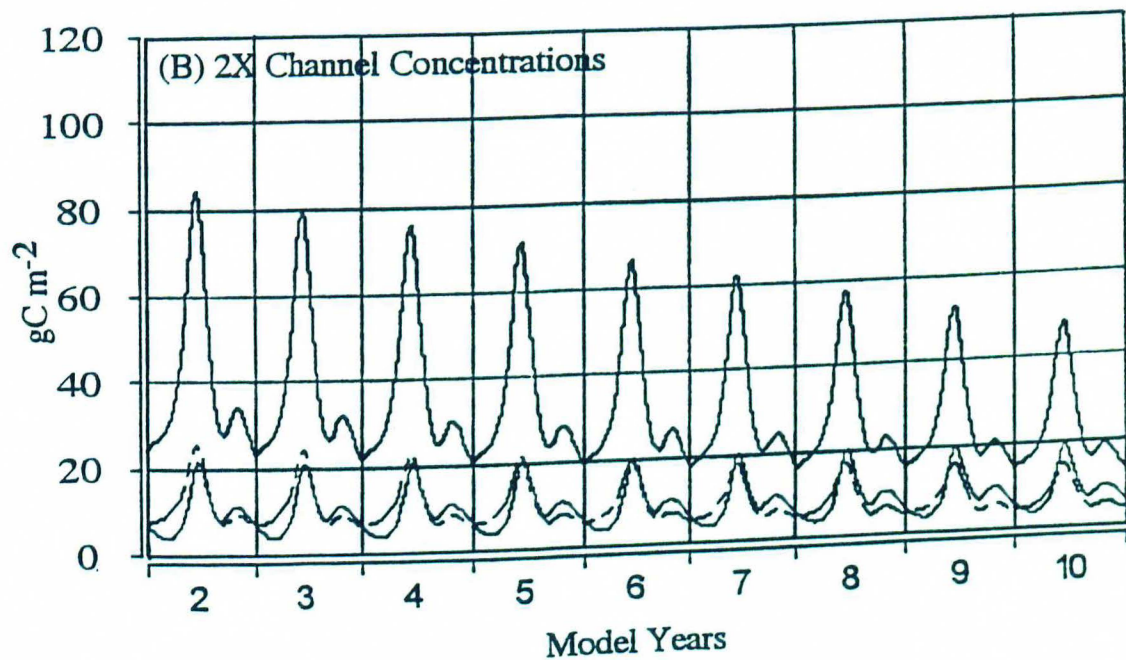
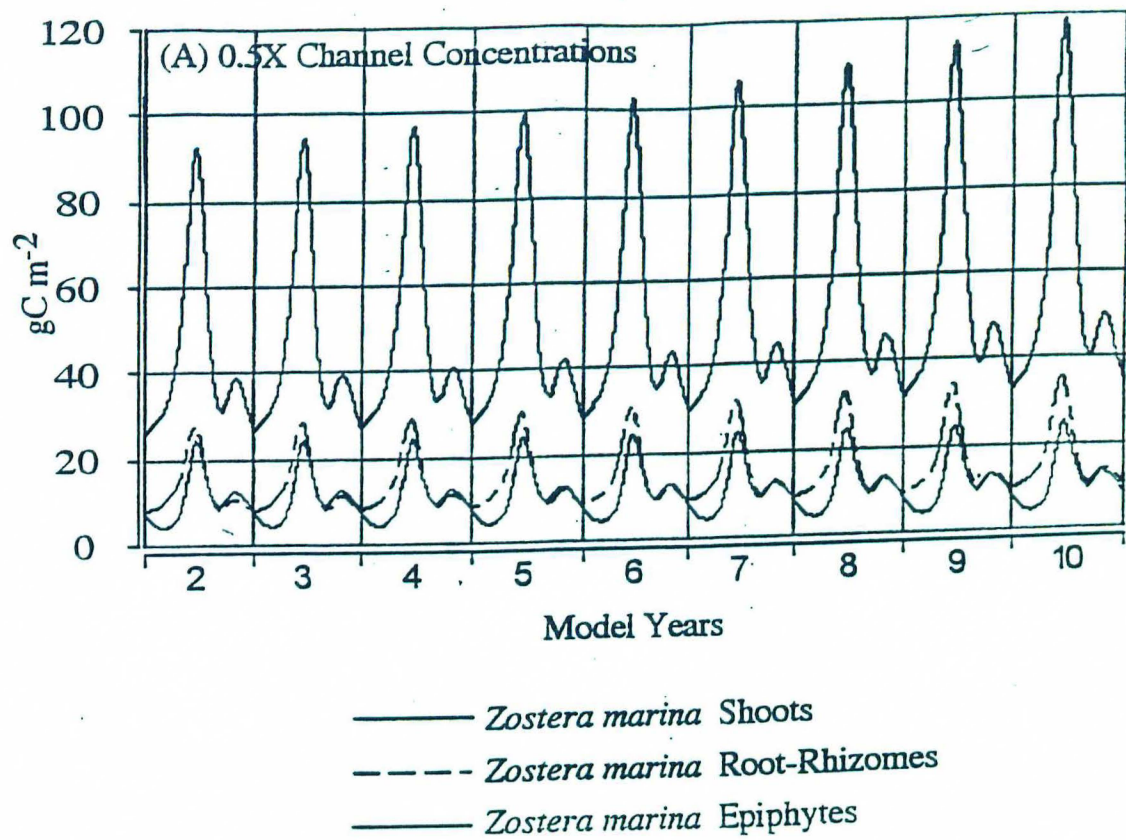


