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Modeling the Lower Chesapeake Bay Littoral Zone & Fringing Wetlands: Modeling the Lower Chesapeake Bay Littoral Zone & Fringing Wetlands: Ecosystem Processes and Habitat Linkages.II. Model Sensitivity Analysis, Validation, and Estimates of Ecosystem Processes

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An Annual Report Submitted to:

United States Environmental Protection Agency
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Special Report No. 335 in
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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 specific habitat criteria and management strategies. 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 lead 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 benefitted 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 conceptual modeling of emergent intertidal marsh communities. 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 this past year revised and expanded this model 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 period has been on the development, calibration, validation, and preliminary simulation analysis of ecosystem process models for specific, highly-distributed components of the estuary emphasizing 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 detrital 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 1995 to May 1996 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 comprised of 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 riverine 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.

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 second in a series on ecosystem process modeling of the lower Chesapeake Bay SAV-Littoral Zone and includes sensitivity analyses and validation of key state variables present in the four littoral zone habitat models of the Goodwin Islands National Estuarine

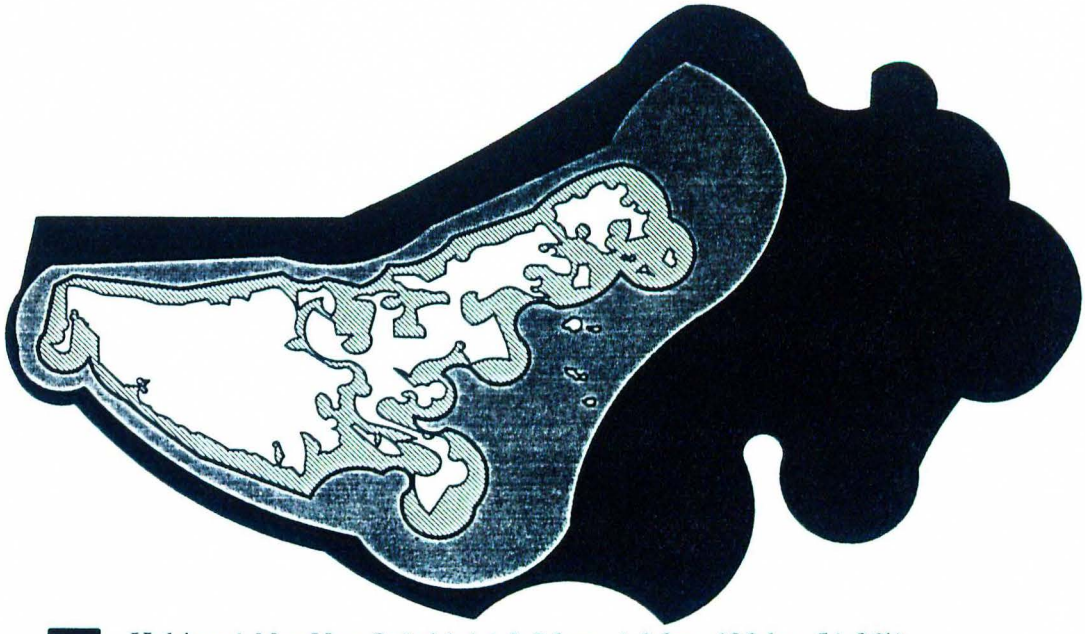
Research Reserve in lower Chesapeake Bay, Virginia (Buzzelli et al. 1995). Following complete calibration and sensitivity analyses the models were used to calculate annual primary production and material fluxes in the Chesapeake Bay littoral zone. The annual net primary production and nitrogen demand and uptake of each model phototroph were calculated along with the annual net carbon production and nitrogen demand of each of the four primary habitats. Annual primary production predicted using the model was compared to estimates derived from the literature. The annual total chlorophyll, particulate and dissolved organic carbon (POC and DOC, respectively), and dissolved inorganic nitrogen (DIN) exchanges were estimated for each habitat. The values for annual net production, nitrogen demand, and material exchanges for each habitat were combined with a GIS of the Goodwin Islands NERR to map the output generated by the four habitat simulation models. The GIS provides a digital geographic representation of ecosystem processes and is a framework upon which to base longer term studies of ecosystem patterns.

METHODS

Model Overview

The Goodwin Islands National Estuarine Research Reserve (NERR) is located in the lower York River estuary (37° 12' 46'' N, 76° 23' 46'' W). The general ecological characteristics of this littoral zone ecosystem have been described in a previous paper (Buzzelli, in review). The littoral zone was defined as the area between the -2.36 m depth (mean sea level) and the salt bush community located near mean higher high water (about +1.5 m). The littoral zone of the Goodwin Islands NERR was divided into four primary habitats between offshore channel environments and forested upland boundaries and include nonvegetated subtidal (NVST), vegetated subtidal (VST), nonvegetated intertidal (NVIT), and vegetated intertidal marsh (VIT; Fig. 1). Conceptual and simulation models were derived for each habitat that include phytoplankton, sediment microalgae, and water column particulate and dissolved organic carbon and dissolved inorganic nitrogen (Fig. 2). The principal forcing variables are tidal water level, solar insolation, and temperature. The vegetated subtidal and intertidal models contain carbon and nitrogen state variables for *Zostera marina* and *Spartina alterniflora*, respectively. Table 1 provides a list of the state variable abbreviations, definitions, and units. The habitats are connected by the volume exchange of suspended materials due to tidal forces. Habitat volume is calculated from the habitat wet area and depth. Wet area (m^2) is constant in the two subtidal habitat models while the intertidal inundation is calculated using a hypsometric curve (Childers et al., 1993). Water column state variables are influenced by production, respiration, loss due to kinetic processes, sedimentation and settling, and horizontal exchange with the adjacent habitats. Sediment microalgal biomass changes due to production, respiration, grazing, and resuspension. Subtidal and intertidal habitat sizes are constant for sediment microalgae although they are limited by light attenuation due to the changes in depth of the overlying water column and seasonal changes in macrophyte biomass (vegetated habitat models only). Macrophyte carbon production is balanced by respiration, loss due to plant mortality, and translocation while nitrogen is absorbed through the shoots and root-rhizomes (*Zostera marina*) or root-rhizomes only (*Spartina alterniflora*) and distributed within the plant to meet nitrogen growth requirements. The formulations for rate processes, tidal functions and horizontal exchanges, and model parameters have been described in a related paper (Buzzelli, in review).

(A) Habitat Map for the Goodwin Islands Littoral Zone



Habitat 1 NonVeg Subtidal (-2.36 to -1.36m, 420 ha, 51.9%)
Habitat 2 Vegetated Subtidal (-1.36m to -0.36m, 150 ha, 18.5%)
Habitat 3 NonVeg Intertidal (-0.36m to 0.00m, 100ha, 12.3%)
Habitat 4 Vegetated Intertidal (0.00m to +0.36m, 75 ha, 11.1%)

(B) Goodwin Islands shoreface profile depicting distribution of littoral zone habitats

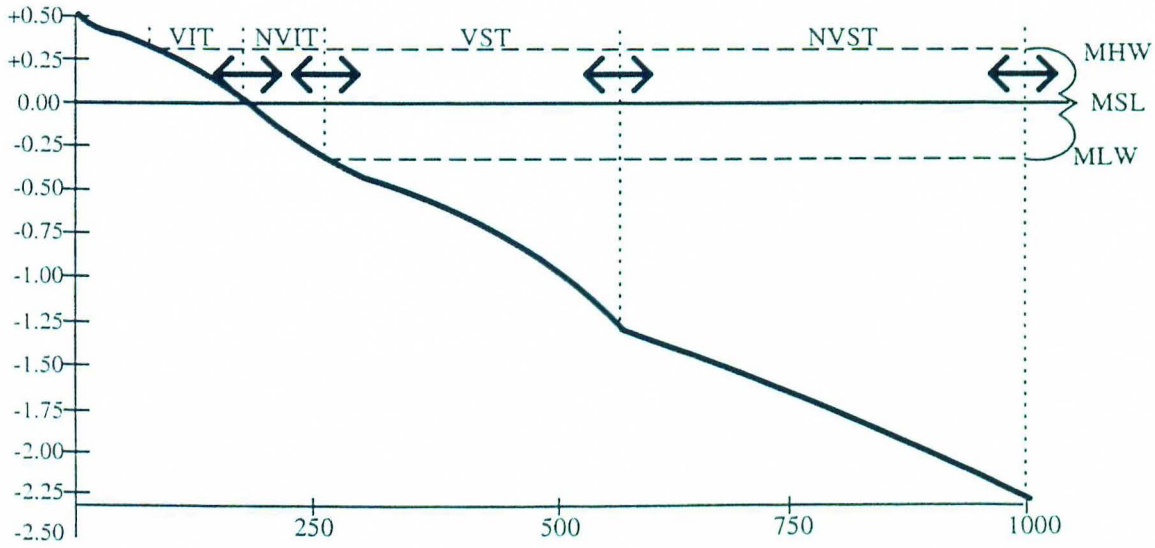


Figure 1. (A) Habitat size and distribution map for the littoral zone of the Goodwin Islands NERR. (B) Shoreline profile for littoral zone of the Goodwin Islands NERR

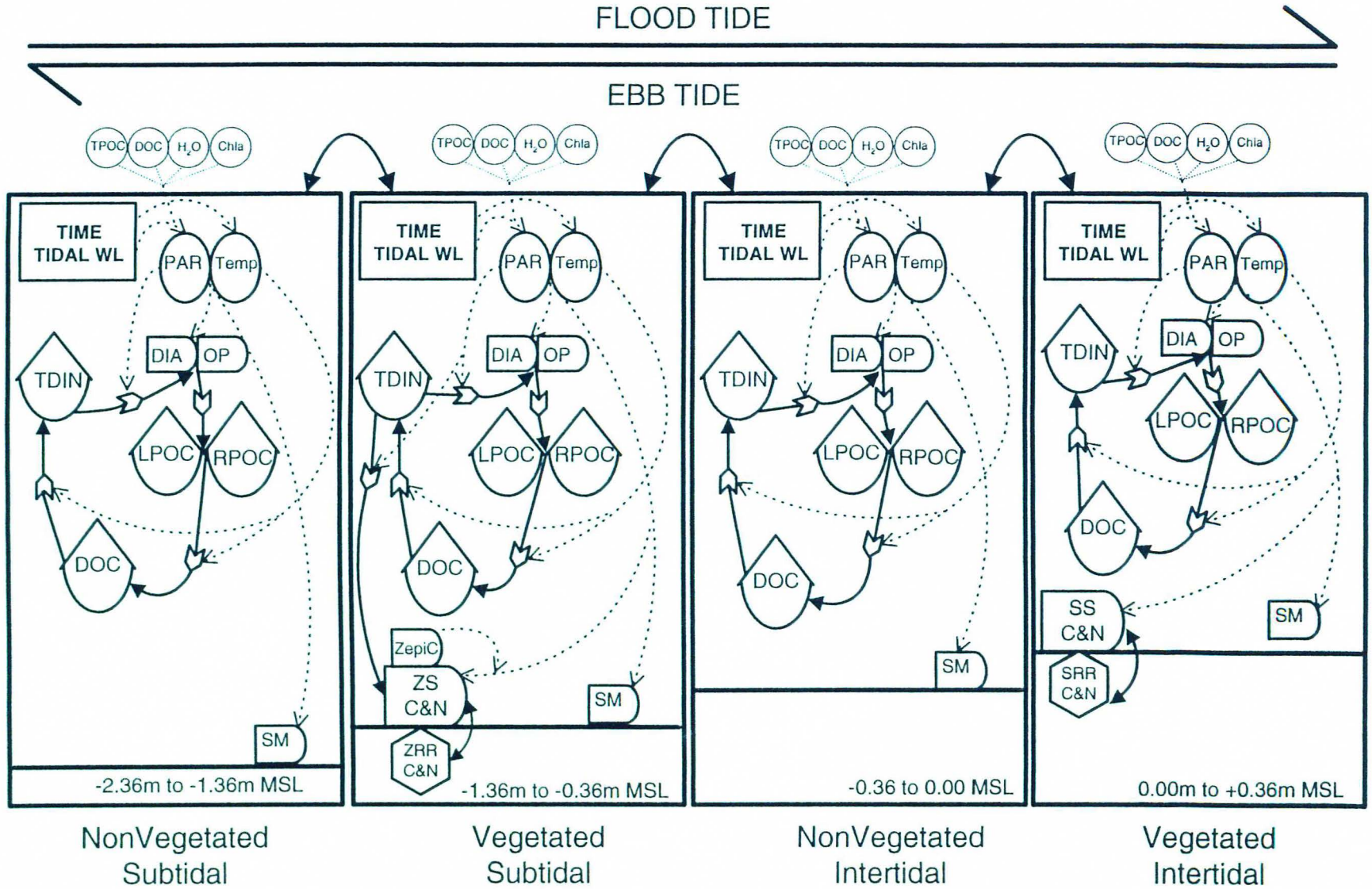


Figure 2. Generalized conceptual diagram for the four habitat models. Dashed lines are information flow while solid lines with workgates represent mass flows. Model time, tidal water level, photosynthetically active radiation (PAR), and water temperature (Temp) influence the six water column state variables (DIA, OP, LPOC, RPOC, DOC, TDIN). The two phytoplankton size classes and the two POC fractions are shown as paired state variables. Each model also includes sediment microalgae (SM). The vegetated subtidal and intertidal models have Zostera marina and Spartina alterniflora shoot and root-rhizome carbon and nitrogen, respectively

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 alternilflora.

