An Ecological Model of the Florida Bay Seagrass Community

Model Documentation

Version II

By

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Introduction

Within the past two decades, the Florida Bay ecosystem has undergone profound changes indicative of environmental degradation. In particular, a dramatic die-off of the seagrass *Thalassia testudinum*, reductions in water clarity, phytoplankton blooms and loss of several important fish species (Robblee et al. 1991) has occurred since the late 1980s. Because of the importance of the seagrass community as a keystone component of the ecosystem, it is imperative to understand the mechanism of seagrass growth and succession, as well as reasons for its degradation and die-off in Florida Bay. Several hypotheses have been advanced to explain seagrass die-off and other changes in the seagrass community, including an altered salinity regime resulting from reduced freshwater flows, changes in circulation patterns, changes in sediment chemistry, disease, over-maturation of the seagrass beds, and increased nutrient inputs. ***The Florida Bay Seagrass Model*** was developed to investigate these potential mechanisms as they may relate to seagrass die-off and to evaluate their effects on seagrass community processes, distribution and survival.

Development of an ecological model of the Florida Bay seagrass community was initiated in 2001 and has produced a dynamic numerical simulation of the *Thalassia-Halodule* seagrass community (Madden and McDonald 2005). This modeling effort was conceived as a means of enhancing scientific understanding and improving coastal management of seagrass systems in general and of the Florida Bay community in particular. The project has produced an operational mechanistic unit model of the *Thalassia-Halodule* community, calibrated for six basins that represent a large part of Florida Bay. Additional basin models are in continuing development and modules for the seagrasses *Ruppia maritima* and *Syringodium filiformi* are being initiated. The model code was developed in STELLA, MATLAB and FORTRAN platforms and the model can be run on a desktop PC. Initial development is being finalized for representative basins in all major areas of Florida Bay, such that linkage of the model to a hydrodynamic or water balance framework is possible, with a subsequent goal of inserting the kernel of the mechanistic biological model into a spatially explicit landscape-based model operating on a geospatial platform. Currently, model runs for all operational basin versions are done in parallel using data

or model-driven forcing to provide salinity and nutrient input files. When in spatially explicit mode, the model will generate water quality information enabling full interaction of the seagrass, phytoplankton and algal community model components.

Ecology of the Florida Bay Seagrass Community

The seagrass community covers an estimated 5,500 km^2 of the greater Florida Bay and Keys area, and is one of the most extensive seagrass resources in the world (Zieman 1982). Seagrasses are a keystone community of this ecosystem, playing roles in many important physico-chemical (Stumpf et al. 1999, Matheson et al. 1999), autotrophic (Fourqurean et al. 2002) and higher trophic (Ley and McIvor 2002, Lorenz et al. 2002) functions of the bay's ecology. Dominated by the turtle grass *Thalassia testudinum*, seagrasses stabilize sediment and sequester nutrients, processes that help reduce epiphyte and phytoplankton blooms (Zieman 1982). The sediment-binding capacity of the rhizomatous macrophytes also serves to ameliorate turbid resuspension events, reduce scouring, promote a clear water column, and contribute to high rates of primary and secondary productivity (Zieman 1982).

Seagrasses provide refuge, spawning areas and a food source for numerous important fish and invertebrate species (Zieman 1982, Sogard et al. 1989, McIvor et al. 1994, Thayer et al. 1999). Fish densities tend to be greater in the seagrass beds than outside the beds (Weinstein et al. 1977), and mixed communities of *Thalassia* and *Halodule wrightii* appear to support higher densities of desirable fauna (Johnson et al. 2005). In Rookery Bay to the west of Florida Bay, Yokel (1975) reported trawl catches in seagrass beds that were 3.5 times greater than those in other habitat types. Pink shrimp favor seagrass habitat (Sheriden 1992), and initiate their development in the protected confines of Florida Bay before moving to the Dry Tortugas. There, the shrimp production supports one of the largest commercial shrimp fisheries in the Gulf of Mexico (Ehrhardt and Legault 1999). As juveniles, spiny lobsters develop in Florida Bay before moving across the Keys to take residence in the reef extending from the Dry Tortugas to Pacific Reef near Miami (Davis and Dodrill 1989). The highest growth rates of juvenile spiny lobsters in the world have been measured in Florida Bay, which is considered to be an optimum habitat for this species (Davis and Dodrill 1989).

The seagrass community is demonstrably vulnerable to system-wide perturbation, and the *Thalassia* population underwent a catastrophic die-off in 1987 (Carlson et al. 1990a,b; Robblee et al. 1991, Durako et al. 2002). Following this die-off event, multiple systemic changes began to occur throughout the bay, including the development of large and persistent phytoplankton blooms, the loss of other seagrass habitat, decreasing water clarity and disappearance of key fauna (Robblee et al. 1991). Subsequently, additional cases of die-off, the development of harmful algal blooms (Phlips and Badylak 1996) and fish, plant and animal kills have occurred since the initial *Thalassia* die-off (Anderson 2005).

The Florida Bay system continues to exhibit signs of impairment, and is subject to smaller-scale "secondary seagrass die-off" and continuing related habitat degradation (Hall et al. 1999, Durako et al. 2002). These events have caused concern about wholesale restructuring or loss of biological communities, degradation of habitat quality, declines in biodiversity and in fish landings, and possible irreversible damage to the ecology of the bay (Durako et al. 2002). Because of their central ecological position in the Florida Bay system, healthy seagrasses are critical to several key biogeochemical cycles and processes and are important in maintaining water quality. A comprehensive research plan, with emphasis on seagrass research and modeling, was recommended in order to increase understanding and our ability to maintain and restore this critical living resource (Florida Bay Science Oversight Panel Report 1999, 2001).

Context for Model Development

Despite vigorous research on and monitoring of Florida Bay seagrasses, synthesis of information into useful forms for interpretation and science-based management has been lacking. Often, the time and space scales of research outputs are not compatible. System components studied in isolation cannot always be counted on to behave predictably in an ecosystem where strong ecological feedbacks are so prevalent. In an ecological system with the biological, spatial and temporal complexity of Florida Bay, we propose that meaningful synthesis can *only* be effectively achieved through dynamic simulation modeling techniques. Simulation models enable the simultaneous numerical description of state variables, major material flows and forcing functions in the target domain, permitting the full interpretation of ecological relationships, prediction of system behavior and hypothesis-testing. Furthermore, the capability to invoke multiple environmental stresses simultaneously is needed to accurately assess the

cumulative effects of forcings that impact seagrasses *in situ*. Thus, there is a need for a modeling tool that can track multiple non-linear relationships simultaneously. Unlike studies in nature, the simulation model provides a means to determine the mechanism and the magnitude of each potential stress or limitation in controlled isolation and in interaction with other factors.

This modeling tool describes the growth, ecology, community composition, physical structure and nutrient dynamics of the seagrass community, and will guide decisions about the restoration of Florida Bay. Several South Florida Water Management District (SFWMD) mandates are served by this model initiative, including rules development for Minimum Flows and Levels for Florida Bay (Hunt et al. 2005), the Modified Waters Project, and several Acceler8 projects under the CERP program, most notably the C111 Spreader Canal Project and the Florida Bay and Florida Keys Feasibility Study. Development of management strategies and infrastructure components require a model framework that can be used to assess alternative formulation.

The process-level and landscape-scale seagrass models currently being developed for Florida Bay will require a close coupling of research and modeling. Throughout the modeling effort, open communication and data sharing between modelers and the wider bay research community has facilitated model development. There is a strong recognition that this model will need to link with other modeling efforts (hydrodynamic, water quality, upper trophic level) in order to access existing and new ecological data. Linked physical-biological models will address the bay's physical and hydrological architecture and, additionally, will synthesize information on nutrients and water quality, basin and bank geomorphology, water turnover rates in basins and salinity structure.

Model Goals, Purpose and Objectives

The goal of the seagrass modeling effort is to accurately simulate the effects of physical and biogeochemical conditions on the growth and survivorship of seagrasses in a tropical/subtropical carbonate-based system. Specifically, the purpose of the resulting model will be to simulate seagrass community growth, species composition and succession and to provide a tool for testing hypotheses about seagrass die-off and response in Florida Bay. The seagrass unit model will be incorporated within a landscape model framework and linked to process-level models of higher trophic levels. The effort to develop the seagrass models will include empirical studies needed to

develop information for the models, evaluation of the assumptions of the models, and the calibration and verification of model outputs. The models will be used in the restoration program for predicting the effects of water management within a landscape model framework.

The objective of these efforts is to use the seagrass model to better understand mechanisms for recent changes in the seagrass community and assist in making management decisions relevant to seagrasses. Specific objectives of the modeling effort include an improved understanding of the physiology and ecology of Florida Bay seagrass communities, their growth, survival and species succession, as well as determination of the factors controlling seagrass productivity, abundance, and distribution in different areas of Florida Bay.

The model currently includes two seagrass species: *Thalassia*, a long term, stable form, and *Halodule*, a rapidly propagating, opportunistic form. *Ruppia*, a generally less halophytic form expected to expand in distribution with additional fresh water introduction to the system, and *Syringodium*, which is generally found in the more saline southern and western areas of the bay, will be added to the model. The model provides a conceptual framework which guides seagrass research priorities and a computational framework that will yield answers to specific questions about how components of the system interact, and which can test the degree to which environmental factors induce changes in seagrasses. Specifically it will:

- Allow quantitative testing and improved planning of field, mesocosm and laboratory experiments in an inexpensive and controllable model environment
- Provide a means for developing management strategies and for testing hypotheses about how the seagrass community will respond to environmental changes, both natural and anthropogenic
- Provide a means to determine small scale spatial factors responsible for differences in seagrass community recruitment, productivity, structure, and composition, including patch dynamics and bed structure
- Provide a means for testing hypotheses about causes of die-off, including salinity, sulfide, temperature, light, diseases and the possible interactions of these components (the multiple stressor hypothesis)

- Develop a predictive capability that will provide long-term simulations, giving insight to impacts on seagrasses due to nutrient enrichment, changes in freshwater flow and salinity regime, eustatic sea level rise, climate change and episodic impacts such as hurricanes and drought events.

The Unit Model Approach

The basis of the unit model approach is to emphasize a detailed mathematical description of internal seagrass processes and their interactions with the environment which produce changes in biomass per unit area. We have modeled the seagrass community at a point in space that represents average conditions for a given relatively homogeneous area of the system. We have developed separate unit models for different regions of the bay. This approach was chosen because of the lack of spatially explicit data on both seagrasses and environmental variables with which to calibrate the model at spatial scales sufficiently resolved to be meaningful. Modeling spatially averaged units for several representative areas of the bay (Figure 1) has a low spatial resolution but yields important information on general trends in space in response to different environmental contexts (see Spatial Domain section below). The time domain of the model is more highly resolved (see Time Domain section below) because significantly more time series data are available on processes affecting seagrasses and on the physiology of the seagrasses themselves, enabling a more precise accounting of the behavior of these units at small temporal scales.