Figure 5. Long term effects of 0.5X (A) and 2.0X (C) channel concentrations on the biomass of *Zostera marina* shoots, roots-rhizomes, and epiphytes over a 10 year simulation.



gC yr<sup>-1</sup>) in the All Zostera trial relative to nominal and a 53.1% increase relative to the No Zostera trial (Table 5). The fraction of sediment microalgae increased to 66.9% when *Zostera marina* was removed from the ecosystem but was reduced to about 25% of the total in the All Zostera trial. The ecosystem imported a similar amount of phytoplankton annually in both the nominal and No Zostera model trials ( $-3.77 \times 10^7$  gC). Annual ecosystem phytoplankton import was reduced to  $-1.93 \times 10^7$  gC in the All Zostera trial (Table 5). There was little variation in annual TDIN import among the model trials (approximately  $-1.8 \times 10^7$  gN). The 45% increase in carbon production required a 28% increase in nitrogen demand from  $1.65 \times 10^8$  gN in the nominal case to  $2.28 \times 10^8$  gN in the all Zostera trial. There was 14.9% less carbon production but there was 6% more nitrogen demand among the nominal and No Zostera trials (Table 5).

Table 5. Comparison of ecosystem properties predicted by the SAV-Littoral Zone model for three SAV scenarios: Nominal version, No SAV (Zostera) condition, and the case where the entire subtidal habitat is populated by SAV (All Zostera). The nominal case represents current conditions with SAV occupying 118 hectares. The All Zostera equals a total area of 498 hectares. A negative flux denotes an annual import of the water column constituent to the littoral zone from the offshore channel.

Property	Model Scenario		
	Nominal	No Zostera	All Zostera
C Production (gC yr <sup>-1</sup> )	$1.68 \times 10^9$	$1.43 \times 10^9$	$3.05 \times 10^9$
SM Production (% Total)	48.4%	66.9%	25.1%
Plankton Flux (gC yr <sup>-1</sup> )	$-3.77 \times 10^7$	$-3.77 \times 10^7$	$-1.93 \times 10^7$
DIN Flux (gN yr <sup>-1</sup> )	$-1.81 \times 10^7$	$-1.78 \times 10^7$	$-1.83 \times 10^7$
N Demand (gN yr <sup>-1</sup> )	$1.65 \times 10^8$	$1.75 \times 10^8$	$2.28 \times 10^8$

## DISCUSSION

The importance of submersed aquatic vegetation (SAV) in Chesapeake Bay has been recognized through the implementation of research programs, modeling efforts, and the establishment of habitat criteria for their conservation and restoration (Batuik et al., 1992; Stevenson et al., 1993; Dennison et al., 1993; Gallegos, 1994; Madden and Kemp, 1996). SAV distribution and abundance is light limited but other factors such as temperature, currents, and nutrient availability also influence plant growth and survival (Pregnull et al., 1984; Dennison, 1987; Fonseca and Kenworthy, 1987; Moore, 1996). The littoral zone makes up ca. 40% of the subtidal Chesapeake Bay and rates of primary production and nutrient cycling are enhanced compared to the mainstem and tributary channels (Malone et al., 1986; Kuo and Park, 1995). Predictive models of biogeochemical cycling within the estuarine littoral zone are necessary to provide information and output for the refinement of larger water quality models (Kuo and Park 1995). The goal of this study was to use a simulation model of the estuarine littoral zone to predict the potential effects of altered water quality upon seagrass habitat properties in the lower Chesapeake Bay tributaries such as the York River.