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	µM
SM	Sediment Microalgae	gC m^{-2}
ZSC	*Zostera marina* Shoot Carbon	gC m^{-2}
ZSN	*Zostera marina* Shoot Nitrogen	gN m^{-2}
ZRRC	*Zostera marina* Root-Rhizome Carbon	gC m^{-2}
ZRRN	*Zostera marina* Root-Rhizome Nitrogen	gN m^{-2}
ZepiC	*Zostera marina* Epiphytic Biomass	gC m^{-2}
SSC	*Spartina alterniflora* Shoot Carbon	gC m^{-2}
SSN	*Spartina alterniflora* Shoot Nitrogen	gN m^{-2}
SRRC	*Spartina alterniflora* Root-Rhizome Carbon	gC m^{-2}
SRRN	*Spartina alterniflora* Root-Rhizome Nitrogen	gN m^{-2}

Model Sensitivity Analysis

There are a large number of factors that potentially influence the resulting state variable concentrations (Buzzelli et al. 1995). The sensitivities of the model state variables to the integration interval (dt), integration routine (Euler vs Runge-Kutta), boundary conditions, and various parameters were investigated using a systematic series of model trial runs. The interval for Eulerian integration (dt) was initially set at 0.0625 d (1.5 hrs). Analyses included a particular state variable over successive years of the same model run as well as the comparison of year two results among a series of different sensitivity runs. The integration interval (dt) was halved during successive calibration runs to check the effects of dt upon the water column concentrations in each habitat model. Euler and Runge-Kutta integration routines were compared at similar values of dt. Four to six individual ecological parameters were selected for each state variable listed in Table 1 to analyze their effects upon the resulting model concentration during year two. Each parameter was varied by +10% and -10% in individual runs and the root mean square deviation (RMS) between the stable, nominal model case and the sensitivity run was calculated (Cerco, 1993).

$$RMS = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(P_i - O_i)^2}$$

Where P_i = model nominal run, O_i= sensitivity run, n = number of dt in year two simulation (n=5840). The RMS was compared to the average mean concentration of the nominal run. In the cases of the carbon state variables of *Zostera marina* and *Spartina alterniflora*, the potential interactions between two or three varied parameters were investigated for year two output.

Model Validation

Validation data from the Goodwin Islands was available only for several model state variables. Graphical validation was performed on the second year of water column chlorophyll a, total particulate organic carbon (TPOC), and total dissolved inorganic nitrogen (TDIN) output from the nonvegetated and vegetated subtidal habitat models. The shoot, root-rhizome, and epiphyte carbon state variables of *Zostera marina*. were compared to data collected at the Goodwin Islands by Moore et al. 1994. *Spartina alterniflora* shoot and root-rhizome carbon biomass were validated using data assembled from the literature including (Mendelssohn, 1973; Smith et al., 1979; Ornes and Kaplan, 1989; Gross et al., 1991). There are no data available at this time to validate model representation of patterns of littoral zone water column DOC dynamics, sediment microalgal production and biomass, and habitat specific and inter-habitat variations in sediment-water and lateral material exchanges.

Model Application

The model processes representing phototrophic net production, phototrophic nitrogen demand and uptake, and the exchanges of total phytoplankton, total particulate organic carbon (TPOC), dissolved organic carbon (DOC), and total dissolved inorganic nitrogen (TDIN) were summed over the third year of simulation to calculate annual rates. Annual carbon and nitrogen dynamics were compared among the autotrophs. Annual carbon production and nitrogen demand were compared among the four habitats. The annual material exchange that each habitat has with each of its two adjacent boundary habitats were then summed to derive an annual import or export estimate for the individual habitat. The annual net carbon production and suspended material budgets for the entire Goodwin Islands NERR were then calculated using the summed process

estimates for each habitat. These estimates were then compared to those derived from studies on other mid-Atlantic coast marsh ecosystems.

RESULTS

Model Sensitivity Analysis

There were no differences between output generated using Eulerian versus Runge-Kutta integration routines for any of the four habitat models (data not shown). The concentrations of water column variables in the subtidal habitat models (NVST and VST) did not change significantly over the range of dt's tested. This was not the case with the intertidal habitat models (NVIT and VIT) where dt and the concentration of chlorophyll in the marsh water column decreased concomitantly (Fig. 3A-D). The annual pattern remained intact as dt was halved, although the spring-neap peaks were accentuated at smaller integration intervals (Fig. 3). The smallest dt was 5.625 minutes (0.00390625 d) and elicited the lowest overall chlorophyll concentrations. A similar pattern was found in the water column TDIN concentration output from the marsh habitat model (Fig. 4A-D). Total dissolved inorganic nitrogen concentrations were halved with dt and spring-neap periodicity was even more predominant than for chlorophyll concentrations (Fig. 4D). While Figure 4 has only the second year of marsh model output for water column TDIN, Figure 5 contains the first two years of output. At large integration intervals of 45 and 22.5 minutes, there were large concentration spikes that occurred over the first 40 days (Fig. 5A and B). These spikes resulted from the interaction between dt, boundary conditions, and the equations for lateral exchange. The initial 40 day peak disappeared when either the TDIN boundary condition was decreased, the exchange was turned off, or dt was decreased significantly (Fig. 5C and D).

The concentrations of DIA, LPOC, SM, and ZepiC from the VST model were not sensitive to most of the parameters tested. DIA, LPOC, and SM were only marginally sensitive to two parameters each as a 10% change in a key parameter triggered only 5-10% changes in average biomass (Table 2). A 10% change in the basal metabolic respiration rate of *Zostera marina* epiphytes (BMRZepi) created an almost 40% change in the year two biomass. Half-saturation irradiance (ZIK), the shoot fall mortality coefficient (ZSFMK), and the translocation potential (ZCPot) had the biggest effects of the *Zostera marina* parameters tested. Shoot and root-rhizome biomass varied by approximately $\pm$8.7% with a $\pm$10% change in the half-saturation irradiance (ZIK; Table 2). A $\pm$10% change in the shoot fall mortality coefficient (ZSFMK) created a 12% change in the shoot and root-rhizome biomass while changing the translocation potential (ZCPot) had a very small effect on the shoots and a larger effect on the root-rhizome biomass (Table 4). Only the combination of increased half-saturation irradiance (ZIKH and L) and shoot fall mortality coefficient (ZSFMKH and L) appeared to interact and decreased the shoot and root-rhizome biomass by approximately 25% (Table 2).

Spartina alterniflora shoot and root-rhizome biomass were greatly influenced by 10% changes in the maximum photosynthetic rate (SPmax), the root-rhizome respiration rate at 20 °C (SRRR@20), and the translocation potential (SCPot; Table 3). A 10% increase in SPmax increased shoot biomass by an average of 65% and root-rhizome biomass by 38% during the second year of output from the VIT model. The effect of increased SPmax upon shoot and root-rhizome biomass over 3 model years is shown in Figure 6A and 6B. A $\pm$10% change in the SRRR@20 created almost a 100% change in shoot biomass and a 25% change in root-rhizome biomass (Table 3). Shoot carbon biomass was also quite sensitive to changes in SCPot while the root-rhizome biomass displayed effects similar to those of SRRR@20 (Table 3). The shoot respiration rate at 20 °C (SSR@20), the shoot basal mortality rate (SSC_{bmort}), and the root-

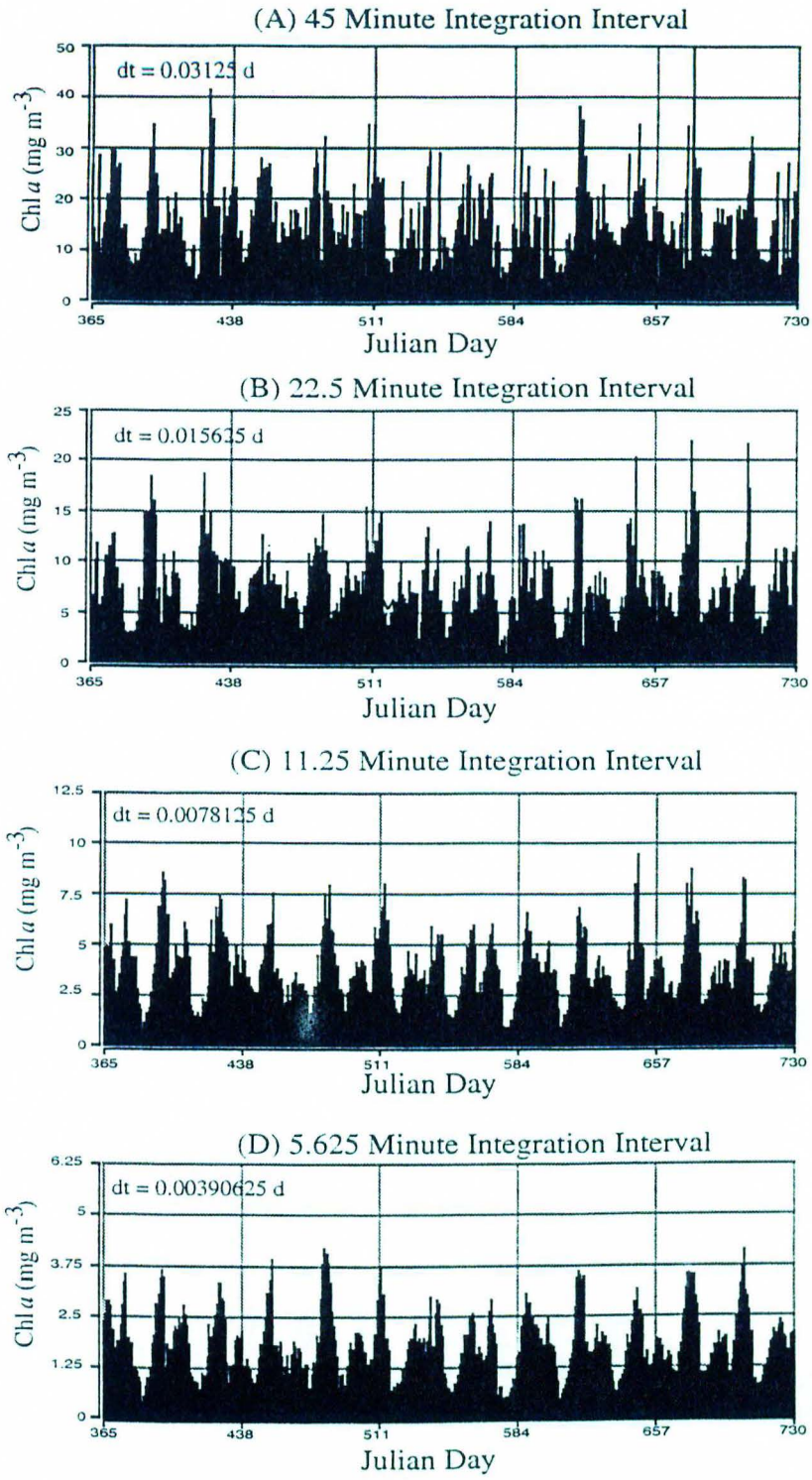


Figure 3. Effect of integration interval (dt) upon the 2nd year of water column chlorophyll *a* (mg m-3) output from the vegetated intertidal model (VIT) of the Goodwin Islands NERR. (A) 45 minute integration interval, (B) 22.5 minute integration interval, (C) 11.25 minute integration interval, (D) 5.625 minute integration interval. Notice that the ordinate scale is halved each time dt is halved.