The initial stage of model development has produced a carbon-based seagrass unit model, calibrated for the Florida Bay *Thalassia testudinum* community in seven basins (from east to west): Duck Key, Trout Cove, Little Madeira Bay, Eagle Key Basin, Whipray Basin, Rankin Lake, and Rabbit Key Basin. Subsequently a module for the seagrass *Halodule wrightii* was implemented and fully integrated into the primary model, invoking inter-specific competition between the two seagrass species. Our approach was to utilize field monitoring data and *in situ* process measurements, augmented by targeted mesocosm studies that accurately measured specific processes and variables (see section on Data Sources below). The model includes information about the physical architecture of seagrass beds as well as interactions of light, nutrients, salinity and sediment properties influencing the growth, survival and succession of seagrasses. This level of detail is achieved at a spatially averaged scale (regional or basin-

wide), and although at the expense of detail about landscape processes or high-resolution spatial variability. The model yields average seagrass biomass, distribution, productivity and species composition per basin. It is important to note that the unit model is not able to predict the dynamics of seagrass population at a particular point in the bay at the sub-basin scale, only the average behavior within a basin. However, the model can be used to explore the environmental characteristics required to produce sub-basin scale spatial variability.

The customization of the unit model for several representative regions of Florida Bay is accomplished through exploitation of publicly available databases at SFWMD as well as from other sources, communication with research scientists, and strong feedback of information requests to the research community.

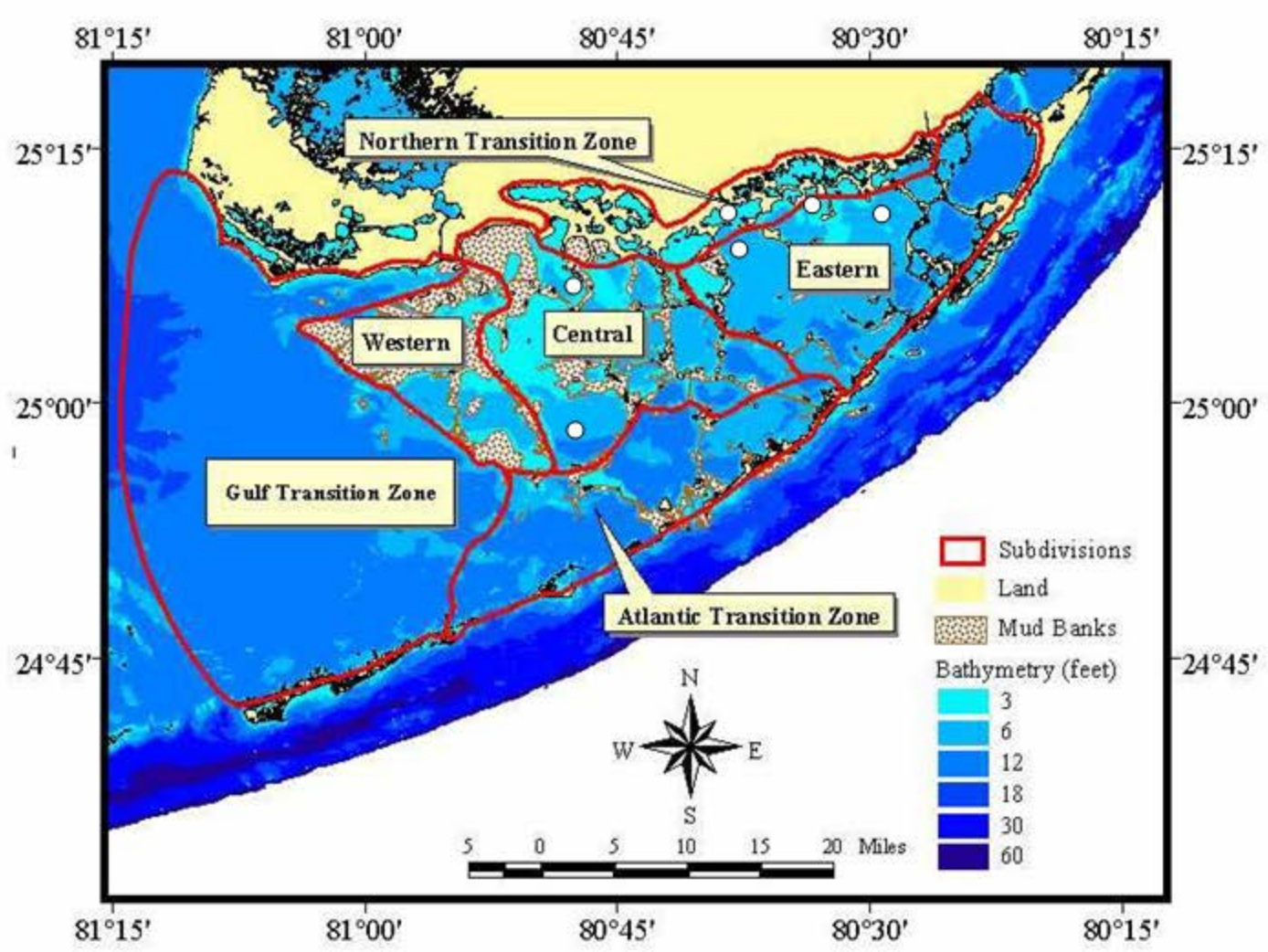

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Figure 1. Florida Bay regions divided into representative areas. The seagrass model calibration emphasizes sites (white dots) in the northern transition zone, the eastern bay and the central bay where land run-off has greatest impact on the system.

Processes specific to sub-tropical Florida Bay that are integrated into the model include: episodic high water temperatures, hypersalinity events, freshwater pulses, carbonate chemistry, diffuse and point source surface and subsurface freshwater inputs, the influence of nutrient inputs from the Gulf of Mexico, the influence of Everglades sheet flow and nutrient inputs, dissolved organic nutrient inputs, bank-basin morphology and depth gradients, organic material inputs, hydrogen sulfide production in sediments, and effects of episodic storms and hurricanes. The totality of the high organic, high sulfide, hypersalinity and high temperature effects, which we refer to as the multiple stressor suite, is likely implicated in the seagrass die-off phenomenon and certainly responsible for sub-lethal effects on seagrass population dynamics. These elements form the basis for several hypotheses regarding seagrass die-off that we use the model to investigate.

Conceptual Model

Model development began with the design of a conceptual model depicting the relevant variables, interactions and processes that are considered important in Florida Bay seagrass ecology (Figure 2). The conceptual model underlies the numerical model, providing a high-level, object-oriented map of the interactions that have been measured in the system or the expected relationships based on scientific literature and expert knowledge. The conceptual model provides a means of showing model variables and their relationships and organizing the structure of the numerical model. This model has also been instrumental in pointing to additional research needs required to fill important gaps in the existing knowledge base. In Figure 2 the blue (lighter shaded) components are fully implemented state variables and forcing functions. The green (darker shaded) components are included in the model but are data driven variables that are not impacted by other model process, although they do impact other variables. Forcing functions in the numerical model are listed along the left side of the conceptual model and include light, dissolved N and P, organic material, temperature and salinity. Along the right side of the diagram are depicted processes such as vegetative and seed propagation, spatial distribution of the population and GIS inputs that are being experimentally implemented in the expansion of a unit model to a spatially articulated landscape model.

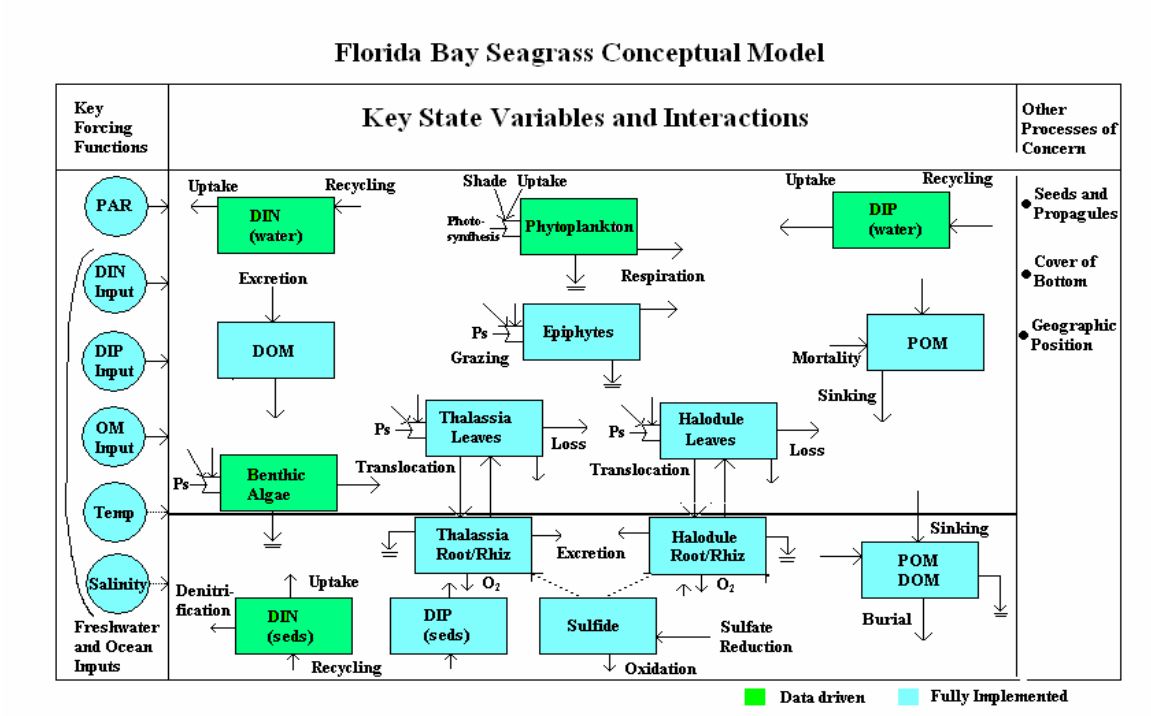


Figure 2. Conceptual model of Florida Bay seagrass community showing state variables, forcing functions and interactions.

In the conceptual model, two seagrass species are the main response variables, regulated by the nutrient cycles, light regime, geology and biology of the bay. The primary seagrass state variables are aboveground (leaves) and belowground (root/rhizome) *Thalassia* compartments and above- and belowground *Halodule* compartments. A state variable representing a generalized community of epiphytes grows on the seagrass aboveground material. We initially conceptualized the seagrass system to most strongly respond to nutrient (positively) and sulfide (negatively) concentrations in the sediment compartment and to light, salinity and temperature in the water column compartment. Epiphytes respond most strongly to nutrients, temperature and light in the water column. Phytoplankton and benthic algae are represented in the model by data functions; they interact with the light regime and nutrients in the water column. Although at present these two variables are fitted with empirical data, they will be converted to state variables following additional conditioning of the data.

Particulate and dissolved organic matter (POM and DOM) pools are partitioned in the water column and sediment pools, whose sizes are influenced by external inputs and detritus formation from plant components and losses to breakdown and remineralization and burial. The dissolved

inorganic phosphorus (DIP) pool in the sediments is largely responsible for regulating seagrass growth as P is the limiting nutrient for autotrophy in Florida Bay (Fourqurean et al. 2002). This pool is increased by a breakdown of sediment organic material (POM, DOM) and small bi-directional diffusive flux between the sediment and water column compartments. Losses from this sediment P pool are from nutrient uptake by seagrasses, buffered by an equilibrium between the dissolved P pool and the solid phase pool of sorbed phosphorus. Dissolved nitrogen (DIN) in sediments is a data-driven variable that we consider to be rarely limiting to seagrass production. Due to the carbonate geochemistry of the system and affinity for P to bind and adsorb to carbonate compounds (forming apatite and oxyhydroxides), P is generally low in concentration throughout the system. However, root exudates released during active seagrass growth can cause dissolution of the carbonate sediments (Madden et al. 2001), which in turn releases the solid-phase phosphate back into the porewater where it can be utilized by seagrasses for growth. N, mostly in the form of ammonium, is generally readily available in sediment pools. The dynamic N state variables will be implemented following full calibration of the P-based model.