Submarine light attenuation ( $k_d$ ) was directly proportional to the concentrations of chlorophyll a and organic carbon in the water column (Fig. 4A-D). The nominal simulated range in  $k_d$  ( $0.2$ - $1.0 \text{ m}^{-1}$ ) was below values reported for the Goodwin Islands nearshore (Moore, 1996) and significantly less than the  $1.5 \text{ m}^{-1}$  required for seagrass survival (Dennison et al., 1993). The  $1.5 \text{ m}^{-1}$  habitat criteria equals approximately 22% of the surface insolation, the minimum light penetration for *Zostera marina* survival (Dennison et al., 1993; Short et al., 1995). The simulated submarine light environment is thus very favorable for seagrasses, epiphytes, and microalgae as 65% and 40% of the surface insolation reaches the *Zostera marina* leaves and the sediment surface, respectively. Based on the model,  $k_d$  approaches  $1.5 \text{ m}^{-1}$  in June when channel concentrations of chlorophyll a and organic carbon are doubled (Fig. 4A). Attenuation coefficients derived from 10 day continuous data collected in the Goodwin Islands seagrass meadow ranged  $0.8$  to  $1.5 \text{ m}^{-1}$  between June 1993 and April 1994 (Moore, 1996). The model does not account for sediment resuspension nor does it include state variables for particulate inorganic materials. Total suspended solids (TSS) includes both inorganic and organic fractions and  $15 \text{ mg L}^{-1}$  has been designated as the seagrass habitat criteria (Dennison et al., 1993). The organic fraction of TSS from the Goodwin Islands samples varied between approximately 50% in the spring to 25% in the summer and fall of 1993-94 (Moore, 1996). The model would predict a maximum  $k_d = 1.07 \text{ m}^{-1}$  in June if a POC fraction of 50% is used to calculate TSS and  $k_d$ . This value is similar to the  $1.13 \text{ m}^{-1}$  measured at the Goodwin Islands by Moore (1996).

Chlorophyll a concentrations predicted by the model were low compared to the habitat criteria of  $15 \text{ mg m}^{-3}$  (Dennison et al., 1993). Only during the spring bloom under the influence of the 2X channel concentrations did chlorophyll a concentrations approach  $14 \text{ mg m}^{-3}$  (Fig. 4B). Chlorophyll a concentration in the seagrass meadow is regulated by light, nitrogen, and the supply of phytoplankton biomass from the sand habitat and offshore channel. Chlorophyll a accounted for approximately 12% of the submarine light attenuation during the spring bloom for nominal model simulations. Phytoplankton biomass is a source of particulate organic carbon to the water column but the model predicts fairly low concentrations of POC ranging  $0.3$ - $1.0 \text{ gC m}^{-3}$  (Fig. 4C). The 3-D water quality model predicts POC concentrations in the range  $0.2$ - $3.0 \text{ gC m}^{-3}$  for surface waters Chesapeake Bay (Cerco and Cole, 1993). Particulate organic carbon concentrations accounted for approximately 15% of submarine light attenuation during the spring bloom. Phytoplankton exudation is a direct source of DOC while particulate organic carbon derived from phytoplankton biomass is rapidly hydrolyzed to DOC. The predicted DOC concentrations were  $0.5$ - $4.5 \text{ gC m}^{-3}$  and were within the range of data from marsh ecosystem studies in the York River, Virginia (Axelrad et al., 1976) and North Inlet, South Carolina (Childers et al., 1993). Based on model simulations, water column DOC concentrations can account for up to 60% of the total light attenuation predicted for the seagrass habitat. The attenuation due to dissolved organic carbon was greater than that due to particulate organic carbon because the DOC concentrations were greater (Fig. 4C and 4D) Attenuation due to POC and DOC concentrations was 72% and 21%, respectively, in a seagrass ecosystem in southwestern Florida (MacPherson and Miller, 1987). Although DOC has been included in channel monitoring efforts (Curling and



Neilson, 1994), its role in littoral zone biogeochemistry and light attenuation is not well understood. The specific role of DOC in the transmission of submarine light warrants further research in order to determine habitat criteria for DOC in Chesapeake Bay and other estuaries. The relationships between spectral attenuation, seagrass growth and survival, and habitat requirements under varying water column composition also require further investigation (Gallegos, 1994; Moore, 1996).