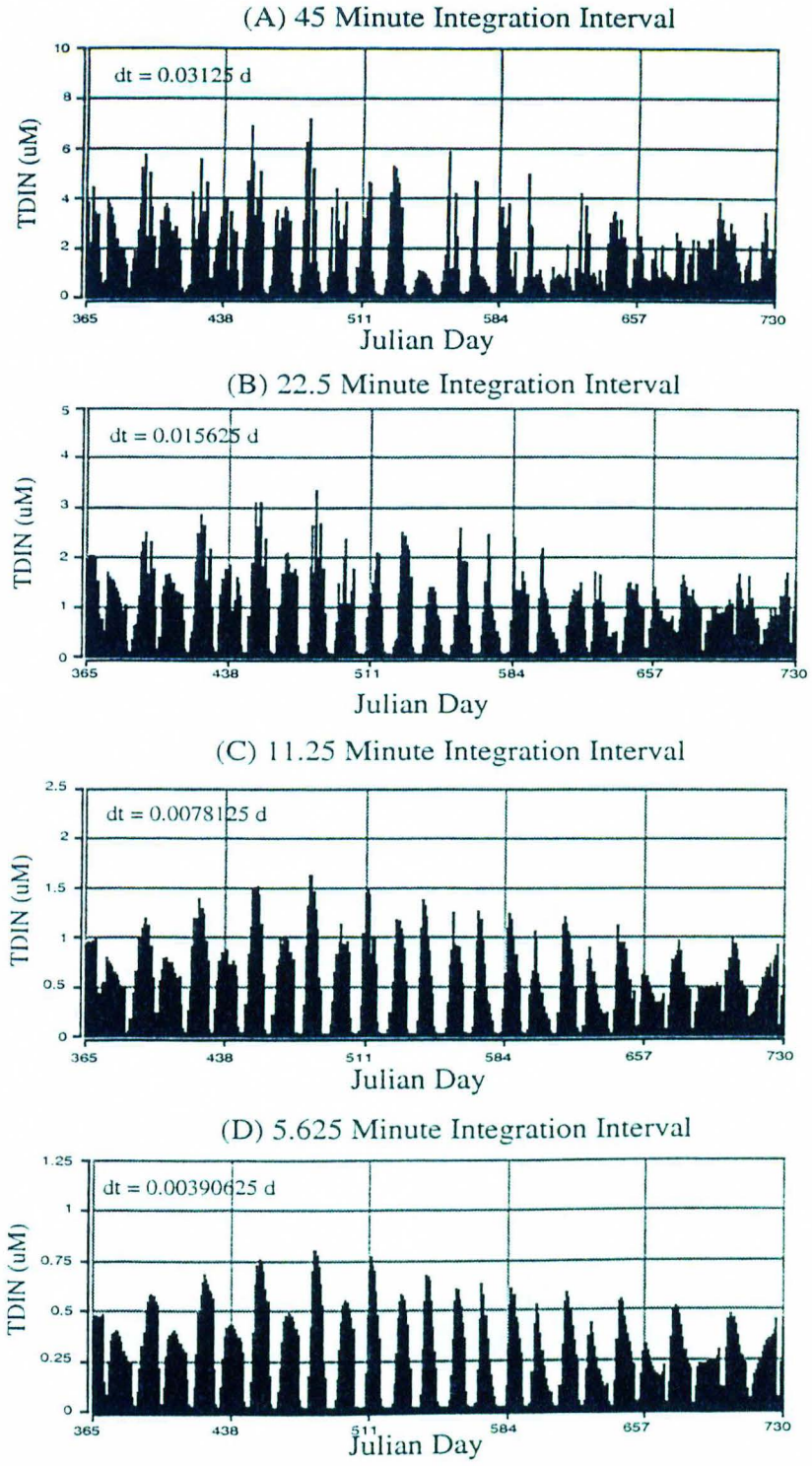


Figure 4. Effect of integration interval (dt) upon the 2nd year of water column of TDIN (mmole m 3 or μM) output from the vegetated intertidal model (VIT) of the Goodwin Islands NERR. (A) 45 minute integration interval, (B) 22.5 minute integration interval, (C) 11.25 minute integration interval, (D) 5.625 minute integration interval. Notice that the ordinate scale is halved each time dt is halved.

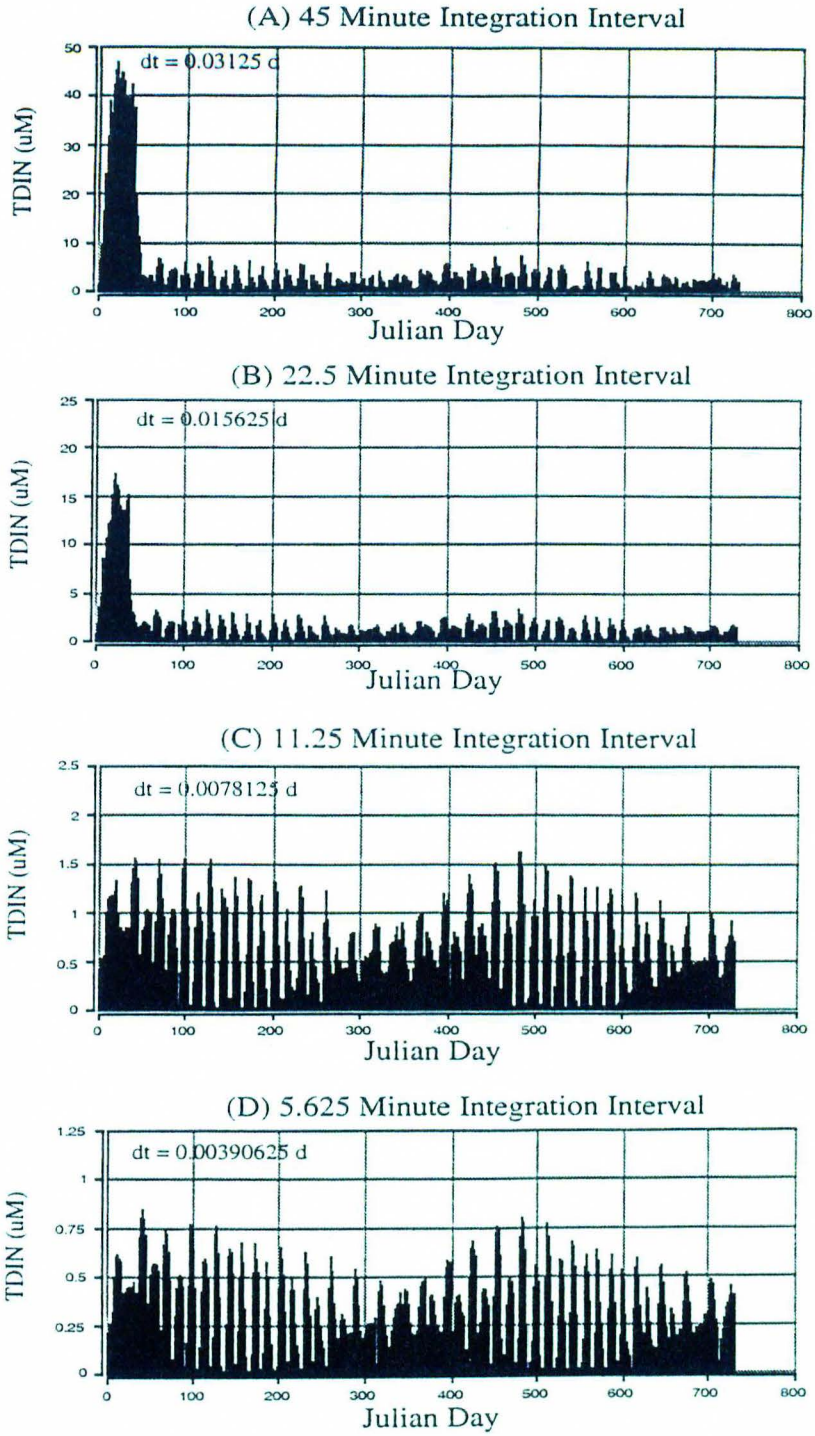


Figure 5. Effect of integration interval (dt) upon the first two years of water column TDIN (mmole m-3 or μM) output from the vegetated intertidal model (VIT) of the Goodwin Islands NERR. (A) 45 minute integration interval. (B) 22.5 minute integration interval. (C) 11.25 minute integration interval. (D) 5.625 minute integration interval. The large pulses of TDIN over the first 40 days of output present in (A) and (B) account for the large ordinate scales. The pulses are not present in (C) and (D) as the scales are an order of magnitude lower than those of (A) and (B), respectively.

Table 2. The results of sensitivity analysis for diatom (DIA), labile particulate organic carbon (LPOC), sediment microalgae (SM), and carbon state variables of *Zostera marina* shoots (ZSC), root-rhizomes (ZRRC), and epiphytes (ZepiC) of the vegetated subtidal habitat model (VST). Refer to Appendix B for parameter definitions and values. The biomass value (Avg. Bio.) is the average over all observations of the nominal run. Root mean square deviation (RMS) were calculated as the difference in state variable concentrations between nominal vs sensitivity runs during year two of simulation. RMS values of paired parameter interactions for *Zostera marina* are provided in the bottom table section. A 10% increase in a parameter value is denoted as high (H) while a 10% decrease in a parameter is labelled low (L).

VARIABLE	PARAMETER	AVG. BIO.	+10% RMS	-10% RMS
DIA2c	DIASdK	0.0716	0.0037	0.0041
	PRRd	($gC\ m^{-3}$)	0.0016	0.0017
LPOC2c	FLPOC	1.299	0.136	0.137
	DetStlV	($gC\ m^{-3}$)	0.064	0.071
SM2C	SMIK	1.748	0.102	0.109
	SMResK	($gC\ m^{-2}$)	0.112	0.112
ZEpiC	BMRZepi	9.686	3.669	3.630
	ZepiGK	($gC\ m^{-2}$)	0.802	0.939

PARAMETER	ZOSTERA SHOOTS (Avg. Bio.=42.47 $gC\ m^{-2}$)		ZOSTERA ROOT-RHIZOMES (Avg. Bio.=12.40 $gC\ m^{-2}$)	
	+10% RMS	-10% RMS	+10% RMS	-10% RMS
ZIK	3.683	4.171	1.084	1.227
ZSFMK	5.138	5.826	1.510	1.171
ZCpot	0.826	0.826	0.936	1.064

PARAMETER	ZOSTERA SHOOTS (Avg. Bio.=42.47 $gC\ m^{-2}$)	ZOSTERA ROOT-RHIZOMES (Avg. Bio.=12.40 $gC\ m^{-2}$)
	RMS	RMS
ZCpotH&ZIKL	4.727	0.404
ZCpotH&ZSFMKL	3.389	0.852
ZCpotL&ZIKH	5.255	0.493
ZCpotL&ZSFMKH	3.711	0.899
ZIKH&ZSFMKH	8.396	2.469
ZIKL&ZSFMKL	10.521	3.093

Table 3. The results of sensitivity analysis for *Spartina alterniflora* shoot and root-rhizome carbon state variables (SSC and SRRC) from the vegetated intertidal habitat model (VIT). Refer to Appendix B for parameter definitions and values. The biomass value (Avg. Bio.) is the average over all observations of the nominal run. The first table section contains the sensitivities of SSC and SRRC to ±10% changes in single parameters. Root mean square errors (RMS) were calculated by comparing state variable concentrations between nominal vs sensitivity runs during year two of simulation. RMS values of paired parameter interactions for *Spartina alterniflora* are provided in the bottom table section. A 10% increase in a parameter value is denoted as high (H) while a 10% decrease in a parameter is labelled low (L).

PARAMETER	SPARTINA SHOOTS (Avg. Bio.=66.45 gC m^{-2})		SPARTINA ROOT-RHIZOMES (Avg. Bio.=577.07 gC m^{-2})	
	+10% RMS	-10% RMS	+10% RMS	-10% RMS
SPmax	43.20	27.75	221.0	147.2
SRRR@20	59.97	66.67	140.6	167.6
SCpot	34.28	63.25	111.5	139.1
SSR@20	11.04	12.88	58.52	62.96
SSC_{bmort}	6.54	7.21	26.20	25.25
SRRKsN	2.56	3.11	17.07	15.55

PARAMETER	SPARTINA SHOOTS (Avg. Bio.=66.45 gC m^{-2})	SPARTINA ROOT-RHIZOMES (Avg. Bio.=577.07 gC m^{-2})
	RMS	RMS
SPmaxH&SRRKsNL	38.79	197.7
SPmaxL&SRRKsNH	29.24	155.7
SPmaxH&SRRR@20H	40.27	192.0
SpmaxL&SRRR@20L	25.97	127.9
SPmaxH&SCpotH	17.30	14.9
SPmaxH&SCpotL	4.05	72.7
SRRR@20H&SCpotH	35.77	131.3

PARAMETER	SPARTINA SHOOTS (Avg. Bio.=66.45 gC m^{-2})	SPARTINA ROOT-RHIZOMES (Avg. Bio.=577.07 gC m^{-2})
	RMS	RMS
SpmaxH.SCPotH. and SRRR@20H	19.07	15.01

rhizome half-saturation concentration for nitrogen uptake (SRRKsN) all elicited individual effects that were greatly reduced relative to SPmax, SRRR@20, and SCPot (Table 3). Paired combinations of parameters were also tested and the effects of SPmax were prevalent (Table 3). Logical combinations such as increased SPmax and decreased SRRKsN were chosen to represent possible changes in marsh edaphic factors. Increased SPmax overwhelmed the effects of increased root-rhizome respiration (Fig. 6 C and 6D). Increased or decreased SPmax was balanced by increased or decreased translocation potential (SCPot; Table 3). This effect is presented in Figure 6 E and 6F as shoot biomass declined slightly over three model years but root-rhizome biomass was fairly consistent between nominal and sensitivity runs. Increased basal rates of root-rhizome respiration (SRRR@20H) and increased translocation (SCPotH) created changes in biomass similar to each of their individual effects (Table 3). The effects of increased rates of photosynthesis, translocation, and root-rhizome respiration upon shoot and root-rhizome biomass were analyzed (Table 3 and Fig.6G and 6H). Once again the effects of increased SPMax were mitigated by changing the other parameters concurrently as the cumulative effects of this combination reduces average shoot biomass by approximately 29% and root-rhizome biomass by only 2.6%.

Validation

Subtidal Water Column Concentrations: The modeled concentrations of chlorophyll *a*, total POC (labile + refractory), and TDIN in the water column of the nonvegetated and vegetated subtidal habitats were validated using data collected during intensive field studies at the Goodwin Islands NERR (Fig. 7; Moore et al., 1994). The intensive field studies were conducted 7-17 June 1993. Figure 7A, 7B, and 7C depict the relationships between the field data and concentrations output from the VST model. VST model chlorophyll *a* is approximately 5 mg m^{-3} while the field data was scattered between 5 and 25 mg m^{-3} (Fig. 7A). Vegetated subtidal model concentrations of TPOC ranged between 1 and 3 gC m^{-3} and are within the range of values recorded in the field (Fig. 7B). Water column TDIN from the VST model are within the range of field data during the first few days of simulation but decline to very low values beginning around 11 June (Fig. 7C). There was some variability in the concentrations measured in the field (0-5 μM). The comparisons between model output and field data for the nonvegetated subtidal habitat are shown in Figure 7D, 7E, and 7F. Model chlorophyll *a* is approximately an order of magnitude lower than field determinations (different vertical scales on Fig. 7D). NVST model chlorophyll *a* concentrations are slightly lower than those output from the VST model while concentrations measured at the Goodwin Islands were slightly increased in the offshore nonvegetated habitat (Fig. 7A and 7D). NVST model TPOC concentrations were slightly lower than those determined in the field (Fig. 7E) while both model output and field data were similar among vegetated and nonvegetated habitats (Fig. 7B and 7E). NVST model TDIN concentrations range 10-16 gC m^{-3} while field observations ranged from 0 to 8 gC m^{-3} (Fig. 7F). The NVST model concentrations are considerably greater than those output from the VST model while field concentrations among the two subtidal habitats were similar (Fig. 7C and 7D).