Spatial Domain of the Numerical Model

The spatial domain encompasses Florida Bay from the northern transitional bays bordering the southern Everglades to the Gulf of Mexico, vertically including the non-stratified water column (1-3 m) and sediments to a depth of 5-15 cm. The horizontal spatial unit is 1 m^2. Because of the spatial coarseness of empirical data and lack of full understanding of the causes of patchiness in seagrass beds, only a moderate amount of spatial information is captured in each of the six basin models in the northeast and central bay (Figure 3). There is a basin and bank version of each unit model, which imparts some degree of spatial heterogeneity to each. Much of the biomass data available is generally obtained in viable seagrass beds, meaning that many datasets are biased toward the higher biomass areas of each basin. Due to the inadequacy of field data alone in defining cause-effect relationships in seagrass growth, the field data are supplemented with mesocosm studies of processes that can be manipulated to produce specific physiological and demographic patterns in seagrass populations (Koch and Durako 2005).

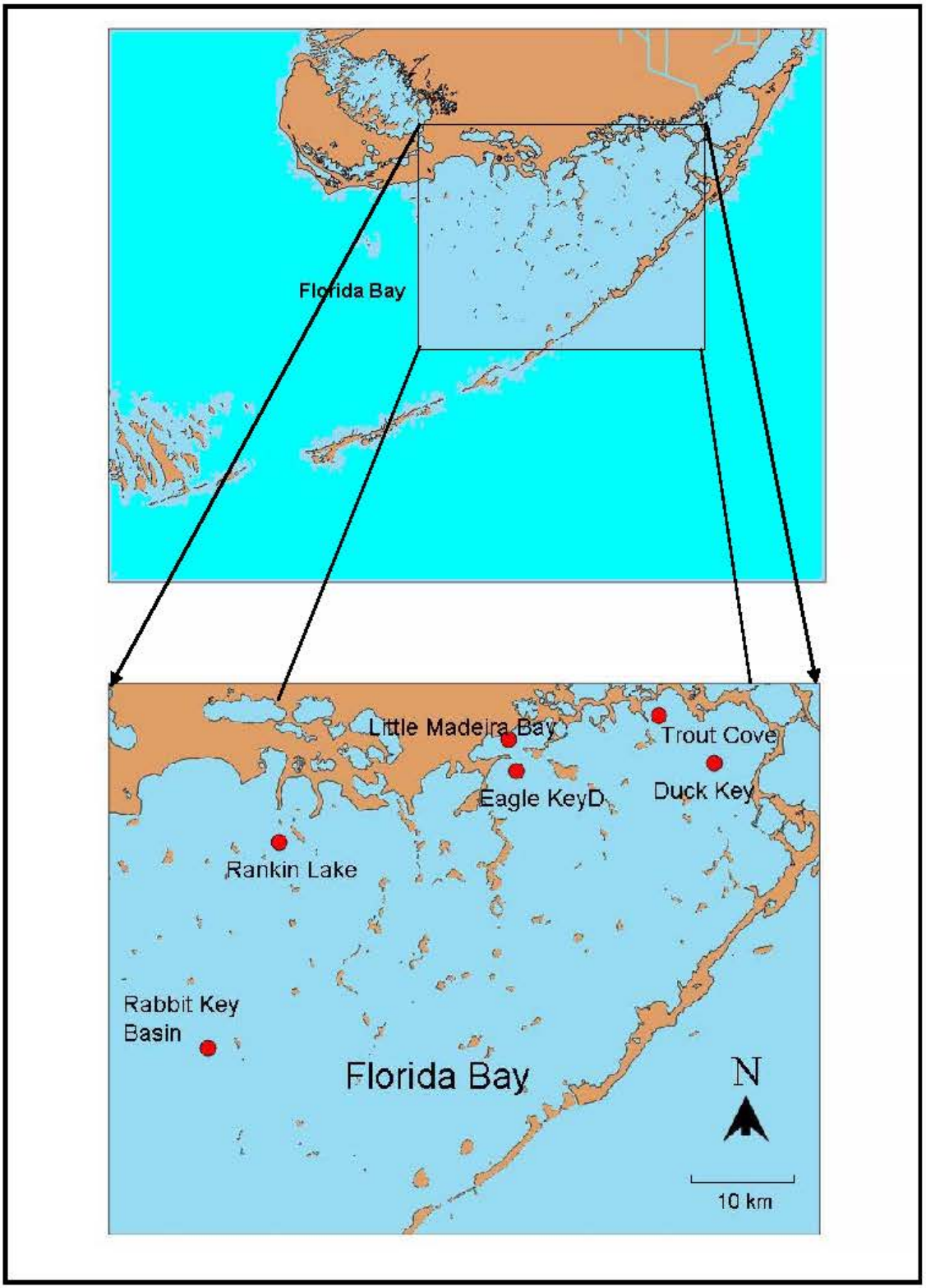


Figure 3. Detailed site locations of unit model basins in Florida Bay.

The unit model approach yields a spatially averaged output, and the models are calibrated and parameterized with distinctive physical, ecological and geomorphological conditions of water quality parameters, water depth, sediment depth and seagrass initial conditions. Combined, all of the unit models offer a means of examining large-scale spatial heterogeneity of seagrass distribution in Florida Bay. Nonetheless, the model is also valuable in that it can simulate variations in conditions each the specific basins of the bay, based solely on ambient nutrient concentrations and salinity levels. Each unit model explicitly incorporates bank and basin morphology and hypsometric characterization via water and sediment depth parameters. External forcings vary among different basins, including nutrient levels in water and sediments, organic material inputs, water depth, sediment depth, basin exchange rates, water turnover time, PAR, turbidity and salinity.

Temporal Domain of the Numerical Model

The temporal domain of the model covers the recent ecological history of Florida Bay for which there are environmental and seagrass data available, about 1960 to the present (Phillips 1960; Tabb and Manning 1961). Standard simulation length is one year, and simulations of two-, five-, ten- and 30-year periods are typically run. The choice of a model timestep of dt=3 hours is based on expert knowledge of the biological and physico-chemical processes important in determining seagrass function and growth patterns. The dt selected represents the timescale of the most rapidly varying processes that materially impact functioning of the seagrass community. The timestep interval represents a compromise between the computational requirements for accurately reproducing the patterns in nature and both the timescale of the available data and computer processing time. The upper limit for the timestep was determined by successively reducing the dt until the model converged on a constant solution.

The model indicates that sediment nutrient pools are drawn down to very low levels during daily productivity processes, below nutrient half-saturation locally around the roots of the seagrass. This emergent property is relevant to P self-limitation in the *Thalassia* state variable itself and is likely for *Halodule* as well. Therefore, a small dt is required to capture biogeochemical interactions operating in such small tolerances. A large dt would generate large productivity rates per timestep and cause the model to “overshoot” available nutrients leading to a negative solution. Other important processes that operate on subdaily timescales are sediment redox

potential (not yet implemented), sediment oxygen concentration (partially implemented), and variations in light regime (implemented). Processes that act on longer timescales that affect seagrass processes include salinity distribution (days to weeks), mean temperature (weeks to months), epiphyte cover (days to weeks), and sulfide production (days to weeks).

Model Specifications

The model is comprised of a system of simultaneous ordinary differential (finite-difference) equations, solved using a second-order Runga-Kutta numerical integration scheme at a dt of 3 hr. Rate equations were derived using information from several sources, including existing models (Madden and Kemp 1996, Cerco 2002), literature values, and empirical relationships derived from field and mesocosm research for this study (Erskine and Koch 1999, Gras et al. 2003, Koch and Durako 2005). The base model describes a non-stratified water column, nominally 1m deep, overlaying a benthic system with which it interacts through sedimentation, diffusive flux, and nutrient translocation. The model tracks biomass in units of organic carbon: seagrass, epiphyte, and detritus stocks are accounted in mg C m^{-2}. Nitrogen and phosphorus are accounted in the model by stoichiometric relationship to carbon. The atom ratio of 280:16:1 for C:N:P (Fourqurean et al. 1992) is fixed for plant tissue and used to index nutrient uptake to carbon flow. N and P in biota and in the nutrient pools are reported on a mg m^{-2} basis.

The base model configuration simulates annual patterns for *Thalassia* and *Halodule*, and will be expanded to include state variables for benthic algae, phytoplankton and other seagrasses. The model has been developed and optimized to elucidate the dynamics of seagrass community growth and species composition. The number of state variables has been kept to the minimum required to realistically model photosynthesis and productivity dynamics without introducing unnecessary and unconstrained error. For example, there is no grazing term in the model for seagrasses, although some small degree of grazing may occur in nature. Groundwater seepage may be important as a nutrient source, but data are too few to accurately quantify this potential input. Thus, this nutrient input is aggregated in the water column nutrient forcing function data.

The baseline period for the dual-species model has been established as 1996-2000 and the unit model provides the following output parameters: specific photosynthetic rate, specific growth rate of aboveground material, total leaf area, mean canopy height, biomass density, biomass

turnover rate, detritus production, epiphyte load, belowground biomass, dissolved nitrogen and phosphorus utilization rate, dissolved nitrogen and phosphorus concentration, deposition of organic matter, hydrogen sulfide concentration, sulfate reduction rate and decomposition rate.

Model Variables

The unit model includes the following state variables: *Thalassia* aboveground biomass (T_a), *Thalassia* below ground biomass (T_b), *Halodule* above ground biomass (H_a), *Halodule* below ground biomass (H_b), epiphyte biomass (E), sediment organic matter (D), porewater hydrogen sulfide (S), porewater phosphate (P_p), sediment adsorbed phosphate (P_s). Units for each of the state variables are as follows:

Variable	Definition	Units
T_a	Thalassia biomass above ground (TAG)	mg C/m^2
T_b	Thalassia biomass below ground (TBG)	mg C/m^2
H_a	Halodule biomass above ground (HAG)	mg C/m^2
H_b	Halodule biomass below ground (HBG)	mg C/m^2
E	Epiphyte biomass	mg C/m^2
D	Sediment organics	mg C/0.1 m^3
S	Sulfide in the porewater	mM S
P_p	Available phosphorous in the porewater	μM P
P_s	Phosphorous adsorbed to sediment	mg P/ 0.1 m^3
t	Time	days

Forcing Functions and Input Data

Forcing functions are energy or materials inputs from outside the model boundaries, such as light and salinity, whose input rates are not influenced by processes occurring within the model boundaries. Data are gathered from the following primary sources as well as from those described in the section Data Sources. Salinity and temperature (Figures 4 and 5) are from USGS instrument deployments at fixed platforms in the basins indicated. These data are collected every 15 min. and averaged per day in the model input files. Data for inorganic as well as dissolved organic nutrients (N_w, P_w) are from the FIU SERC monthly monitoring program at stations in each indicated basin (Figure 6). Subsurface PAR (photosynthetically active radiation) data (not pictured) are from the USGS-funded monitoring of daily light regime at surface- and bottom-sensor deployments at platforms in each basin.