The concentration of dissolved inorganic nitrogen for nominal model runs was always less than the habitat criteria of  $10 \mu\text{moles l}^{-1}$  (Dennison et al., 1993; Fig. 5E). The DIN concentration exceeded  $10 \mu\text{moles l}^{-1}$  in the winter and summer under the 2X model scenario, but these are the times of reduced production and biomass by *Zostera marina* in Chesapeake Bay (Moore, 1996). Maximum DIN concentrations were similar among nominal and 0.5X model scenarios. It is interesting that the minimum DIN concentration in May and June at the 0.5X trial was over twice that of the nominal or 2X trials (Fig. 4E). This result is due to reduced nitrogen removal during the spring bloom due to low phytoplankton biomass in the 0.5X trial (Fig. 4B). Nominal water column DIN was reduced to  $< 2.0 \mu\text{moles l}^{-1}$  in May and June due to the combined effects of increased horizontal exchange and uptake by phytoplankton (Fig. 4E). Phytoplankton nitrogen removal rates were of a similar magnitude as the rates of DIN influx from the sand habitat in late May. The transport, production, and uptake of dissolved inorganic and phytoplankton biomass are tightly linked and phytoplankton are the major sink for DIN (Fisher et al., 1988.; Buzzelli et al., in review). The specific relationships between primary production and nitrogen cycling and the potential ecological significance are under further investigation using the nominal and altered model versions (Buzzelli, unpublished data).

A doubling of channel boundary concentrations had a greater effect upon annual primary productivity rates than a corresponding 0.5X decrease in every case (Tables 3 and 4). The greatest effects were evident in the rates of phytoplankton productivity and contribution to annual production within the seagrass meadow (Tables 3 and 4). Phytoplankton production decreased by 45% with 0.5X channel concentrations but increased 69% when concentrations were doubled. It is reasonable that the channel chlorophyll a concentration has a significant influence upon littoral zone plankton dynamics since phytoplankton biomass in the SAV habitat is ultimately linked to the channel boundary. Phytoplankton are intricately linked to water column cycles of carbon and nitrogen and increased biomass can reduce light available to the epiphytes, seagrass leaves, and sediment algae (Twilley et al., 1985).

The annual rate of primary production by epiphytes of *Zostera marina* decreased with reduced channel DIN concentration but increased with improved submarine light (Table 3). The reverse was true when channel concentrations were doubled as epiphyte production rates increased by 6% with 2X nitrogen but decreased by 11.3% when all channel constituents were doubled. The model results suggest that epiphytes are sensitive to both nitrogen and light availability, but that light has a greater effect. This modeling result is consistent with mesocosm experiments where epiphytic growth responded more to changes in light than nutrients (Short et al., 1995; Moore, 1996). Epiphyte net



production is closely regulated by submarine light, inorganic nutrient availability, and biomass loss to leaf surface grazers (Howard and Short, 1986; Neckles et al., 1993; Moore, 1996). Long term epiphyte biomass stabilized in both decreased and increased channel concentration scenarios (Fig. 5). Under normal turbidity levels in lower Chesapeake Bay there is a limited epiphyte nutrient response, but any factor that alters the balance between production and loss processes could change epiphyte response to nutrients (Moore, 1996). Unknown factors may include changes in the resident fish population that regulate the grazer population to exert top down control (Short et al., 1995; Moore, 1996). Epiphytic cover influences PAR at the leaf surface and exerts control over the photosynthetic rates of *Zostera marina* (Twilley et al., 1985; Short et al., 1995).

Long term changes in the submarine light regime are largely responsible for the widespread variations in seagrass coverage in Chesapeake Bay (Orth and Moore, 1984; Dennison et al., 1993; Moore, 1996). For both the increased and decreased channel concentration scenarios, submarine irradiance had a greater influence over *Zostera marina* shoot and root-rhizome production than dissolved inorganic nitrogen (Tables 3 and 4). A 0.5X decrease in channel concentrations caused a 4% increase in the annual rate of the *Zostera marina* shoots and provided a 25% increase in the maximum biomass over ten years (Fig. 5A). A 2X increase in channel concentrations caused a 12% decrease in the annual rate that lead to a 47% decrease in maximum biomass over ten years (Fig. 5B). Increased nitrogen input does have indirect effects in the model and the estuary because nutrients stimulate epiphytic growth and shade the leaves (Twilley et al., 1985; Short et al., 1995). Nutrient enrichment favors a shift towards algal dominated communities and negatively impacts seagrass growth (Short et al., 1995). Decreased rates of primary production could negatively affect reproductive success and lead to eventual changes in seagrass meadow extent.