Zostera marina Biomass: Graphical validation of *Zostera marina* shoot, root-rhizome, and epiphytic biomass are shown in Figure 8. The validation data were collected at the Goodwin Islands NERR in 1993 by Dr. K.A. Moore, Virginia Institute of Marine Science (Moore et al., 1994). The model sufficiently represents the annual patterns in the biomass of these three state variables. While the model predicts summer shoot biomass of approximately 30 gC m^{-2}, actual shoot biomass was below 20 gC m^{-2} (Fig. 8A). Predicted root-rhizome biomass is consistent with field data except for the large peak in biomass recorded at the Goodwin Islands NERR in April 1993 (Fig.8B; Orth and Moore, 1986). Although there was not as much data collected for

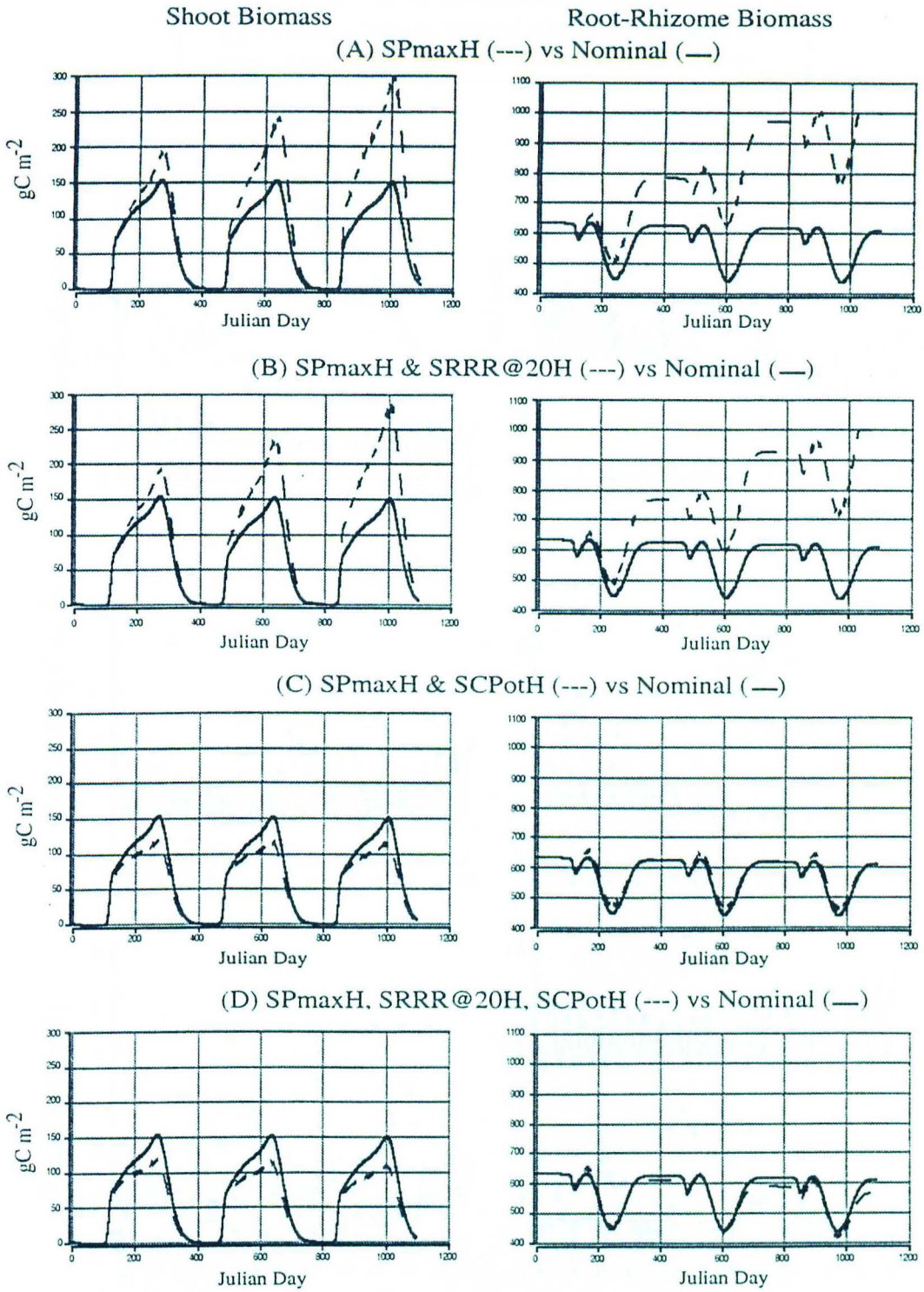


Figure 6. Sensitivity results for shoot and root-rhizome carbon biomass (gC m-2) of *Spartina alterniflora*. The effects of the maximum photosynthetic rate (SPMax) are shown as a singular factor in (A) and (B), as a two-way factor with increased root-rhizome basal respiration rate (SRRR@20) in (C) and (D), as two-way factor with increased translocation potential (SCPot) in (E) and (F), and as a three-way factor with SRRR@20 and SCPot in (G) and (H).

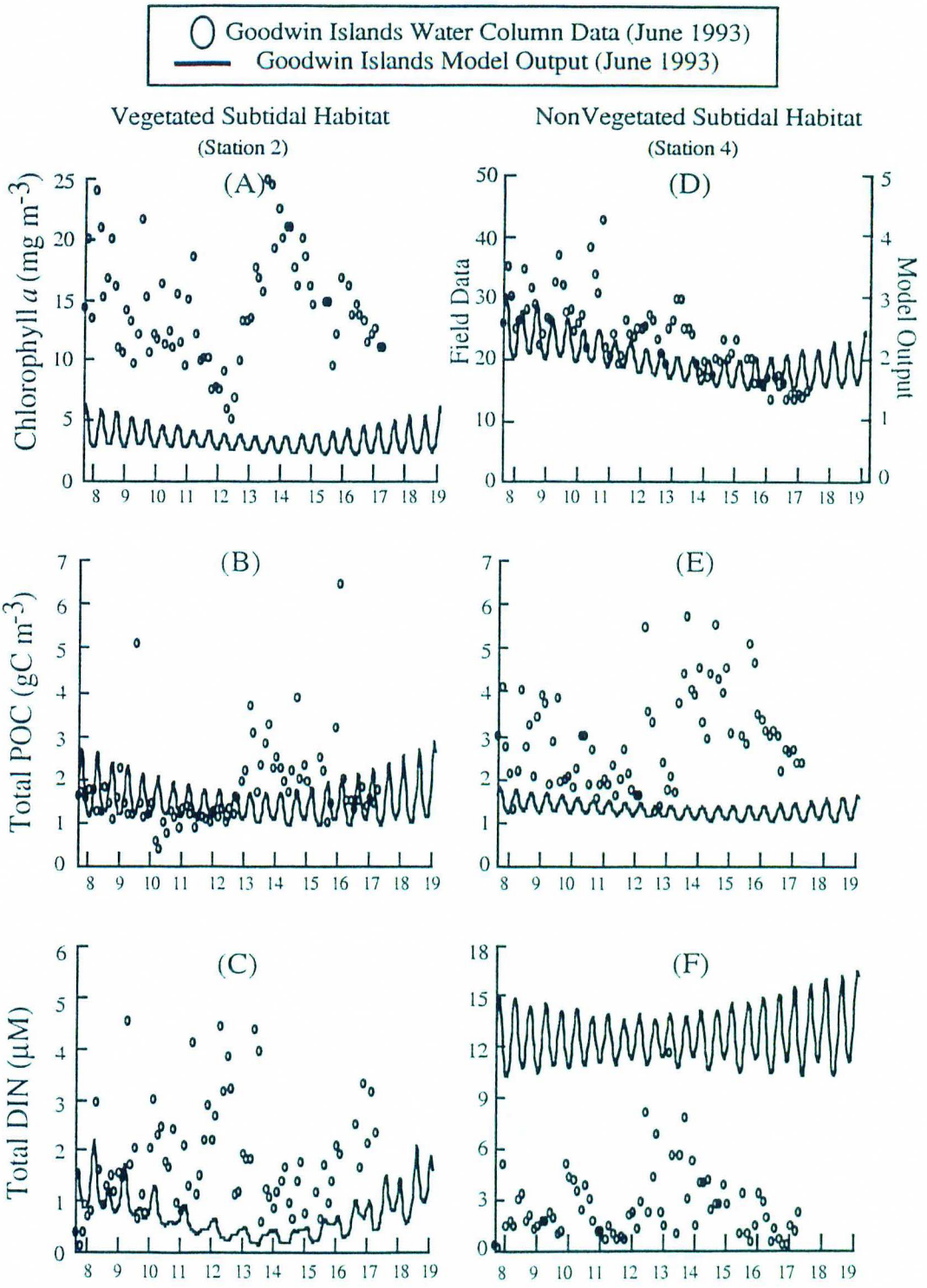
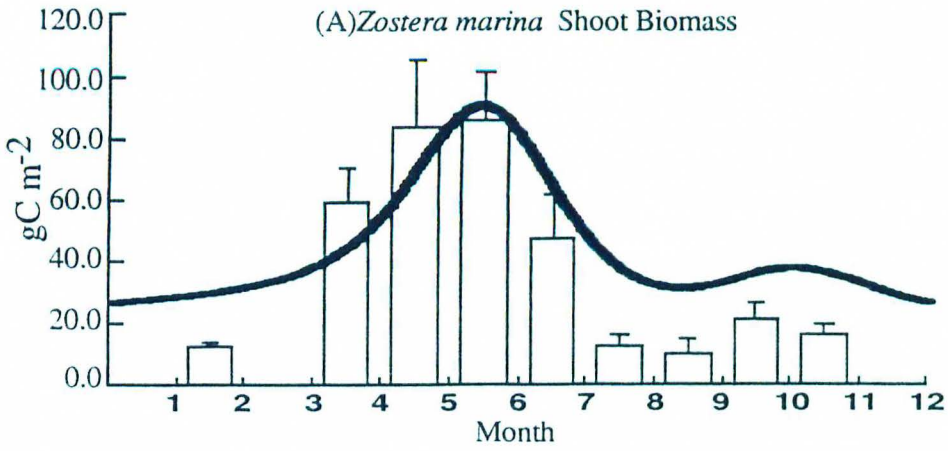
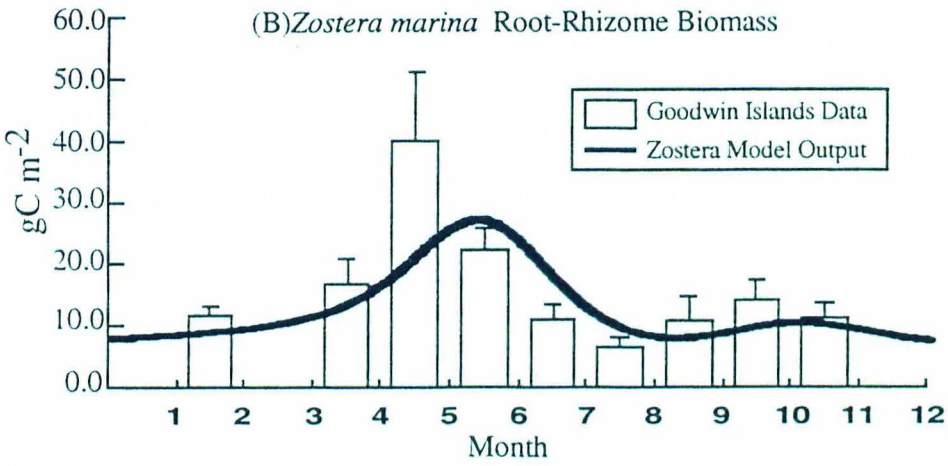


Figure 7. 1993 validation results for water column chlorophyll *a* (A and D; mg m-3), total particulate organic carbon (B and E; gC m-3), and total dissolved inorganic nitrogen (C and F; µM) from the vegetated and nonvegetated subtidal habitat models of the Goodwin Islands NERR. Data from the Goodwin Islands intensive study were collected 7-17 June 1993 and are shown as circles. Station 2 was located within the vegetated habitat while Station 4 was in the offshore nonvegetated habitat. 10D includes different vertical axes for model (left axis) and data (right axis). All other plots have only one vertical axis.