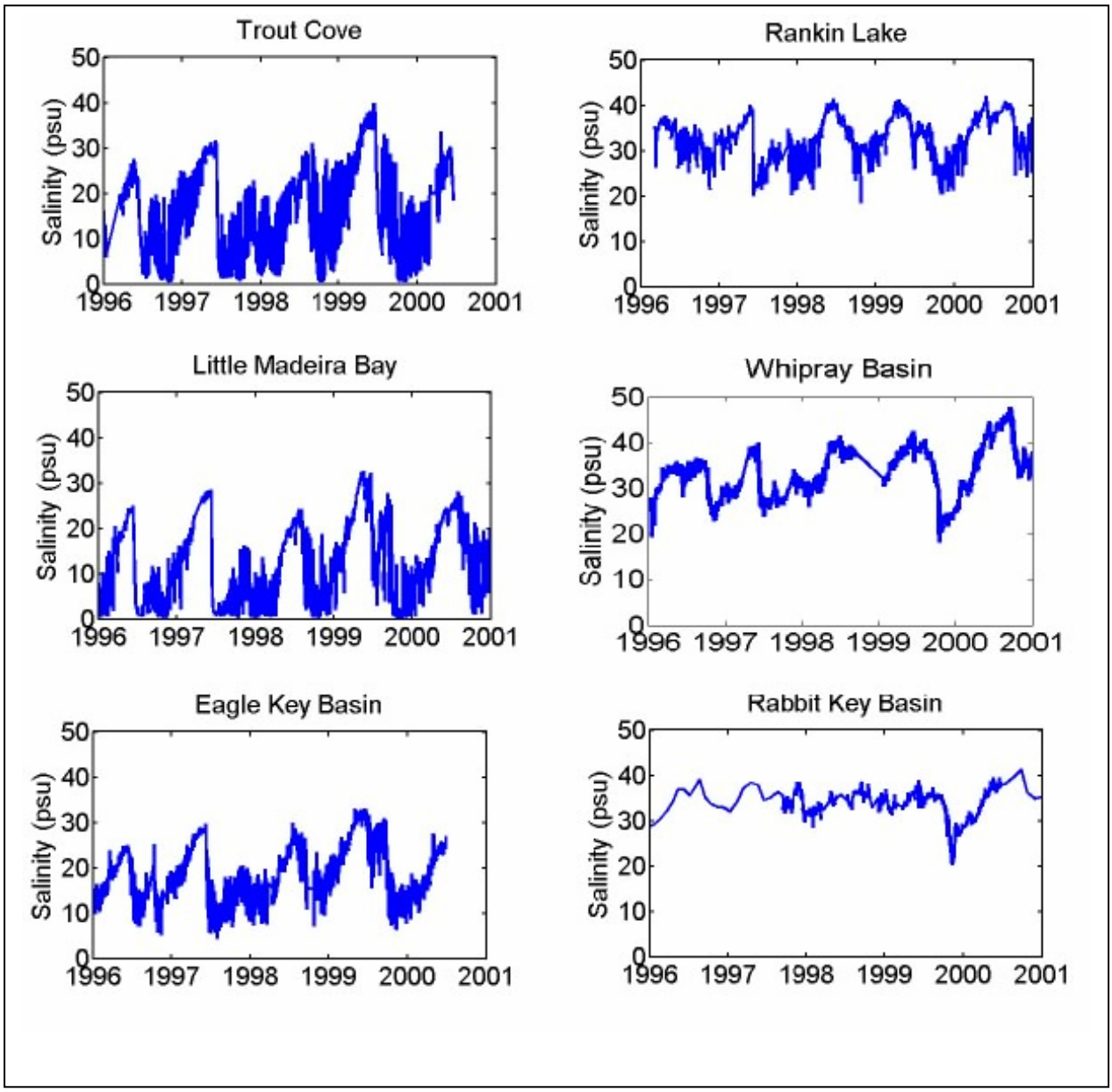


Figure 4. Hourly salinity input data from long-term, platform-based instrument deployments for six unit models (USGS).

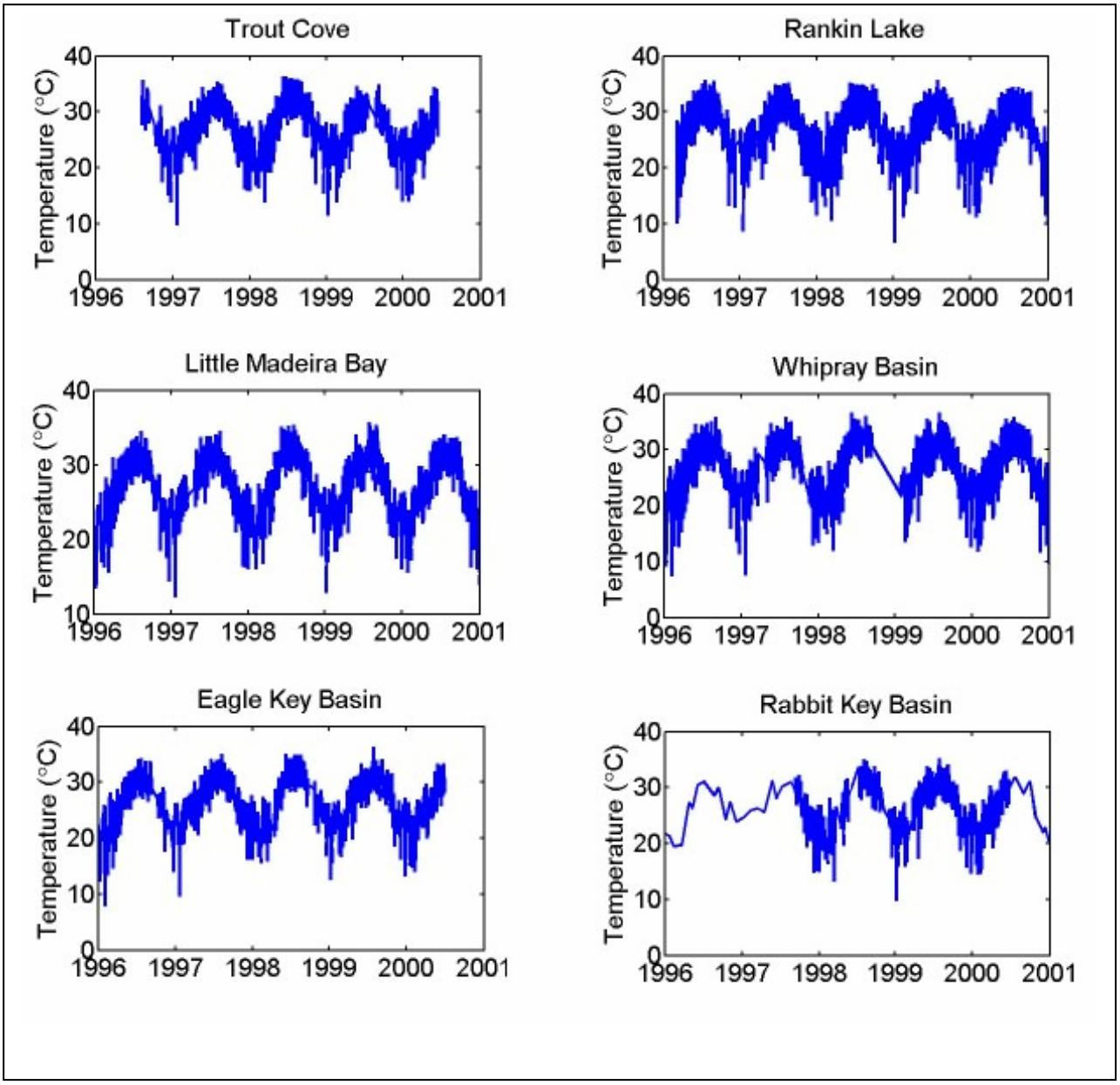


Figure 5. Hourly temperature input data from permanent, platform-deployed instruments for six unit models (USGS).

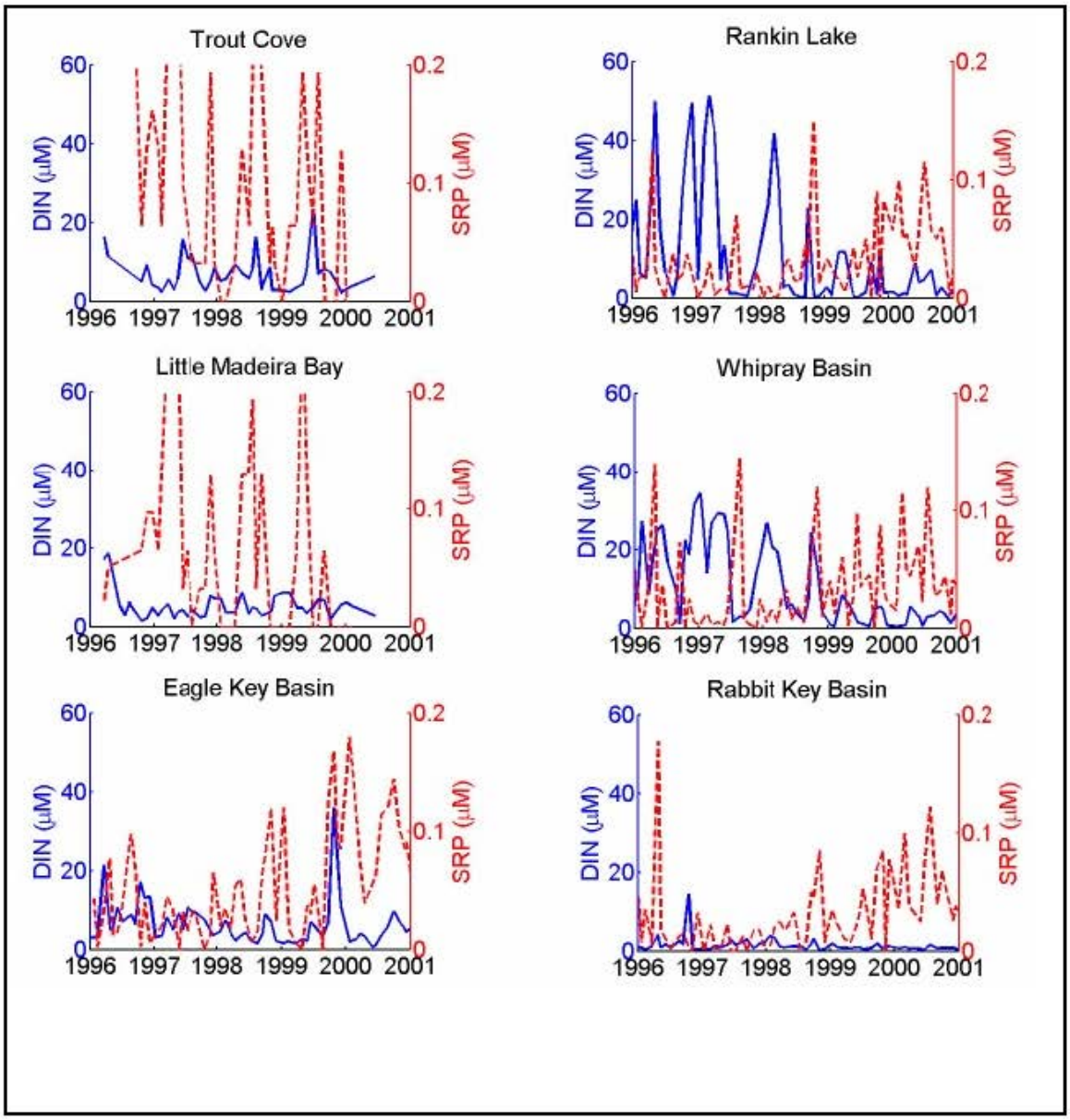


Figure 6. Monthly nutrient (DIN, DIP) input data from ship-based water quality surveys for six unit models (FIU-SERC).