Chesapeake Bay has experienced widespread variation in SAV distribution during this century with stable or increased coverage recorded during the 1990's (Orth and Moore, 1984; Orth et al., 1994). At its current size (118 ha), the seagrass meadow accounts for 34% of the annual primary of the Goodwin Islands littoral zone (Buzzelli, in review; Buzzelli et al., in review). Changes in spatial coverage of SAV could have a significant impact upon the primary production and material cycling within the estuarine littoral zone. The estimated annual primary production of the Goodwin Islands littoral zone increased from  $1.68 \times 10^9$  gC to  $3.05 \times 10^9$  gC when the seagrass meadow size was increased to 498 ha (Table 5). Sediment microalgae contribution to total production increased to 67% when *Zostera marina* was removed but decreased to 25% when the seagrass coverage was extended across the entire subtidal habitat. The decrease in microalgal contribution resulted from the reduction in sediment surface light over a greater area due to increased seagrass coverage (Table 5). The phytoplankton imported into the Goodwin Islands littoral zone annually decreased by 45% when the seagrass meadow was enlarged (Table 5). Despite a large decrease in phytoplankton import and the close relationship between phytoplankton and nitrogen removal, annual nitrogen import did not change with changes in seagrass coverage ( $-1.81 \times 10^7$  gN yr<sup>-1</sup>). The seagrass leaves



became a more important sink for water column DIN in the ecosystem when *Zostera marina* habitat size was increased. The removal of *Zostera marina* creates a water column dominated littoral zone where phytoplankton with low C:N ratios and high rates of turnover are favored. An increase in seagrass coverage drives the system towards a macrophyte dominated littoral zone with high C:N ratios and longer turnover times.

## SUMMARY

The simulation model of the littoral zone of the Goodwin Islands NERR site is based upon a concentric series of hydrodynamically linked estuarine habitats. The water column concentrations exhibit semi-diurnal and spring/neap tidal periodicity and the habitats are connected through 2-D finite difference exchange equations. The dynamics of phytoplankton, particulate and dissolved organic carbon, and inorganic nitrogen within the water column of each habitat are interdependent in the mathematical structure (Cercu and Cole, 1994; Kuo and Park, 1994; Buzzelli et al., in review). The model can provide carbon and nitrogen budgets at the habitat scale to incorporate into a geographic information system (GIS) and track longer term patterns (Buzzelli, in review). The model is a source of specific rate information integrated on the scale of the individual, community, and ecosystem for use in other studies of estuarine primary production and water quality. The model is currently being used to investigate carbon and nitrogen dynamics at the ecosystem and macrophyte scales by examining photosynthesis and nitrogen uptake in phytoplankton and *Zostera marina*, respectively. The role of seagrass canopy biomass in sediment deposition and resuspension and the effects of inorganic water column fractions on submarine light attenuation are being considered as modifications for future model versions (Moore, 1996).

This modeling study supports the widely held opinion that submarine light quantity is singularly critical to the stability and long term survival of *Zostera marina* communities, particularly in the lower Chesapeake Bay (Dennison, et al., 1993; Gallegos, 1994; Moore et al., 1996). The lower Chesapeake Bay has exhibited fewer characteristics of nutrient enrichment relative to the upper Chesapeake Bay (Fisher et al., 1988). Increased channel nitrogen did stimulate epiphytic growth, but light effects predominated in every other model scenario. Water quality predicted by the model is well above the standards established by Dennison et al. (1993) and explain the healthy seagrass currently present at the Goodwin Islands NERR location. The nominal version was based upon the current, pristine state of the Goodwin Islands NERR location and deteriorated water quality had much larger effects than improved conditions in the channel. Increased material loading to the littoral zone leads to poorer submarine light availability, less productive seagrass, more phytoplankton, less ecosystem production, faster nitrogen turnover, and less vegetated habitat for resident and transient fauna.



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