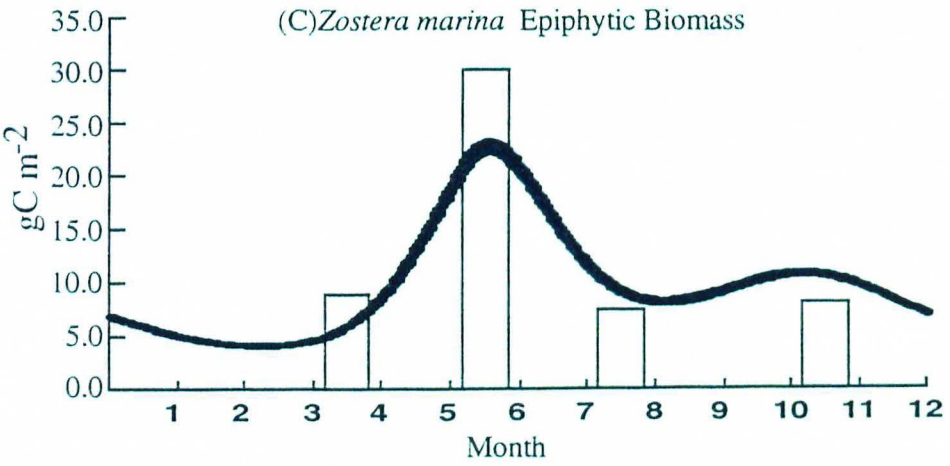


Figure 8. Validation results for carbon state variables (gC m-2) representing *Zostera marina* shoot (A), root-rhizome (B), and epiphytic (C) biomass for the vegetated subtidal habitat model (VST) of the Goodwin Islands NERR.

epiphytic biomass at the Goodwin Islands NERR, model output is within the range and agrees with other data collected in the York River, Virginia (Moore, unpublished data).

Spartina alterniflora Biomass: The model was calibrated using field data collected at the Goodwin Islands NERR and the annual patterns in shoot and root rhizome biomass of *Spartina alterniflora* generated by the model were validated with data assembled from the literature (Fig. 9). Shoot biomass was compared to data from the York River, Virginia and South Carolina (Mendelssohn, 1973; Ornes and Kaplan, 1989) while the root-rhizome output was validated with data collected in New Jersey and Delaware (Smith et al., 1979; Gross et al., 1991). Shoot carbon biomass was initialized at 3 gC m^{-2} and stays low until the spring pulse of carbon translocated from below ground stocks (Fig. 9A). Root-rhizome carbon biomass was initialized at 635 gC m^{-2} and decreases in April due to the upward carbon translocation to shoots (Fig. 9B). Shoot and root-rhizome carbon biomass increase through May and June. Shoot biomass continues to increase reaching a maximum of 160 gC m^{-2} by early September while the root-rhizome biomass declines during the summer due to increased below ground respiration which results from higher temperatures (Fig. 9). Shoot carbon biomass shows a precipitous decline in the fall as carbon is translocated belowground to the root-rhizome pool as both state variables return to their initial values. Shoot carbon biomass predicted from the model agrees with field data from South Carolina (Ornes, 1989) while root-rhizome carbon biomass is within the range of data reported for other marshes at similar latitude as Chesapeake Bay (Smith et al., 1979; Gross et al., 1991).

Processes and Exchanges

Annual production by the diatom and other plankton phytoplankton state variables of the Goodwin Islands NERR habitat models was estimated at 66.0 gC m^{-2} (Table 4). The nonvegetated and vegetated subtidal areas were added to the average inundated area of each of the two intertidal habitats in order to calculate the total ecosystem size for phytoplankton production (671 m^2). The annual phytoplankton production was 442.7 x 10^6 gC which comprised 15.8% of the total annual production in the Goodwin Islands NERR. The annual net areal production rates (gC m^{-2} yr^{-1}) of sediment microalgae varied among the four habitats. The nonvegetated intertidal (NVIT) habitat model predicted the highest rate at 169.0 gC m^{-2} yr^{-1}, followed by the intertidal marsh (VIT) at 162.5 gC m^{-2} yr^{-1}, the nonvegetated subtidal (VST) at 127.6 gC m^{-2} yr^{-1}, and the seagrass meadow habitat (VST) had the lowest at 101.2 gC m^{-2} yr^{-1} (Table 4). The NVST habitat provided 535.9 x 10^6 gC which accounted for 19.1% of the total for the littoral zone of the Goodwin Islands NERR. The VST, NVIT, and VIT habitats contributed 4.3%, 6.0%, and 4.9% of the total annual primary production of the ecosystem, respectively (Table 4).

The *Zostera marina* community includes productivity due to the shoots, attached epiphytes, and the root-rhizomes. *Zostera marina* epiphytes and root-rhizomes produced at a similar rate of approximately 55 gC m^{-2} yr^{-1} (Table 4). These two state variables made up 4.6% of total ecosystem production. The shoots of *Zostera marina* had a net annual rate of 241.3 gC m^{-2} yr^{-1} and accounted for about 10% of total ecosystem production. The *Zostera marina* community of the Goodwin Islands NERR produced approximately 421.7 x 10^6 gC yr^{-1} (Table 4). The shoots of *Spartina alterniflora* had the greatest annual net productivity of any of the model autotrophs at 830.8 gC m^{-2} yr^{-1} while the root-rhizome net productivity was 319.7 gC m^{-2} yr^{-1} (Table 4). Over the 85 hectares of the intertidal marsh habitat *Spartina alterniflora* shoots and root-rhizomes produced 977.9 x 10^6 gC yr^{-1} and accounted for 34.9% of the total ecosystem production predicted by the four habitat models.

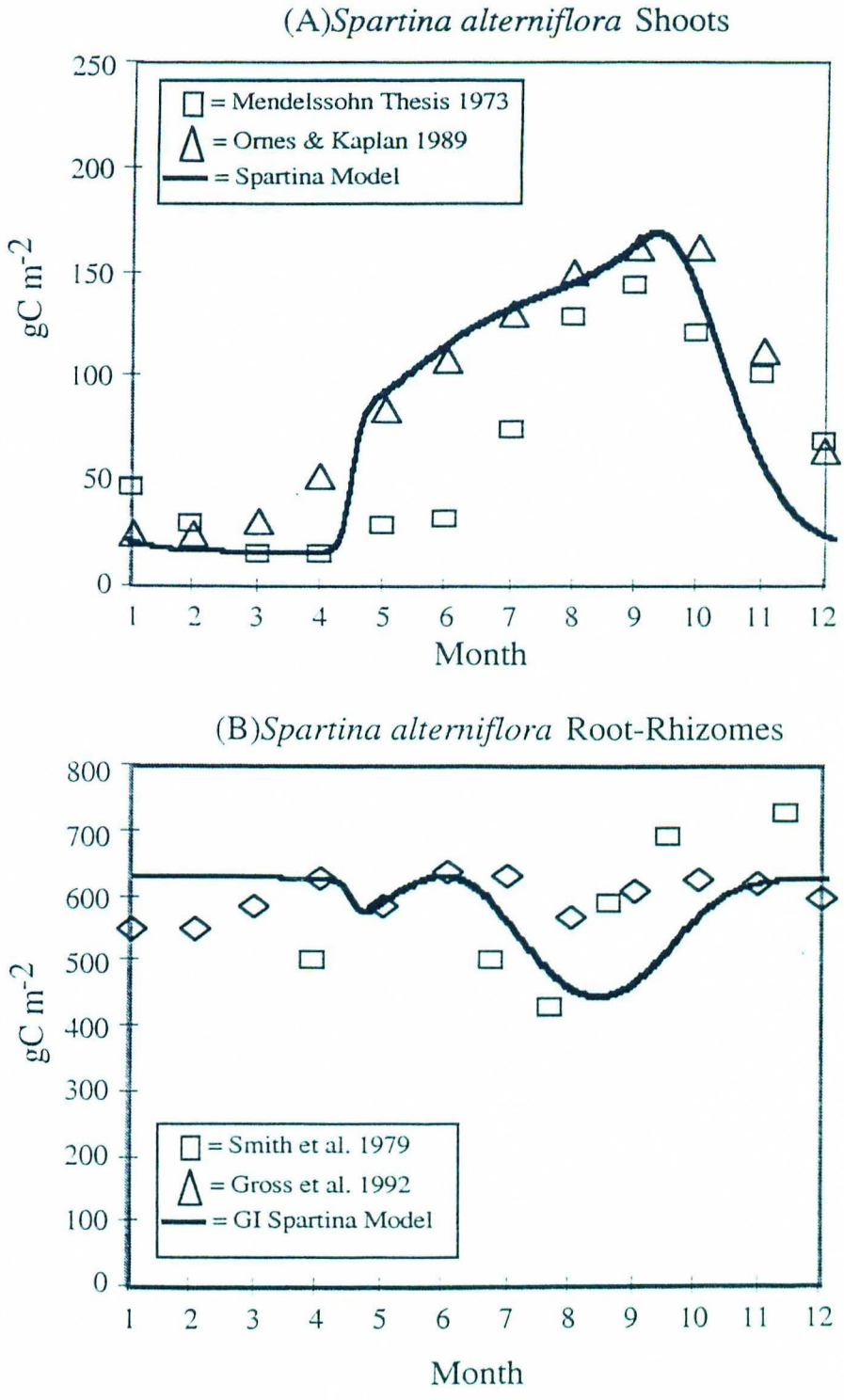


Figure 9. Validation results for carbon state variables (gC m-2) representing *Spartina alterniflora* shoot (A) and root-rhizome (B) biomass for the vegetated intertidal habitat model (VIT) of the Goodwin Islands NERR.

Table 4. Estimates of annual net production and contribution to ecosystem production in the littoral zone of the Goodwin Islands NERR using the four habitat models. Phytoplankton productivity was summed over all 4 habitats and intertidal habitat size used in this summation is the average areal inundation during model simulation time (m^2). The habitats are nonvegetated subtidal (NVST), vegetated subtidal (VST), nonvegetated intertidal (NVIT), and vegetated intertidal (VIT).

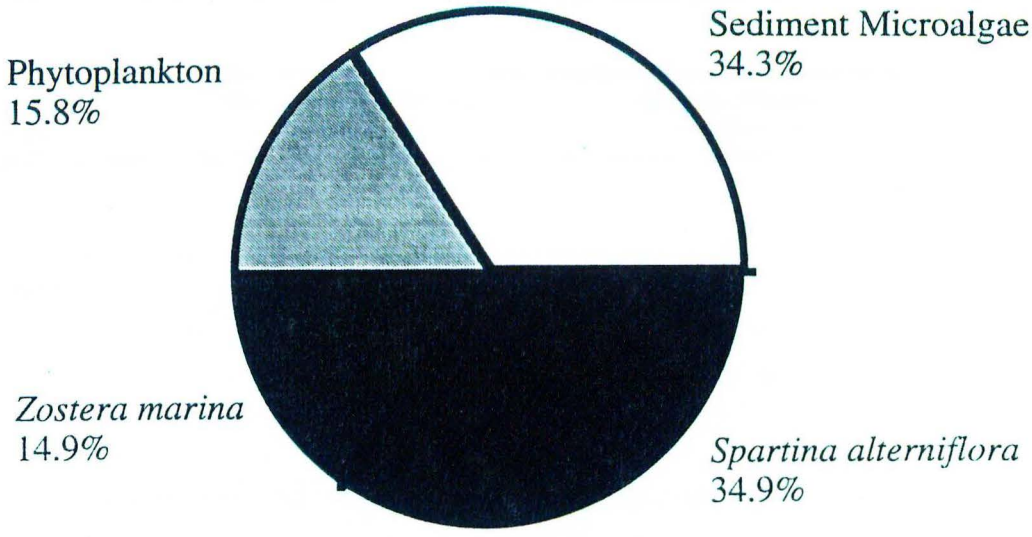
Photoautotrophic Component	Annual Net Production	Habitat Size	Annual Net Production	Percent of Total Ecosystem
	$gC\ m\text{-}2\ yr^{-1}$	$10^4\ m^{-2}$	$10^6\ gC\ yr^{-1}$	%
Phytoplankton	66.0	671	442.7	15.8
Sed. Microalgae				
NVST	127.6	420	535.9	19.1
VST	101.2	120	121.4	4.3
NVIT	169.0	100	169.0	6.0
VIT	162.5	85	138.1	4.9
Zostera marina				
Epiphytes	55.9	120	67.1	2.3
Shoot	241.3	120	289.6	10.3
RR	54.2	120	65.0	2.3
Spartina alterniflora				
Shoot	830.8	85	706.2	25.2
RR	319.7	85	271.7	9.7
TOTAL			2806.7	99.9

The fractions of each phototrophic contribution to total ecosystem production of the Goodwin Islands NERR were plotted for comparison to the results from a study of another Atlantic coastal marsh-estuarine ecosystem, the North Inlet, South Carolina (Pinckney and Zingmark, 1993a). The North Inlet study utilized photophysiological models of sediment microalgal production to integrate annual primary production and then estimated the contribution by the other autotrophs using empirical data gathered from other studies (Pinckney and Zingmark, 1993a). Phytoplankton accounted for 15.8% of total ecosystem production in the Goodwin Islands NERR compared to 20.8% in the North Inlet ecosystem (Fig. 10). Sediment microalgal contribution among the two ecosystems compared favorably with approximately 30% of the annual net production by sediment microalgae (Fig. 10). *Spartina alterniflora* productivity was responsible for approximately 35% of total production among the two ecosystems while the productivity of *Zostera marina* in the Goodwin Islands NERR (14.9%) was similar to that contributed by macroalgae in the North Inlet ecosystem (13.5%). Some preliminary collections made at the Goodwin Islands NERR revealed extremely sporadic distribution and an overall low abundance of macroalgae (C.P. Buzzelli, unpublished data).