Salinity response curves for both species used in the model show that *Halodule* has a broader range of optimal salinities. The curve for *Halodule* has a plateau because the data used to build the curve showed no significant differences between 10 and 35 psu.

Numerical Model Description

Growth in autotrophic compartments is controlled by maximum photosynthetic rates for both seagrass species and epiphytes. Maximum potential growth is modified by dimensionless terms called primary growth factors characterizing light sufficiency, nutrient sufficiency, salinity, sulfide concentration and temperature relative to optimal or saturating requirements. The relationships between these growth factors and photosynthesis are described by mathematical functions of the forms depicted in Figure 7. Secondary factors that act to influence the level of the primary growth factors include turbidity from phytoplankton, epiphytes and suspended particulates which all reduce PAR at the seagrass leaf surface, and nutrients in the water column and from recycled nutrients that support seagrass and phytoplankton growth. Inorganic nutrient concentrations regulate photosynthesis in accordance with Michaelis-Menten kinetics. Biomass change in the autotrophic components of the model is calculated through environmental inputs and species-specific response curves created to fit experimental data. The effects of environmental influences on photosynthesis are multiplicative, and they attenuate the maximum growth rate of 0.7 d^{-1} for epiphytes, 0.3 d^{-1} for *Thalassia* and 0.3 d^{-1} for *Halodule*. Total biomass change for each state variable for each time step is calculated as the sum of gain and loss terms to yield a new biomass at time t+1.

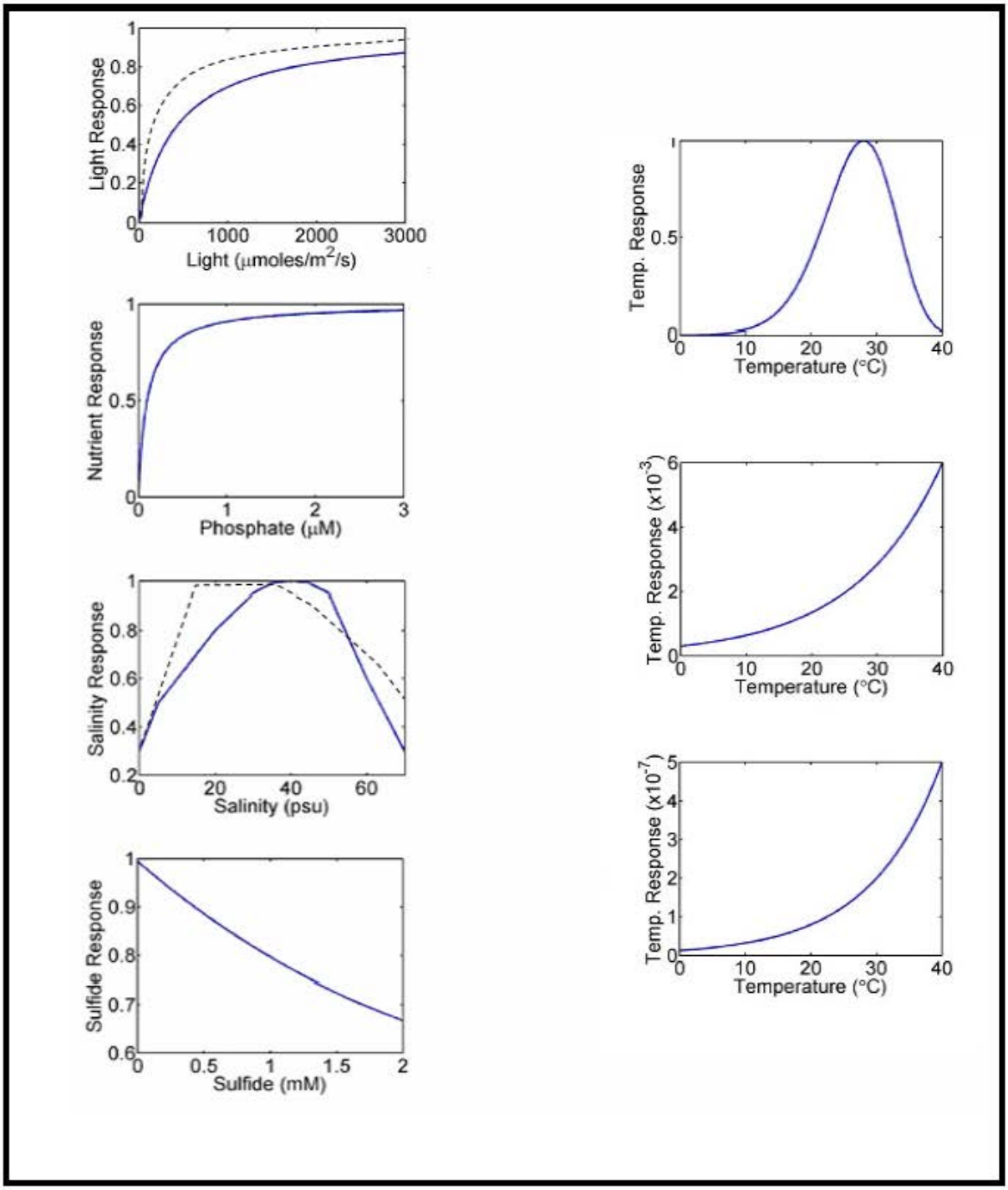


Figure 7. Graphical depictions of seagrass response functions to environmental factors. In the left column are four functions that affect the rate of photosynthesis (Ps): light, phosphorus concentration, salinity and sulfide concentration. Where two lines are shown, dashed line is for *Halodule*, solid for *Thalassia*. *Halodule* is not affected by H_2S in the model. In the right column, top shows the temperature optimum function effect on Ps, and temperature functions for carbon losses due to respiration rate and mortality rate. All Ps response functions are relative to the maximum Ps rate. Loss functions are specific rates in units of mg per mg carbon.

Seagrass State Variables

The state variable for aboveground *Thalassia* biomass is represented by the differential equation:

$$\frac{dT_a}{dt} = (1-\chi_{Ta})g_T T_a - r_{Ta}T_a - m_{Ta}T_a + \chi_{Tb}T_b \qquad (1)$$

The terms are: increase due to photosynthetic growth, loss from respiration, loss from mortality and increase from carbon translocated from belowground tissue. Mortality includes plant death as well as leaf sloughing but does not include a grazing term. Direct grazing on seagrasses is not widely observed in Florida Bay and is likely a second-order process.

The photosynthetic production equation for *Thalassia* is:

$$g_T = V_T \xi_T \left(\tanh \frac{I_T}{l_T}\right) \eta_T \left(1 - \left(\frac{T_a}{\kappa_T} + \frac{H_a}{\kappa_H}\right)^2\right) R_T \psi_T \qquad (2)$$

Growth of the seagrasses is controlled by light and nutrient availability, water column salinity, porewater sulfide concentration, self-limiting density and water temperature with parameters as detailed in Table 1. Light available for seagrass use is determined by the amount of light reaching the seagrass canopy (data-driven forcing function) as modified by epiphyte density on the surface of seagrass blades. The reduction of light (PAR) at the SAV leaf surface in the model is characterized by the expression from Frankovich and Zieman (2005):

$$I_e e^{-0.11 \frac{E\delta_e}{\phi_T}} \qquad (3)$$

The light-coupled term governing photosynthetic rate uses the hyperbolic tangent function (Jassby-Platt 1976). Nutrient uptake is governed by a Michaelis-Menten function for P and N of the form:

G=KnC/K+C

where G=nutrient-based growth rate, K is the half saturation coefficient for a particular nutrient form, n, and C is the concentration of the nutrient. Uptake is calculated using the minimum of a separate uptake velocity calcuation for each nutrient concentration, N and P, as detailed in Table 1. The model assumes that plants acquire phosphorus from the sediment porewater since water column phosphorus concentrations are generally low (less than 0.1 uM) and epiphytes generally have higher nutrient uptake affinities than seagrass leaves out-competing seagrasses for water column nutrients. This also represents a simplifying assumption to reduce error as the effect of surface epiphytes presents an unknown boundary layer effect on nutrient uptake via seagrass leaves. The effects of sulfide toxicity, temperature and salinity on seagrass production are expressed as response curves whose development is described further in the section entitled Parameterization of the Biological Model.

The density limiting function (Table 1) is described as a simple inverse logarithm with variable species-specific density maxima (L). For *Thalassia*, we employ a critical value of δ_{maxTA}=400 g C m^{-2}, which yields minimal effect on photosynthesis at densities from 0-50 g C m^{-2}, progressing to a 50% reduction in photosynthesis between 50-150, and about a 80% reduction above 200 g C m^{-2}.

Thalassia above ground losses occur in the form of temperature-dependent mortality and respiration, as well as translocation to the below ground compartment. Below ground *Thalassia* material accrues solely from downward translocation (Equation 4). Losses occur from mortality, respiration and the fractions of below ground material from the root/rhizome biomass compartment that is transported upward to support growth of shoots.

$$\frac{dT_b}{dt} = \chi_{Ta} g_T T_a - m_{Tb} T_b - r_{Tb} T_b - \chi_{Tb} T_b \qquad (4)$$

Table 1: *Thalassia testudinum* parameters

Parameter	Definition	Value	Source
χ_{Ta}	Proportion of TAG production transported to TBG	0.4	calibrated
χ_{Tb}	Proportion of TBG that is used for TAG growth	0.0005	calibrated
δ_a	TAG dry weight to carbon ratio	2.94	Rudnick and Kelly (unpub)
δ_u	Phosphorous to carbon ratio for T uptake	0.00134 gP/gC	Rudnick and Kelly (unpub)
m_{Ta}	Intrinsic mortalilty rate of TAG	0.001 /day	calibrated
m_{Tb}	Intrinsic mortalilty rate of TBG	0.0001 /day	calibrated
η_T	Nutrient limitation effect on TAG	$\min(\frac{N_p}{N_p+k_{TN}}, \frac{P_p}{P_p+k_{TP}})$	
r_{Ta}	Respiration rate for TAG	0.01/day	Fourqurean and Zieman (1991)
r_{Tb}	Respiration rate for TBG	0.0025 /day	Fourqurean and Zieman (1991)
κ_T	Saturation density (carrying capacity) for TAG	400,000 $\frac{\text{mg C in } T_a}{\text{m}^2}$	Zieman
k_{TN}	Thalassia N half-saturation constant	0.04 μM	
k_{TP}	Thalassia P half-saturation constant	0.1 μM	
I_T	PAR at T_a layer	$I_e e^{-0.11\frac{E\delta_e}{\phi_T}}$	Frankovich
l_T	Light saturation parameter for Thalassia	407 $\frac{\mu\text{mole}}{sm^2}$	Fourqurean and Zieman (1991)
V_T	Maximum photosynthetic rate for Thalassia	0.208 /day	Fourqurean and Zieman (1991)
W_t	Thalassia dry weight to surface area conversion	1.7 $\frac{\text{mg } T_a \text{ dry weight}}{\text{cm}^2 \text{ of leaf surface}}$	Madden (unpub)
ξ_T	Salinity affect on T production	response curve	Koch (2003); Lirman et al. (2003)
ϕ_T	Thalassia leaf surface area in cm^2	$\frac{2T_a\delta_a}{W_t}$	
R_T	Temperature effect on Thalassia production	$e^{0.07(w_t-28)}$	Arrhenius function
ψ_T	Response of Thalassia Growth to porewater sulfide	response curve	Erskine and Koch (2000)