While the nitrogen demand of each phototroph was calculated using the net carbon production rate and the optimal C:N ratio, nitrogen uptake was calculated for only the phytoplankton and the two macrophytes, *Zostera marina* and *Spartina alterniflora*. Nitrogen uptake was calculated for the macrophytes and phytoplankton state variables of each habitat model using Michaelis-Menten kinetics. There are no formulations to represent nitrogen uptake by sediment microalgae although dissolved inorganic nitrogen is exchanged vertically within each habitat model based upon empirical data (Buzzelli, in review). Table 5 summarizes the annual nitrogen demand and uptake by each of the phototrophic components of the Goodwin Islands NERR habitat models. Based upon an annual production rate of 66.0 gC m^{-2} yr^{-1} and the Redfield C:N weight ratio (5.7), the annual phytoplantkon nitrogen requirement was 11.5 gN m^{-2} yr^{-1} (Table 6). Annual phytoplankton nitrogen uptake estimated by the models was 15.7 gN m^{-2} yr^{-1}. Based upon the areal production rates provided in Table 4 and a C:N of 5.7 sediment microalgae required 22.4, 13.8, 29.6, and 28.5 gN m^{-2} yr^{-1} in the NVST, VST, NVIT, and VIT habitats, respectively (Table 6). The annual nitrogen requirement for *Zostera marina* shoots and root-rhizomes was 16.0 gN m^{-2} yr^{-1} while the actual nitrogen uptake was 5.95 gN m^{-2} yr^{-1}. The annual nitrogen requirement of *Spartina alterniflora* was 27.5 gN m^{-2} yr^{-1} while the root-rhizome uptake rate was 11.5 gN m^{-2} yr^{-1} (Table 5).

The annual carbon production and nitrogen demand of each of the autotrophs in the habitat models was calculated to compare the four different littoral zone habitats (Table 6). The nonvegetated subtidal habitat model (NVST) predicted 740 x 10^6 gC yr^{-1} which was 28.6% of the total ecosystem annual net primary production. The NVST habitat required 130 x 10^6 gN for this rate of primary production and the nitrogen requirement was over 50% of the nitrogen requirement of the entire ecosystem (Table 6). The vegetated subtidal habitat model (VST) generated an annual net carbon production of 562 x 10^6 gC which represented 21.7% of total ecosystem production. The VST habitat required 440 x 10^6 gN to sustain this level of production and the VST nitrogen requirement was 17.4% of the total predicted for the littoral zone of the Goodwin Islands NERR (Table 6). The nonvegetated intertidal habitat model predicted 170 x 10^6 gC of annual net production and was 6.6% of the ecosystem total. Approximately 30 x 10^6 gN or 11.9% of the ecosystem total nitrogen demand was required to sustain this level of production in the NVIT habitat. The vegetated intertidal marsh habitat model (VIT) predicted the highest annual net carbon production among the four habitats at 1116 x 10^6 gC which comprised 43.1% of the total. The nitrogen required to sustain this net productivity was 47 x 10^6 gN which made up the final 19.0% of the total ecosystem nitrogen demand (Table 6).

(A) Goodwin Islands NERR Ecosystem Primary Production



(B) North Inlet, SC Ecosystem Primary Production

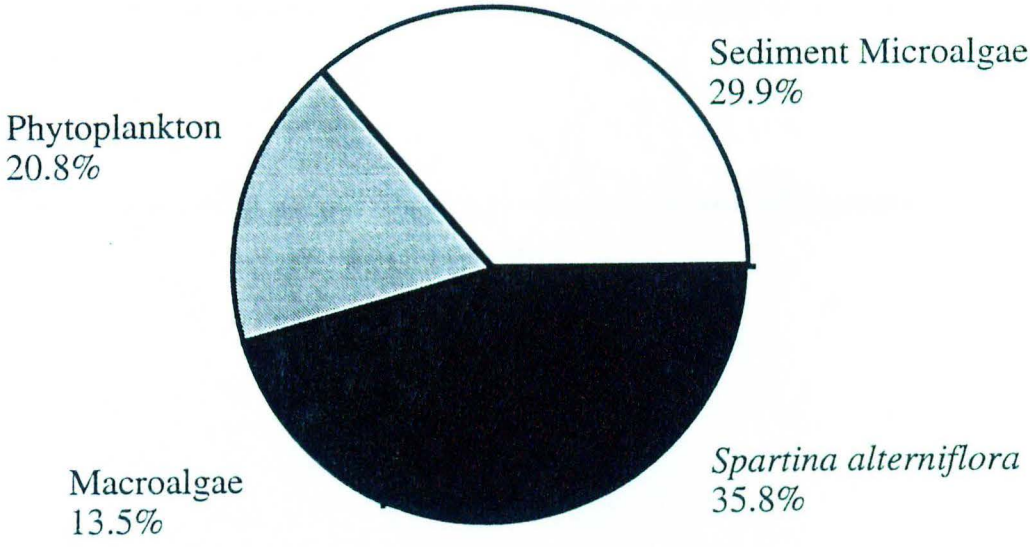


Figure 10. Comparison of the contributions of various autotrophs to net ecosystem primary production between the (A) Goodwin Islands NERR, and the (B) North Inlet, South Carolina ecosystem (from Pinckney and Zingmark, 1993a).

Table 5. Estimates of annual nitrogen demand and uptake for estuarine autotrophs using the Goodwin Islands habitat models. Demand is calculated using the net carbon production and the optimal C:N ratio. Uptake is calculated using a Michaelis-Menten relationship based upon external nitrogen concentration, a half-saturation value, and the maximum uptake rate. Phytoplankton nitrogen processes were summed over the four separate habitat models. The habitats are nonvegetated subtidal (NVST), vegetated subtidal (VST), nonvegetated intertidal (NVIT), and vegetated intertidal (VIT).

Photoautotrophic Component	Annual Nitrogen Demand gN m^{-2} yr^{-1}	Annual Nitrogen Uptake gN m^{-2} yr^{-1}
Phytoplankton	11.5	15.7
Sediment Microalgae		
NVST	22.4	na
VST	17.8	na
NVIT	29.6	na
VIT	28.5	na
Zostera marina		
shoots	15.1	2.09
root-rhizomes	0.89	3.86
total	16	5.95
Spartina alterniflora		
shoots	26	na
root-rhizomes	1.53	11.5
total	27.5	11.5

Table 6. Estimates of net annual carbon production and nitrogen demand of each of the four littoral zone habitats of the Goodwin Islands NERR using the four habitat simulation models. The habitats are nonvegetated subtidal (NVST), vegetated subtidal (VST), nonvegetated intertidal (NVIT), and vegetated intertidal (VIT). Each habitat model includes diatoms, other plankton, and sediment microalgae. In addition to algae the vegetated subtidal and intertidal habitat models include the net shoot and root-rhizome production by *Zostera marina* and *Spartina alterniflora*, respectively.

Habitat	Size (ha)	Percent of Total Size	Annual C Production gC	Percent of Total C Production	Annual N Demand gN	Percent of Total N Demand
NVST	420	51.9%	740×10^6	28.6%	130×10^6	51.7%
VST	120	18.5%	562×10^6	21.7%	44×10^6	17.4%
NVIT	100	12.3%	170×10^6	6.6%	30×10^6	11.9%
VIT	85	11.1%	1116×10^6	43.1%	47×10^6	19.0%

The four habitat models were used to estimate the annual net material fluxes for each habitat as well as the entire littoral zone of the Goodwin Islands NERR (Table 7). The water column constituents included total phytoplankton (gC yr^{-1}), TPOC (gC yr^{-1}), DOC (gC yr^{-1}), and TDIN (mmolesN yr^{-1}). Net import is designated as a negative flux while net export is shown as a positive flux. The nonvegetated subtidal habitat model (NVST) predicted imports of phytoplankton C and TPOC equal to -3.9 x 10^7 gC yr^{-1} and -4.7 x 10^7 gC yr^{-1}, respectively, from the surrounding boundary environments. The NVST habitat was an annual source of DOC to the estuary (1.4 x 10^8 gC) and a sink for TDIN (-1.1 x 10^9 mmolesN; Table 7). The vegetated subtidal habitat model (VST) also predicted annual imports of phytoplankton and TPOC equal to -1.4 x 10^7 gC and -1.7 x 10^8 gC, respectively. The VST annually exported 2.4 x 10^7 gC of DOC to the surrounding habitats and imported -2.2 x 10^8 mmoles TDIN (Table 7). The nonvegetated intertidal habitat model (NVIT) predicted annual imports of -4.5 x 10^6 g phytoplankton C, -4.7 x 10^7 g TPOC, -1.0 x 10^7 g DOC, and -4.7 x 10^7 mmoles TDIN (Table 7). The vegetated intertidal habitat model (VIT) predicted that the marsh annually imports -1.4 x 10^6 g phytoplankton C, -1.4 x 10^7 g TPOC, -1.0 x 10^7 g DOC, and -1.5 x 10^7 mmoles TDIN. In order to assess the interactions between the Goodwin Islands littoral zone and the surrounding estuary the annual total exchanges were summed among the habitats. The totals that were calculated using the four habitat models provide annual imports of phytoplankton C (-5.9 x 10^7 gC), TPOC (-2.7 x 10^8 gC), and TDIN (-1.4 x 10^9 mmolesN) and an annual export of DOC (1.5 x 10^8) for the littoral zone of the Goodwin Islands NERR.

DISCUSSION

This study utilizes a unique and innovative approach to the simulation of coastal zone ecosystem dynamics. The model series was organized and developed following differences in sediment elevation and biotic composition among littoral zone habitats of the Goodwin Islands National Estuarine Research Reserve in Virginia in order to simulate primary production and water column processes (Buzzelli, in review). These models have been used to integrate research methods (field and geographic data collection), to link distinct aquatic habitats within the ecosystem mosaic, and to link water quality and living resources in the analysis of ecosystem dynamics. The models also provide a framework to assemble available data, identify missing information, estimate ecosystem and habitat productivity, and investigate the potential impacts of altered environmental factors upon ecosystem dynamics in the Chesapeake Bay littoral zone.

Water column concentrations in the intertidal habitat models were very sensitive to changes in the integration interval (dt; Figures 3 and 4). The patterns evident over the sensitivity series depicted in Figures 3 and 4 were caused by the interactions between dt and tidal inundation. Water column concentration (gC or mmoleN m^{-3}) are calculated using the change in volume that results from the exchanges with the adjacent habitats. Since the marsh is not inundated for various periods of the tidal cycle, a large dt causes very large and sudden changes in flooded area and tidal prism volume. These effects are mitigated when dt is reduced to time scales consistent with those that regulate changes in tidal height (minutes). A smaller dt creates smoother hypsometric and volume curves to calculate marsh inundation and tidal volume. Based upon considerations for model complexity and output versus computer time an integration interval of 11.25 minutes (0.0078125 d) has been chosen as the time step for the intertidal habitat models.

Table 7. Estimates of annual material exchanges for the four littoral zone habitats of the Goodwin Islands NERR using the four habitat simulation models. The habitats are nonvegetated subtidal (NVST), vegetated subtidal (VST), nonvegetated intertidal (NVIT), and vegetated intertidal (VIT). The exchanges of phytoplankton carbon,total particulate organic carbon (TPOC), dissolved organic carbon (DOC), and total dissolved inorganic nitrogen (TDIN) between a habitat and its two adjacent boundaries were integrated annually and summed to calculate net import (-) or export (+).

	Phytoplankton ($gC\ yr^{-1}$)	TPOC ($gC\ yr^{-1}$)	DOC ($gC\ yr^{-1}$)	TDIN ($mmoles\ N\ yr^{-1}$)
NVST	-3.9×10^7	-4.7×10^7	1.4×10^8	-1.1×10^9
VST	-1.4×10^7	-1.7×10^8	2.4×10^7	-2.2×10^8
NVIT	-4.5×10^6	-4.7×10^7	-1.0×10^7	-4.7×10^7
VIT	-1.4×10^6	-1.4×10^7	-1.0×10^7	-1.5×10^7
TOTALS	-5.9×10^7	-2.7×10^8	1.5×10^8	-1.4×10^9

The concentrations of DIA, LPOC, and SM during year two of simulation in the vegetated subtidal model were very robust with respect to %10 deviations in key controlling parameters. Most of the mathematical expressions for these state variables have been calibrated and utilized for a number of years (Cerco and Cole, 1994; Kuo and Park, 1994). The flood/ebb signal present in the subtidal model output of water column concentrations was not as apparent in the field data (Fig. 7). In most cases the concentrations of water column chlorophyll *a* , TPOC, and TDIN output by the nonvegetated and vegetated subtidal models are consistent with data recorded at the Goodwin Islands NERR (Moore et al., 1994). These data are also within the range of longer term measurements made in the lower York River (Batuik et al., 1992). The primary exceptions are for model output of chlorophyll *a* concentrations (Fig. 7A and 7D). The model output is an order of magnitude less than field data for the nonvegetated subtidal habitat (Fig. 7D). The comparatively low values of chlorophyll *a* generated by the NVST model result from the very large volume used to calculate the concentrations. The mass of diatoms and other plankton in each of the habitat models are greatly influenced by the inter-habitat exchanges as the magitudes of the exchange rates are much greater than those associated with production and loss terms. Model chlorophyll *a* concentrations are lower than those predicted for the surface waters of the mainstem Chesapeake Bay (10-20 mg m^{-3}; Cerco, 1993). The TPOC concentrations from the Goodwin Islands subtidal habitat models are similar to those reported in Cerco (1993). The TDIN concentrations from the subtidal models are within the range of the surface and bottom values predicted in Cerco (1993).

Model simulation of *Zostera marina* shoot, root-rhizome, and epiphytic biomass were also fairly robust during sensitivity analysis although epiphytic biomass could change by 40% if its basal metabolic rate is increased or decreased by 10% (Table 2). The model replicates the annual changes in *Zostera marina* biomass and has been used to estimate net annual primary production for eelgrass meadows of lower Chesapeake Bay (Figure 11). The equations that represent *Spartina alterniflora* are highly parameterized and the shoot and root-rhizome carbon biomass was sensitive to changes in shoot maximum photosynthetic rate (SPMax), the root-rhizome basal respiration rate (SRRR@20), and the carbon translocation potential (SCPot; Table 3). The connectivity between above and below ground carbon pools is demonstrated by the effects of these three parameters upon both shoot and root-rhizome carbon state variables. Net production is translocated downward, a pulse of carbon is translocated upwards in the spring, and a large fraction of shoot carbon remaining in the fall is translocated to the root-rhizomes. SPmax appears to be the most dominant parameter and values calculated from the literature vary with methods, geographic locations, and conversion units and range 0.01-0.36 d^{-1} (Table 8). The maximum rate of 0.15 d^{-1} used in this study is the average value calculated from the other studies of *Spartina alterniflora* primary production (Table 8).

The dynamics of 37 different state variables can be represented by these four littoral zone habitat models (Figure 2). The output of only a few of these state variables have been validated in this summary. While one of the objectives of this modeling project was to organize data relevant to Chesapeake Bay littoral zone ecology, another was to identify information that was lacking. Data is required in several areas including the annual variation in the productivity and biomass of sediment microalgae in all habitats and the relationships between sediment microalgal production and the effects of macrophyte canopy shading; the spatial and temporal dynamics of dissolved organic carbon in shoal waters of lower Chesapeake Bay; the processes of gross and net photosynthesis, nitrogen uptake, and internal carbon and nitrogen translocation in *Spartina alterniflora*; and the horizontal exchange of dissolved and particulate materials between the vegetated intertidal marsh and the surrounding habitats.

Table 8. Comparison of Spartina alternilflora maximum photosynthetic rates (d^{-1}) calculated from literature sources. The research method referenced in the literature source is provided. A 12 hour day was used to convert between hourly and daily rates.

METHOD	RATE (d^{-1})	SOURCE
Gas flux chambers	0.01[a]	Blum et al., 1978
Gas flux chambers	0.13[b]	Giurgevich and Dunn, 1979
Gas flux chambers	0.04[c]	Drake and Read, 1981
Curve fit from growth study	0.26[d]	Morris, 1982
Gas flux chambers	0.36[e]	Morris et al., 1984
Gas flux chambers	0.06[f]	Pezeshki et al., 1987
Nitrogen uptake experiments	0.36[g]	Morris and Bradley, 1990
Goodwin Islands model	0.15[h]	This study

[a]Estimated using 0.4 gC gdw^{-1} and 1045 gdw m^{-2}.
[b]Estimated empirically from data provided.
[c]Estimated using 0.4 gC gdw^{-1} and 500 gdw m^{-2} for a *Spartina patens* community.
[d]Estimated assuming 30 °C
[e]Estimated using 0.43 gC gdw^{-1}
[f]Estimated using 0.4 gC gdw^{-1} and 900 gdw m^{-2}
[g]Estimated using 0.006 gN gdw^{-1} root-rhizome tissue
[h]Average calculated from other studies listed for use in Goodwin Islands model

One of the main objectives of this modeling study was to estimate the annual rate of net primary production by phytoplankton, sediment microalgae, *Zostera marina*, and *Spartina alterniflora* of the Goodwin Islands NERR (Table 4). The net annual rate of phytoplankton production (66.0 gC m^{-2} yr^{-1}) accounted for 15.8% of total annual ecosystem production (Fig. 10A) and was within the range of values reported in the literature (Table 9). The annual chlorophyll *a* biomass curves generated using the subtidal habitat models are similar to long term patterns evident in data collected in the lower York River, Virginia (Batuik, 1992; Buzzelli, in review). Using regression equations provided in the literature the annual net rate calculated for the mainstem Chesapeake Bay was 20.26 gC m^{-2} yr^{-1} while that calculated for Narragansett Bay, Rhode Island was 101.6 gC m^{-2} yr^{-1} (Malone et al., 1986; Keller, 1989). An empirical model of Narragansett Bay provided an average rate of 91.25 gC m^{-2} yr^{-1} (Keller, 1988) while estimates of annual net phytoplankton productivity for North Carolina estuaries ranged 52-500 gC m^{-2} yr^{-1} (Boyer et al., 1993; Mallin, 1994; Table 9).

The net annual productivity of sediment microalgae predicted by the four habitat models of the Goodwin Islands NERR ranged 101-169 gC m^{-2} yr^{-1} (Table 4) and accounted for 34.3% of the total annual littoral zone production (Fig. 10A). The rate in the nonvegetated intertidal habitat (NVIT) was greater than that of the other three habitats. This results from the reduced combined effects of light attenuation due to the depth of the overlying water column (NVST and VST habitats) and sediment shading by the canopy biomass (VST and VIT habitats). Light attenuation due to overlying water was reduced in the NVIT habitat because it was inundated only 46% of the time over the third year of simulation (21,505 of 46,720 time steps). The effects of canopy shading are particularly evident in the differences between the productivity in the deeper sand habitat (NVST; 127.6) relative to the shallower seagrass habitat (VST; 101.2). Although sediment microalgal productivity estimates vary with geographic location and habitat, the rates estimated using the Goodwin Islands habitat models were in overall agreement with those calculated from the biomass data collected as well as literature values (Table 9). A shallow nonvegetated subtidal habitat in Denmark averaged 89.0 gC m^{-2} yr^{-1} (Colijn and deJonge, 1984) while mudflats in England and Massachusetts averaged 143.0 and 250.0 gC m^{-2} yr^{-1}, respectively (Joint, 1978; Gould and Gallagher, 1990). Sediment microalgal production in a Mississippi seagrass meadow was estimated to be 339.0 gC m^{-2} yr^{-1} while that of a Mississippi *Spartina alterniflora* marsh was 57.4 gC m^{-2} yr^{-1} (Sullivan and Moncreiff, 1988; Daehnick, Sullivan and Moncreiff, 1992). Sediment microalgal production over different habitats of the North Inlet, South Carolina salt marsh ecosystem ranged between 55-234 gC m^{-2} yr^{-1} (Pinckney and Zingmark, 1993b; Table 9).

Zostera marina shoot net annual productivity generated by the VST model was 241.3 gC m^{-2} yr^{-1} and was approximately four times that calculated for the epiphytes (55.9) or root-rhizomes (54.2; Table 4). *Zostera marina* community productivity accounted for about 15% of the total production in the littoral zone of the Goodwin Islands NERR (Fig. 10A). The annual biomass curves for the three carbon state variables related to *Zostera marina* are similar to field data collected in the Goodwin Islands seagrass meadow and are within the range of long term data for the lower York River, Virginia (Orth and Moore, 1986). The Goodwin Islands *Zostera marina* shoot productivity was within the range of values reported from Massachusetts (155-345) (Roman and Able, 1988) and the Netherlands (160-412) (van Lent and Verschuure, 1994) (Table 7). The Goodwin Islands *Zostera marina* root-rhizome productivity was at the low end of values reported from North Carolina (55-102; Kenworthy and Thayer, 1984) and the Netherlands (53-132; van Lent and Verschuure, 1994; Table 9).

Table 9. Summary of annual net production rates (gC m^{-2} yr^{-1}) taken from published literature. [1]Estimated using linear regression equation provided. [2] Averaged from values provided.

Phototroph/Location	Annual Rate	Literature Source
Phytoplankton		
Chesapeake Bay	20.26[1]	Malone et al. 1986
Narragansett Bay	101.61	Keller 1989
Narragansett Bay	91.25[2]	Keller 1988
Neuse River, NC	373.4	Boyer et al. 1993
North Carolina Estuaries	52-500	Mallin 1994
Goodwin Islands Models	66.0	This Study
Sediment Microalgae		
Mudflat in England	143.0	Joint 1978
Subtidal in Denmark	89.0	Colijn and DeJong 1984
Marsh in Mississippi	57.4	Sullivan and Moncreiff 1988
Mudflat in Massachusetts	250.0	Gould and Gallagher 1990
Seagrass meadow in Mississippi	339.0	Daenick et al. 1992
Marsh ecosystem in South Carolina	55-234	Pinckney and Zingmark 1993
Goodwin Islands Models	101-169	This Study
Zostera marina		
Shoots in Massachusetts	155-345	Roman and Able 1988
Shoots in Netherlands	160-412	Van Lent and Verschuure 1994
Goodwin Islands Model-Shoots	241.3	This Study
Root-Rhizomes in Netherlands	53-132	Van Lent and Verschuure 1994
Root-Rhizomes in North Carolina	55-102	Kenworthy and Thayer 1984
Goodwin Islands Model-RR	54.2	This Study
Spartina alterniflora		
Shoots in South Carolina	289-875	Dame and Kenny 1986
Shoots in Georgia	749-1421	Dai and Wiegert in press
Goodwin Islands Model-Shoots	830.8	This Study
Root-Rhizomes in South Carolina	945-2178	Dame and Kenny 1986
Root-Rhizomes in Georgia	397-872	Dai and Wiegert in press
Root-Rhizomes in Virginia	270-857	Blum 1993
Root-Rhizomes in New Jersey	880.0	Smith et al. 1979
Goodwin Islands Model-RR	319.7	This Study

The *Spartina alterniflora* annual shoot and root-rhizome biomass changes predicted using the model agree with literature values and the model estimates of primary production are similar to those calculated using Goodwin Islands biomass data. *Spartina alterniflora* shoot and root-rhizome productivity were estimated at 830.8 and 319.7 gC m^{-2} yr^{-1}, respectively, and these rates were similar to the short form shoot and root-rhizome annual productivity predicted by Dai and Wiegert (in press) using a canopy model (749 and 397 gC m^{-2} yr^{-1}; Table 9). The similarities among the model of the Goodwin Islands *Spartina alterniflora* and those estimated for short form *Spartina alterniflora* from Georgia (Dai and Wiegert, in press) result primarily from the inclusion of seasonal cycles of internal carbon translocation in both models (Buzzelli Chapter 2). *Spartina alterniflora* whole plant production accounted for almost 36% of the total ecosystem production in the Goodwin Islands littoral zone (Fig. 10A). The shoot productivity estimate agreed with the range of empirical estimates for South Carolina (Dame and Kenny, 1986) and model estimates for Georgia (Dai and Wiegert, in press; Table 9). *Spartina alterniflora* root-rhizome productivity generated using the VIT model of the Goodwin Islands marsh habitat was much lower than those reported for South Carolina (Dame and Kenny, 1986) and New Jersey (Smith et al., 1979) but are within the range of values in Georgia (Dai and Wiegert, in press) and the eastern shore of Virginia (Blum, 1993). The processes representing belowground dynamics in the marsh were calibrated and initialized using data collected at the Goodwin Islands NERR and the annual biomass curves for the *Spartina alterniflora* shoot and root-rhizome carbon state variables reflect those reported in the literature.

The annual Goodwin Islands phytoplankton nitrogen demand was estimated to be 11.5 gN m^{-2} based upon a C:N weight ratio of 5.7 (Table 5). The annual phytoplankton nitrogen uptake rate was estimated to be in excess of nitrogen demand at 15.7 gN m^{-2}. This disparity resulted because unlike *Zostera marina* and *Spartina alterniflora* there are no mechanisms in the model that limit nitrogen uptake as a function of internal C:N ratio. It is hypothesized that this difference reflects potential luxury nitrogen uptake by phytoplankton. The differences in the nitrogen requirement of sediment microalgae among the four habitat models resulted from the differences in the net annual carbon productivity (Tables 4 and 5). Although nitrogen uptake by sediment microalgae is not modeled explicitly, the models include a vertical exchange of TDIN between the water column and sediment based upon empirical data collected in subtidal and intertidal habitats (Neikirk 1996). These empirical studies measured community vertical exchanges only during the daytime and further studies are being conducted to determine the diel variability of sediment-water biogeochemcial fluxes in littoral zone environments of lower Chesapeake Bay (K.A. Moore and I. C. Anderson, Virginia Institute of Marine Science).

Nitrogen is taken up from the water column by the shoots and from the sediments by the root-rhizomes of *Zostera marina*. Other studies have determined that the sediment is the primary source of nitrogen for eelgrass (Iizumi and Hattori, 1982; Short and McRoy, 1984). Nitrogen is translocated from root-rhizomes to the shoots in order to meet the shoot nitrogen requirement for growth in the Goodwin Islands model (Buzzelli, in review). Nitrogen uptake by the shoots and root-rhizomes is influenced both by the external concentration and by feedback limitation terms based upon the maximum and minimum C:N ratios of the tissues (Buzzelli, 1991). The difference between the annual nitrogen demand of *Zostera marina* (16.0 gN m^{-2} yr^{-1}) and the annual nitrogen uptake (5.95 gN m^{-2} yr^{-1}) was attributed to the role of translocation and internal recycling (Table 6). Based on the Goodwin Islands model, approximately 63% of the macrophyte nitrogen requirement was met through internal recycling. This value is within the range of annual estimates made by Borum et al. (1989; 64%) but is approximately twice the short term rates of translocation measured by Buzzelli and Wetzel (in review; 34%). Later refinements to this model will include bi-directional nitrogen translocation within individual plants as well as carbon and nitrogen

translocated from adjacent root-rhizomes connected in the belowground matrix of the eelgrass meadow.