Above ground and below ground *Halodule* equations (Eqn 5, 6) function exactly as for *Thalassia* but with coefficients as listed in Table 2.

$$\frac{dH_a}{dt} = (1-\chi_{Ha})g_H - r_{Ha}H_a - m_{Ha}H_a + \chi_{Hb}H_b \tag{5}$$

$$\frac{dH_b}{dt} = \chi_{Ha}g_H H_a - m_{Hb}H_b - r_{Hb}H_b - \chi_{Hb}H_b \tag{6}$$

Table 2: *Halodule wrightii* parameters

Parameter	Definition	Value	Source
χ_{Ha}	Proportion of HAG production transported to HBG	0.34	Burd and Dunton (2003)
χ_{Hb}	Proportion of HBG that is used for HAG growth	0.00001	calibrated
δ_{uH}	Phosphorous to carbon ratio for H uptake	0.001211 gP/gC	Fourqurean (LTER)
m_{Ha}	Intrinsic mortalilty rate of HAG	0.004 /day	Burd and Dunton (2003)
m_{Hb}	Intrinsic mortalilty rate of HBG	0.0004 /day	Burd and Dunton (2003)
η_H	Nutrient limitation effect on HAG	$\min(\frac{N_p}{N_p+k_{HN}}, \frac{P_p}{P_p+k_{HP}})$	
r_{Ha}	Respiration rate for HAG	0.029/day	Burd and Dunton (2003)
r_{Hb}	Respiration rate for HBG	0.011 /day	Burd and Dunton (2003)
κ_H	Saturation density (carrying capacity) for HAG	667,000 $\frac{\text{mg C in } H_a}{\text{m}^2}$	Burd and Dunton (2003)
k_{HN}	Halodule N half-saturation constant	0.04 μM	
k_{HP}	Halodule P half-saturation constant	0.1 μM	
I_H	PAR at H_a layer	I_e	
l_H	Light saturation parameter for Halodule	319 $\frac{\mu\text{mole}}{\text{s}m^2}$	Burd and Dunton (2003)
V_H	Maximum photosynthetic rate for Halodule	0.29 /day	Burd and Dunton (2003)
ξ_H	Salinity affect on H production	response curve	Koch (2003); Lirman et al. (2003)
R_H	Temperature effect on Halodule production	$e^{0.07(w_t-31)}$	Arrhenius function

Epiphyte State Variable

Epiphytes colonize SAV leaf surfaces, intercepting light and reducing SAV productivity. They obtain nutrients and light directly from the water column and SAV provides a substrate on which to grow. The epiphyte community is actually a consortium of plant, animal, bacterial and abiotic components. The abiotic parts include sediments, mucous and detritus. Photosynthetic rates of the autotrophic component are characterized similarly as for SAV: a temperature-related potential growth rate defines maximum specific growth rate of 0.7 per day, modified by the product of P-I based and nutrient-based growth rates. A density-dependent function limits

epiphyte growth from self-shading, and with increasing epiphyte density per area of SAV leaf, an exponential decline in growth rate is invoked, using a maximum of δ_{maxE}=20 mg cm^{-2}. Growth is reduced by 50% per 0.5 mg cm^{-1} increase in density, and at 5.0 mg cm^{-1}, growth rate is 30% of the maximum potential rate. If no seagrass is present as a substrate for growth, the density limiting function goes to zero, and production ceases.

Epiphyte biomass is represented by the differential equation:

$$\frac{dE}{dt} = V_e \left(1 - \left(\frac{E\delta_e}{\kappa_e \phi_T}\right)^2\right) \left(\frac{I_e}{I_e + l_e}\right) \eta_e E - m_{Ta} E - r_e E^2 - m_e E^2 \qquad (7)$$

Loss pathways from epiphytes are respiration, grazing and mortality, applying coefficients listed in Table 3. Additionally, a quantum loss of epiphyte material is associated with substrate losses via seagrass leaf sloughing, calculated as the product of leaf death rate and epiphyte density. A constant relates mortality to the square of biomass, simulating natural mortality, stripping by wave action, and sedimentation such that 2-6% of the biomass is removed by this pathway daily.

Table 3: Epiphyte parameters

Parameter	Definition	Value	Source
δ_e	Epiphyte dry weight to carbon ratio	$9\ \frac{\text{mg } E \text{ dry weight}}{\text{mg C in } E}$	Donovan (unpub)
η_e	Nutrient limitation effect on HAG	$\min(\frac{N_p}{N_p+k_{eN}}, \frac{P_p}{P_p+k_{eP}})$	
k_{eN}	Epiphyte N half-saturation constant	2.86 μM	
k_{eP}	Epiphyte P half-saturation constant	0.16 μM	
m_e	2nd order Epiphyte mortality/loss rate	0.00005 /day	
r_e	2nd order Epiphyte respiration rate	0.00001 (mg C)$^{-1}$m^{2}day^{-1}	
l_e	Light half saturation constant for E	$150\ \frac{\mu\text{mole}}{sm^2}$	Biber (2002)
κ_e	Saturation density (carrying capacity) for E	$20\ \frac{\text{mg } E \text{ dry weight}}{\text{cm}^2 \text{ of leaf}}$	Twilley
V_e	Maximum growth rate for epiphytes	0.7 /day	

Mortality losses from seagrass and epiphyte compartments enter the organic matter pool (D) in the sediments. Other sources of organic matter are detritus from benthic algae and of planktonic organisms, fixed as a constant.

$$\frac{dD}{dt} = m_{Ta}E + m_{Ta}T_a + m_{Tb}T_b + m_{Ha}H_a + m_{Hb}H_b + m_B B + m_z Z + \chi_w - \sigma\tau_D D - \chi_D D \quad (8)$$

A proportion of the sediment organic matter is lost through export and burial, while another portion is remineralized to release nutrients into the porewater. The remineralization process releases inorganic nutrients and produces hydrogen sulfide (S) as a byproduct of sulfate reduction, accumulating sulfide in the porewater. Some of the sulfide is oxidized through seagrass oxygen production and exudation from the roots and via natural diffusion of oxygen from overlying water.

$$\frac{dS}{dt} = \left(r_s\delta_s\sigma\tau_D D - K_s S\nu_S\right)/\nu_S \quad (9)$$

Phosphate released during remineralization accumulates in the porewater fraction (P_p) as dissolved inorganic phosphorus DIP and sorbs to the calcium carbonate sediment matrix (P_s) that is a major component in Florida Bay sediments (Table 4). A portion of the sorbed phosphate is incorporated into the sediment matrix, sequestration that effectively makes the P unavailable to plants. Seagrass growth can lower pH in the sediments via acid excretion, causing dissolution of the carbonate sediments (Jensen et al. 1998) and releasing phosphorus from the solid phase into the porewater where it can be utilized by seagrass for growth. Phosphate released during remineralization accumulates in the porewater and adsorbs to the calcium carbonate sediment matrix. A portion of the adsorbed phosphate is incorporated into the sediment matrix allowing more phosphate to adsorb to the sediment surface.

$$\frac{dP_p}{dt} = \left(\sigma\tau_D\delta_p D + (K_d - \delta_{uT})g_T T_a - \delta_{uH}g_H H_a + (P_s K_p - P_p\nu_p)\right)/\nu_p \quad (10)$$

$$\frac{dP_s}{dt} = -\left(P_s K_p - P_p\nu_p\right) - \beta_p P_s \quad (11)$$

Parameterization of the Biological Model

In addition to light and nutrient control of photosynthesis, three mechanisms are critical to plant response: sediment sulfide concentration, salinity and temperature. The effect of sulfide

concentration is to limit *Thalassia* photosynthesis. Erskine and Koch (1999) determined that higher sulfide concentrations had a negative effect on growth. While there was a sharp decline in leaf elongation to approximately 50% of maximum when sulfide concentration increased from 0 uM to 2 uM, there was no further decrease in elongation rate between 2 uM and 6 uM. At 10 uM, there was again a large decrease in elongation rate. A response curve was created to exhibit this relationship in the model. Because *Halodule* belowground biomass is positioned

Table 4: Other parameters

Parameter	Definition	Value	Source
B	Benthic cholorophyll concentration (living biomass)	30 mgC	Rudnick and Kelly (unpub)
β_p	Burial rate of adsorbed phosphorous	0.0003 mg P/day	
χ_D	Sediment organic matter export rate	0.0001 /day	
δ_p	Phosphorous to carbon ratio in sediments	0.002 gP/gC	Chambers (LTER)
δ_s	Sulfide to carbon ratio	2.8 gS/gC	
r_s	Anaerobic portion of sediment respiration	0.1	
K_d	Dissolution rate of phosphorous from Thalassia	$0.0006 \frac{\text{mg } P}{\text{mg C in } T_a}$	
K_s	Sulfide oxidation rate	$0.01 + 0.2 g_T Ta$ /day	
K_p	Equilibrium coefficient for phosphorous adsorption	0.02	
m_B	Mortality of Benthic organisms	0.25 /day	
m_z	Mortality of Plankton organisms	0.325 /day	
χ_w	Organic matter addition to the sediment	100 mg/day	calibrated
σ	Decomposition rate of D	0.006 /day	
τ_D	Temperature effect on decomposition rate	$e^{0.3(\omega_r - 28)}$	Arrhenius function
Z	Planktonic chlorophyll biomass	10 mg C	Boyer
ν_s	concentration to mg conversion for S	32*volume mgS/mM S	
ν_p	concentration to mg conversion for P	0.031*volume mgP/ μM P	

superficially in the sediments, primarily in the oxidized microzone and is less affected by sulfide, there is no sulfide effect on *Halodule* growth conceptualized in the model.

Salinity data were compiled from multiple sources to produce a response curve for *Thalassia* that has optimal growth centered at 40 psu (Koch and Durako 2004; Lirman and Cropper 2003; McMillan and Moseley 1967). Literature suggests that *Thalassia* is more sensitive to higher salinities than lower salinities, which would imply a sharper slope above 40 psu. However, Koch and Durako (2005) showed that *Thalassia* can be more productive in higher salinities if the salinity increase is gradual (0.5 psu d^{-1}), thus producing the flatter response curve in the upper limb, which is used in the model. *Halodule* has a broader optimum and better tolerance for lower salinities Lirman and Cropper (2003), yielding a flattened curve centered at 25 psu, with optimum salinity range extending from 15-35 psu. While McMillan and Mosely (1967) found that *Halodule* was more resilient at high salinities, Lirman and Cropper (2003) showed a decline that began at around 40 psu, and evidence from multiple Florida Bay researchers suggest that *Thalassia* is more resilient than *Halodule* at high salinities.