Whole plant nitrogen demand and root-rhizome uptake of *Spartina alterniflora* were calculated using the vegetated intertidal marsh model. A similar approach to that used to model the nitrogen relationships of *Zostera marina* was adopted for the shoot and root-rhizome nitrogen state variables of *Spartina alterniflora* except that there is no nitrogen uptake by the shoots . As the case in eelgrass, the whole plant nitrogen requirement for growth of *Spartina alterniflora* (27.5 gN m^{-2} yr^{-1}) was in excess of nitrogen taken up by the macrophyte (11.5 gN m^{-2} yr^{-1}; Table 5). Approximately 58% of the plant nitrogen requirement was met through internal recycling and these results agree with the 54% estimated in an empirical study in a Georgia marsh (Hopkinson and Schubauer, 1984). Further field and laboratory studies should include the determination of the actual short and long term rates of carbon and nitrogen uptake and translocation in *Spartina alterniflora* using photophysiological methods, carbon and nitrogen stock assessments, and the stable isotope, ^{15}N, as a tracer. A refinement that is being made to the model is the inclusion of bi-directional translocation of nitrogen to synchronize with seasonal carbon translocation (Buzzelli, in review).

Despite the fact that the VIT is the smallest habitat the annual production by phytoplankton, sediment microalgae, and *Spartina alterniflora* (1116 x 10^6 gC) accounted for 43.1% of total in the littoral zone of the Goodwin Islands NERR (Table 6). Over 80% of the intertidal primary production and 34.1% of the total for the littoral zone was attributable to *Spartina alterniflora* (Fig. 3A). This characteristic explains the comparatively low fraction of the total ecosystem nitrogen demand required by the vegetated intertidal habitat (Table 6) because the C:N ratio of *Spartina alterniflora* shoots and root-rhizomes is 7-10 times that of the phytoplankton or sediment microalgae. Conversely, phytoplankton and sediment microalgae primary production in the nonvegetated subtidal habitat (NVST) was only 28.6% of the total production in the littoral zone of the Goodwin Islands NERR although it is the largest of the four habitats (Table 6). The NVST did require 51.7% of the total littoral zone nitrogen demand due to the low C:N ratio as compared to the habitats that include macrophytes. The annual C production by the vegetated subtidal habitat (VST; 562 x 10^6 gC) was approximately half that of the vegetated intertidal habitat (1116 x 10^6 gC) but the annual nitrogen demand and fraction of total ecosystem nitrogen requirement were similar (44 x 10^6 vs 47 x 10^6 gN). The nonvegetated intertidal habitat had the least influence upon the annual ecosystem carbon production (6.6%) and nitrogen requirement (11.9%) of the four littoral zone habitats.

The nonvegetated and vegetated subtidal models (NVST and VST) both predicted net annual imports of phytoplankton, particulate organic carbon, and dissolved inorganic nitrogen and predicted net annual exports of dissolved organic carbon (Table 7). The nonvegetated and vegetated intertidal models (NVIT and VIT) both predicted net annual imports of all four water column constituents including dissolved organic carbon (Table 7). Figure 11 A-D depicts the annual net exchanges for each habitat and water column constituents. An arrow into the habitat denotes a net annual import into the habitat from the adjacent habitats while an arrow out of a habitat represents a net export of the constituent across its two boundaries. The subtidal net DOC production and export were caused by the increased exudation of the comparatively large phytoplankton population that was imported (Fig. 11A and 11C). The intertidal net DOC imports resulted from the decreased exudation and import of phytoplankton as compared to the subtidal habitat models (Fig. 11A and 11C). Over an annual cycle the nonvegetated intertidal habitat was inundated 46% of the time while the vegetated intertidal habitat was inundated only 25% of the

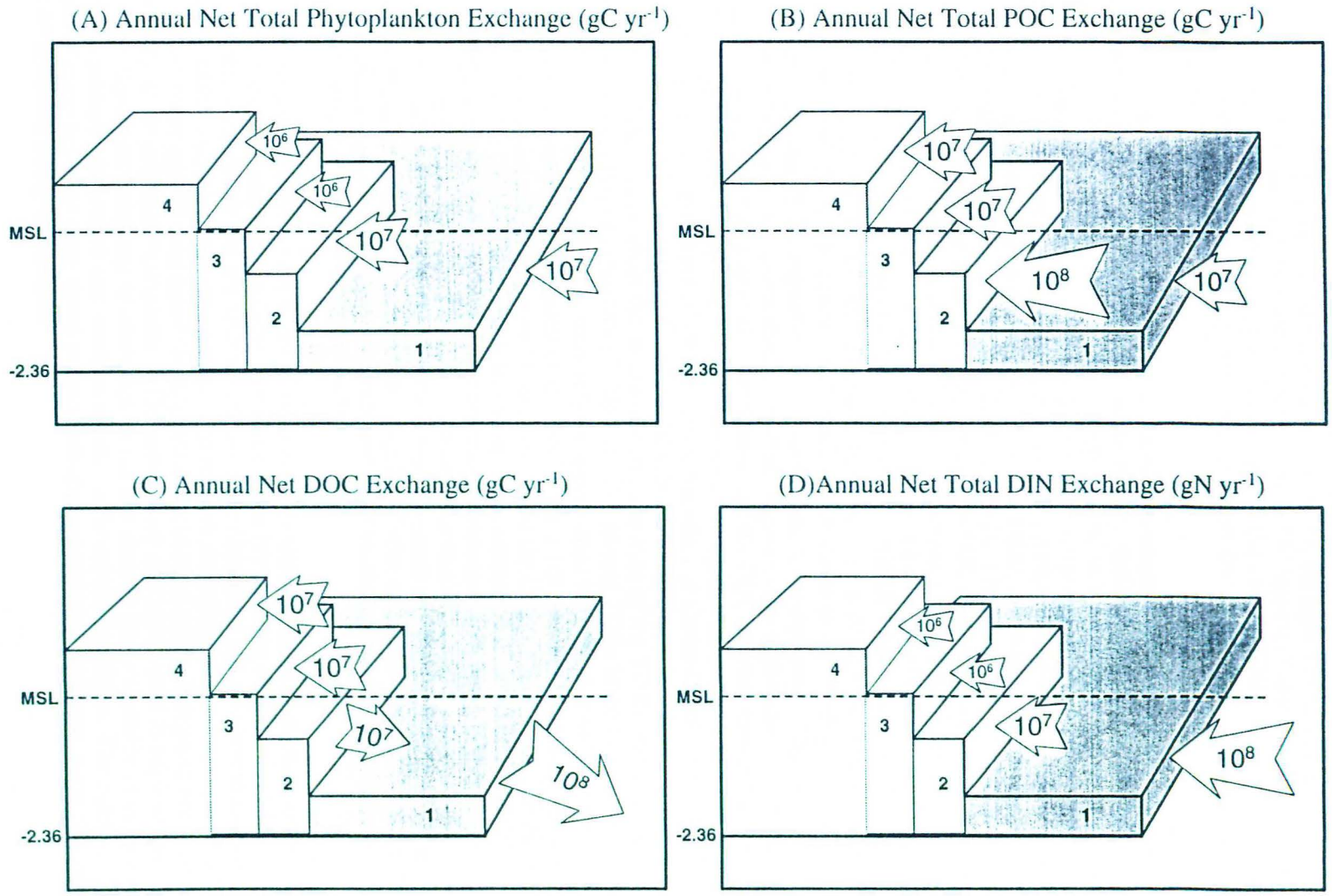


Figure 11. Comparison of annual net exchanges of (A) total phytoplankton, (B) total particulate organic carbon, (C) dissolved organic carbon, (D) total dissolved inorganic nitrogen in the nonvegetated subtidal (1), vegetated subtidal (2), nonvegetated intertidal (3), and vegetated intertidal (4) habitats. (A-C) are in units of gC yr^{-1} while (D) is in gN yr^{-1}. An arrow pointing intoa habitat denotes a net annual import of the water column constituent while an arrow pointing out denotes a net annual export.

time. The decreased inundation time and phytoplankton import of the intertidal habitats relative to the subtidal habitats did not translate to decreased TPOC import into the intertidal habitats (Table 7 and Fig 11B). The vegetated subtidal habitat imported the greatest TPOC annually (-1.7 x 10^8 gC) while the other three habitats were similar relative to TPOC import (Table 8 and Fig. 11B). All four habitats imported dissolved inorganic nitrogen and the annual TDIN imported was correlated to the annual phytoplankton mass imported as phytoplankton remove nitrogen from the water column (Fig. 11A and 11D).

Coastal marshes possess biogeochemical relationships with their surrounding environments based upon their geomorphologic developmental history, basin configuration, and hydroperiod (Childers et al., 1993; Rozas, 1995). The hydroperiod of an individual marsh is unique and has a significant influence upon the horizontal and vertical material exchanges (Vorosmarty and Loder, 1994). Despite the differences in geomorphology and hydroperiod among marshes, it is useful to compare and contrast the flux characteristics among marshes as a way to synthesize information and identify spatial or temporal pattterns (Childers, 1992). The material exchange estimates generated for the littoral zone of the Goodwin Islands NERR were compared to annual flux estimates derived from empirical studies (Table 10; Axelrad et al., 1976; Wolaver et al., 1983; Dame et al., 1991; Correll et al., 1992). Carter Creek is a mainland estuarine marsh located approximately 15 km upriver from the Goodwin Islands NERR. Axelrad et al. (1976) estimated that the Carter Creek, Virginia marsh annually exported 1.17 x 10^7 g POC, imported -2.5 x 10^7 g DOC, and imported -2.6 x 10^7 mmole N (Table 10). Wolaver et al. (1983) provided a similar estimate for an annual TDIN import of -2.0 x 10^7 mmole N for the same 10 hectare marsh. The Goodwin Islands marsh model predicted a net POC import to the marsh annually (Table 10). The difference between the POC export at Carter Creek and the POC import predicted using the Goodwin Islands model is attributed to the absence of an upland connection at the Goodwin Islands NERR and the proximity of the terrestrial boundary at Carter Creek (pers. observation). The annual import of DOC into the Goodwin Islands marsh is approximately four times that imported into Carter Creek while the magnitude and direction of the TDIN import is similar among the two York River marsh ecosystems (Table 10). The annual TDIN import calculated for the Goodwin Islands marsh (-1.5 x 10^7 mmoleN) is approximately twice that estimated for a marsh on the Rhode River, Maryland by Correll et al. (1992; -8.6 x 10^6 mmoleN) although the Goodwin Islands marsh is about six times larger (Table 10). Like the Carter Creek marsh on the York River, Virginia, the Rhode River marsh has an upland connection (Correll et al. 1992). The Bly Creek marsh, South Carolina is a geologically young pristine marsh basin (Dame et al., 1991). Although the tidal range in South Carolina is about twice that of lower Chesapeake Bay, the net exchange of POC and TDIN into the Goodwin Islands marsh are similar in magnitude and direction to those determined for the marsh in the Bly Creek ecosystem, South Carolina (Table 10). The DOC exchanges for the Goodwin Islands and Bly Creek marshes are of similar magnitudes but have opposite net directions of transport.

These studies employed a series of simulation models to calculate annual carbon production and nitrogen demand and water column dynamics in the littoral zone of the lower Chesapeake Bay. These models were developed not only to address these objectives but also investigate potential change in habitat and ecosystem properties. The models are being used to assess potential effects of decreased water quality (increased chlorophyll *a*, suspended solids, inorganic nitrogen) upon productivity in the eelgrass community. The models are also being used to explore the possible effects that significant increases or decreases on the distribution and abundance of eelgrass might have upon primary production and nitrogen uptake in the subtidal habitats. The potential effects of changes in mean sea level upon intertidal productivity and material exchange properties are also being investigated using the models.

Table 10. Summary of marsh ecosystem flux estimates assembled from published literature. Negative flux (-) denotes net import to marsh, positive flux (+) denotes net export from marsh.

Location	Size (ha)	POC flux gC yr^{-1}	DOC flux gC yr^{-1}	DIN flux mmoleN yr^{-1}	Literature Source
Carter Creek, Virginia	10	1.17×10^7	-2.5×10^6	-2.6×10^7	Axelrad et al. 1976
Carter Creek, Virginia	10	na	na	-2.0×10^7	Wolaver et al. 1983
Rhode River, Maryland					
Low marsh	13	na	na	-8.6×10^6	Correll et al. 1992
Bly Creek, South Carolina					
Marsh	12	-2.1×10^7	1.8×10^7	-1.2×10^7	Dame et al. 1992
Goodwin Islands Marsh Model	85	-1.4×10^7	-1.0×10^7	-1.5×10^7	This Study

These models were designed to be coupled to coarser scale models of water quality in the Chesapeake Bay watershed (Cerco, 1993). Of course, many important physical and biogeochemical processes are currently not present in the models. The development of the sediment state variables and processes and linkages to the overlying water column must be included in order to better investigate production and material cycling in shallow and irregularly flooded littoral zone habitats. Phosphorus dynamics, the contribution of living and dead macrophytes to DOC production and exchange, and the nitrogen relationships of sediment microalgae would help complete the biogeochemical portions of the models. The secondary productivity within the different littoral zone habitats should be included as a vehicle to transfer energy and nutrients between the autotrophs and higher trophic levels and to provide additional mechanisms to link the habitats in time and space.

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