Temperature influences several processes in the model, including photosynthesis, mortality and respiration of seagrasses as well as decomposition rate of sediment organic matter through the metabolism of microorganisms. Arrhenius functions were used to model the temperature effects with an Arrhenius parameter of 0.07. The reference temperature was set to the temperature condition under which the rates were measured (ranged from 25ºC to 28ºC).

Basin and Bank Model Versions

For the standard model formulation developed for the deeper parts of each of the targeted basins of Florida Bay, selected parameters are adjusted to yield a “bank” version for each unit model. Banks are found throughout Florida Bay and are shoal areas that tend to have thicker sediment layers over bedrock, shallower water columns, higher water temperatures, increased light, and often higher salinity relative to the adjacent deeper waters of the basin. These conditions can result in a more lush seagrass biomass (Zieman 1982). For the bank versions of the unit models, we are incorporating an active root zone that is on average 2.5 times deeper than the basin version, yielding a larger nutrient pool from which roots can draw, higher % organic matter in the sediments, 50% more light reaching the epiphyte surface and seagrass canopy, increased

variance of salinity around a 30% higher mean salinity value and increased variance of temperature around a 20% higher mean temperature value. Development of these bank versions is in progress, but preliminary model runs indicate that stable, viable seagrass populations result, with greater average biomass. The biomass increase is due largely to the deeper sediment depth, providing access to larger phosphorus porewater volume and higher mean light and temperature regimes (Figure 8).

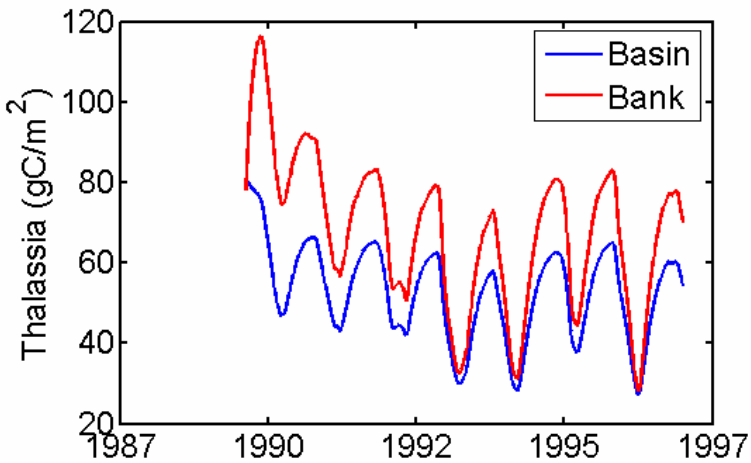


Figure 8. Bank and basin proof-of-concept model run for Rabbit Key Basin *Thalassia* population.

Interspecific Competition

The two target seagrass species in the current version of the model, *Thalassia* and *Halodule*, can be found coincident in space at the spatial resolution (1 m^2) represented by the model. The model reproduces the competitive interaction of these species for nutrients, light and space within the same parameter space. Allelopathy is not considered, as no evidence of this process is noted in the literature. Both modeled species draw from the same pool of sediment nutrients for growth and are thus competing for the same resources. Both have the same nutrient kinetics parameters, meaning that nutrient affinities are identical. However, due to the architecture of *Thalassia*, with greater belowground biomass and occupation of a deeper zone in the sediment compartment, there is a larger volume of nutrient porewater available to this species. Each species can compete for nutrients equally on a local concentration basis, but *Thalassia* occupies a larger physical space. Secondarily, *Halodule* is more tolerant of lower and mid salinities,

while *Thalassia* is slightly more tolerant of high salinities. Therefore when hypersaline conditions persist, *Thalassia* is favored.

In terms of density, *Halodule* presents a lower and smaller profile and, thereby, reduced shading influence on *Thalassia* per unit biomass than *Thalassia* on *Halodule*. Furthermore, *Halodule* is more efficient at photosynthesizing at lower light intensities due to its lower saturation onset parameter (Ik). Thus, *Halodule* can tolerate the presence of shading and crowding by *Thalassia* to some degree, but the massive profile of *Thalassia* can and does present a competitive challenge for *Halodule* at some "tipping" point beyond which a positive feedback loop is generated, maintaining *Thalassia* in a dominant configuration.

Calibration of the Seagrass Community Model

Calibration of the single-species model

Initially, we developed the *Thalassia* single-species model, including all state variables described above, excluding *Halodule*. Calibration for each basin unit model was achieved through least-squares optimization of the summed squared error for *Thalassia* aboveground biomass. The free parameters allowed to vary during the optimization routines were:

- Rate of translocation of carbon between above and below biomass portions
- Mortality rate for aboveground *Thalassia* biomass
- Mortality rate for belowground *Thalassia* biomass
- Import rate of organic matter

The calibration period was selected to cover a period of record where data for all variables were available, which for sites in northeast Florida Bay (Duck Key, Trout Cove, Little Madeira Bay and Eagle Key Basin) was from 1989 to 1995. Figure 9 shows the calibrated *Thalassia* output for Rankin Lake and Rabbit Key Basin. The general decline of *Thalassia* in the Rabbit Key Basin data after 1992 was not captured by the model initially, and the model required an adjustment of the chlorophyll data to reflect the initiation of blooms in that year. A validation exercise was performed using the calibrated models extended until 2000 (Figure 10), and model output tracked the empirical data reasonably well.

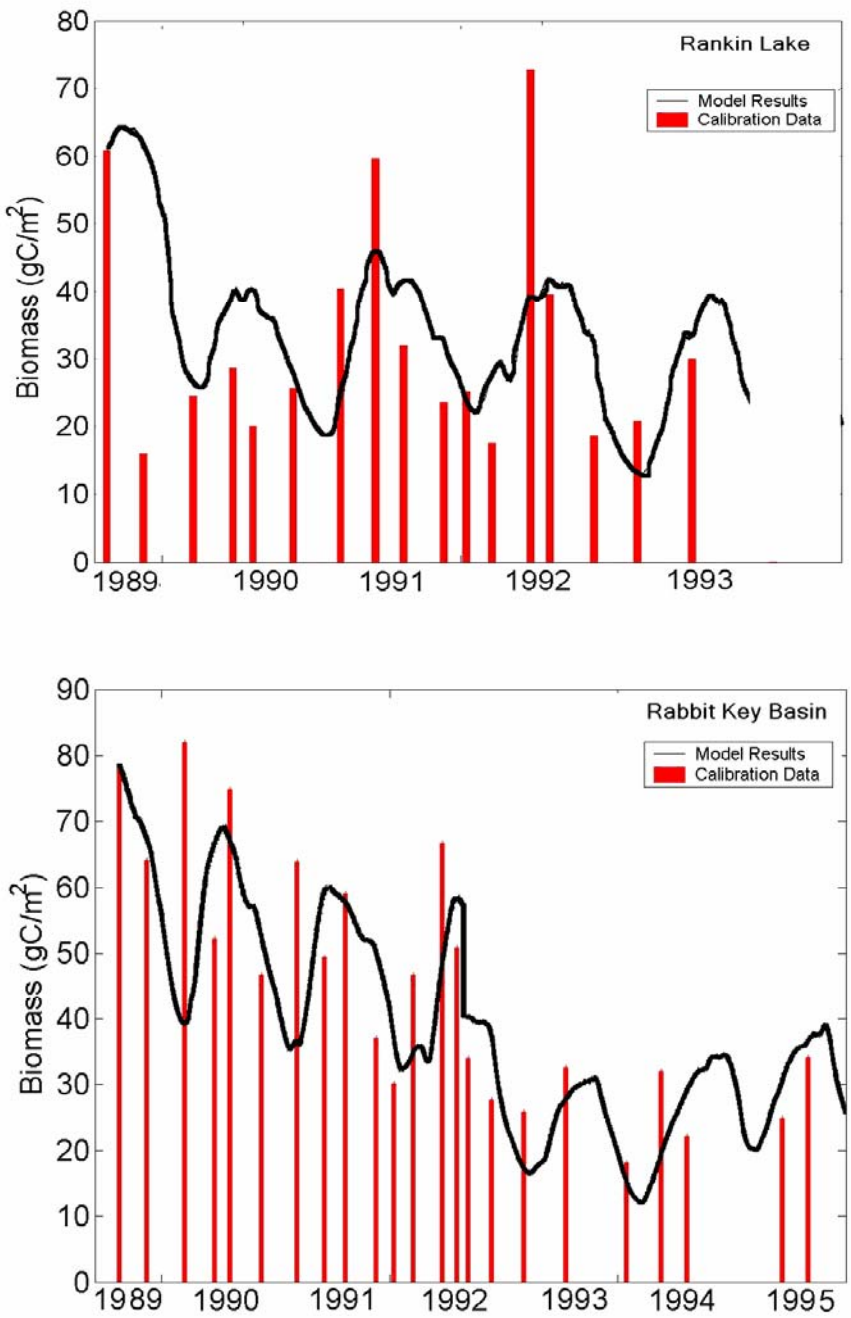


Figure 9. Calibration of single-species *Thalassia* model for Rankin Lake and Rabbit Key Basin. Red columns represent field biomass data.

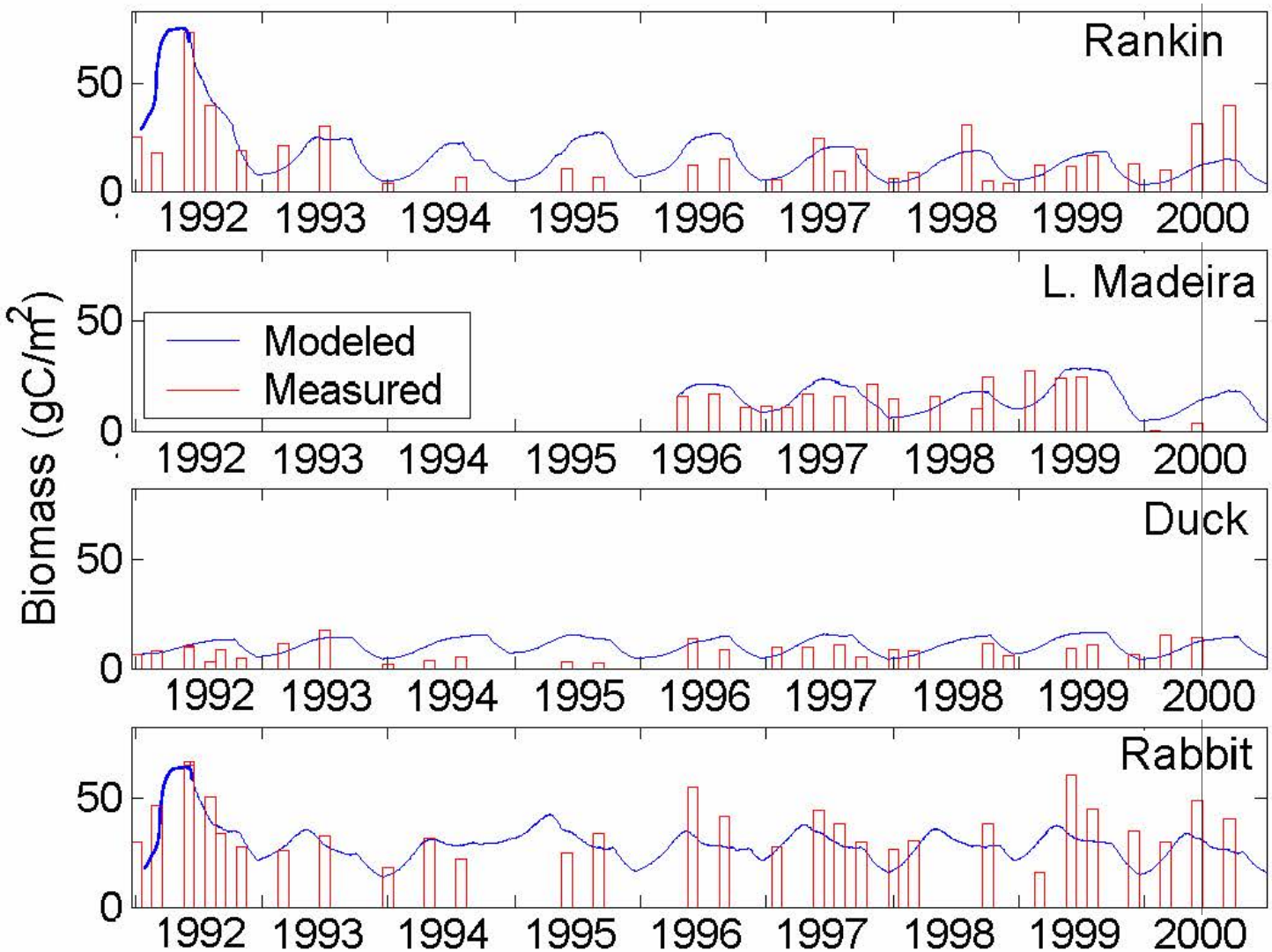


Figure 9. Validation model runs for four basins for single-species *Thalassia* model.

Calibration of the dual-species model

A dual-species version of the Florida Bay seagrass model was calibrated for four northeastern basins using biomass data collected by Miami-Dade Department of Environmental Resources Management (Miami-Dade DERM) from fall 1996 to spring 2000 (M-D DERM 2004). Calibration runs were done for *Halodule* and *Thalassia* in Little Madeira Bay, Eagle Key Basin, Whipray Basin and Trout Cove against empirical data from those sites between 1997 and 2000 or 2001 (Figure 11). Calibration for each basin unit model was achieved through least-squares optimization of the summed squared error for both *Thalassia* and *Halodule*. Model output (solid lines) for *Halodule* is total plant biomass and for *Thalassia* is aboveground biomass, in g C m^{-2}.

Thalassia biomass data were compartmentalized into three components: leaf, shoot/sheath and root/rhizome. The shoot/sheath and root/rhizome data were aggregated as belowground biomass. For *Thalassia* only the above ground biomass was assessed in the calibration routine. Because belowground biomass is collected to a depth of 30 cm (which is outside of the active layer in the model), it is not possible to calibrate the model for belowground biomass without a depth distribution for biomass. However, the overall visible trend was noted (decrease, increase or stable).

Halodule biomass is not apportioned at collection so the *Halodule* state variable is calibrated as total (aboveground plus belowground) biomass. This could introduce errors, as belowground biomass for *Halodule* was also sampled to 30 cm, which is deeper than the active zone in the model. However, in model development, we assume that *Halodule* does not reside in deep sediments, and that this error is likely to be minimal. Parameters assigned from literature values or calculated from empirical data were not allowed to vary.

Because *Halodule* is a small-biomass component occupying a distinct niche, competition with *Thalassia* for resources, particularly light, may be considered to be minor, and indeed, *Thalassia* parameters changed little with the introduction of the *Halodule* state variable. However, *Thalassia* has a strong influence on *Halodule* in a mixed community and a competitive advantage under stable, undisturbed situations.

The free parameters allowed to vary during the optimization routines were:

- Rate of translocation of carbon between above and below biomass portions
- Mortality rate for aboveground *Thalassia* biomass
- Mortality rate for belowground *Thalassia* biomass
- Mortality rate for total *Halodule* biomass
- Import rate of organic matter

The calibration output in Figure 11 shows that the model intersects the data at a number of points for both species. Although the model undergoes seasonal oscillations, the actual data are not sufficiently temporally resolved to show seasonal patterns. In general, the level of biomass is appropriate for each species, and the biomass level predicted by the model conforms ordinally to the biomass abundance at each calibration site. Only where there is a highly variable "unexpected" change in the biomass data did the model fail to capture the pattern, probably indicating a process that is not anticipated in the model. This might be most prevalent at highly variable sites such as Little Madeira Bay, near the Taylor River discharge. Nonetheless, the model shows stability and the ability to track some long term trends (e.g. *Halodule* in Trout Cove). The error analysis in Table 5 reflects that the model tracks data reasonably well, and the coefficient of determination for the regression analysis in Figure 12 indicates a relatively high predictive ability.

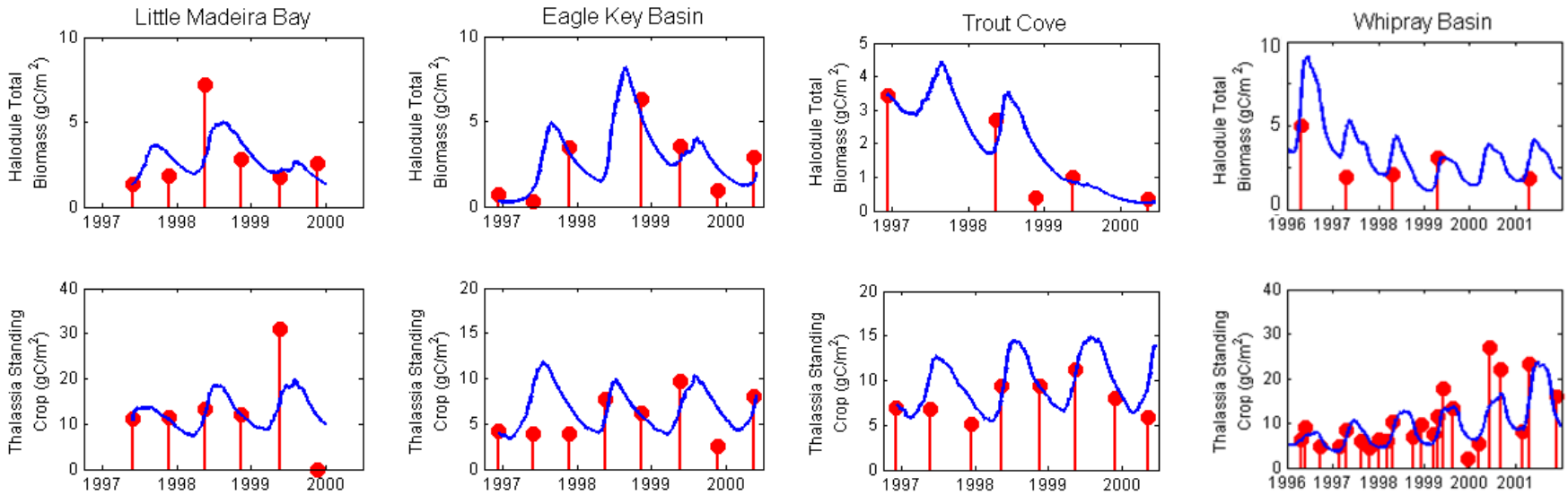


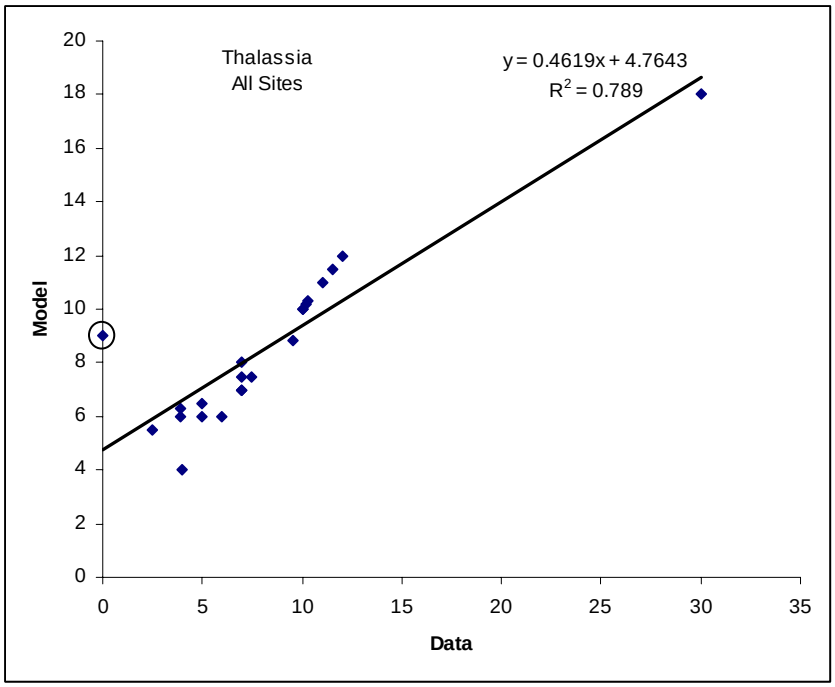
Figure 11. Calibration runs for *Halodule* (top) and *Thalassia* (bottom) species in the SAV model for the inner Little Madeira Bay, Eagle Key Basin, Trout Cove and Whipray Basin. Model output (solid lines) for *Halodule* is total plant biomass, and output for *Thalassia* is aboveground biomass, both in g C m^{-2}. Note scale differences for locations. Solid circles represent data from field measurements.

Error Analysis

Model uncertainty was examined using Root Mean Squared Error (RMSE) calculation for multi-year runs during the calibration period. RMSE values for *Halodule* were 1.9 g C m^{-2} in Little Madeira Bay, 1.0 in Eagle Key Basin and 0.8 in Trout Cove. RMSE values for *Thalassia* biomass were 7.9 g C m^{-2} in Little Madeira Bay, 3.1 g C m^{-2} in Eagle Key Basin and 2.7 in Trout Cove. The r^2 values are low in some cases due to the sparseness of biomass calibration data taken for both species concurrently. The *Thalassia* r^2 value is reduced due to the inability to capture the extremes that occurred in 1999. The model is used as a predictive tool, but we are careful in interpreting results due to the uncertainties in both the model and the data that are used in calibration. We have confidence that the model faithfully represents the major processes and interactions in the seagrass community, though components are still in the process of being refined.

Table 5. Calibration statistics for the three northeastern Florida Bay transition zone sites. SSE = summed squared error; RMSE = root mean squared error; r^2 = coefficient of determination. n=18 for *Halodule* and n=22 for *Thalassia*; *= linear regression recalculated excluding one extreme outlier (circled in Figure 12) in the empirical data for each species.

Statistic	Little Madeira Bay	Eagle Key Basin	Trout Cove	ALL	ALL*
Halodule wrightii					
SSE	17.8	6.1	2.7		
RMSE	1.9	1.0	0.8		
r^2	0.50	0.87	0.75	0.68	0.83
Thalassia testudinum					
SSE	311.3	68.6	38.1		
RMSE	7.9	3.1	2.3		
r^2	0.93	0.70	0.97	0.79	0.90



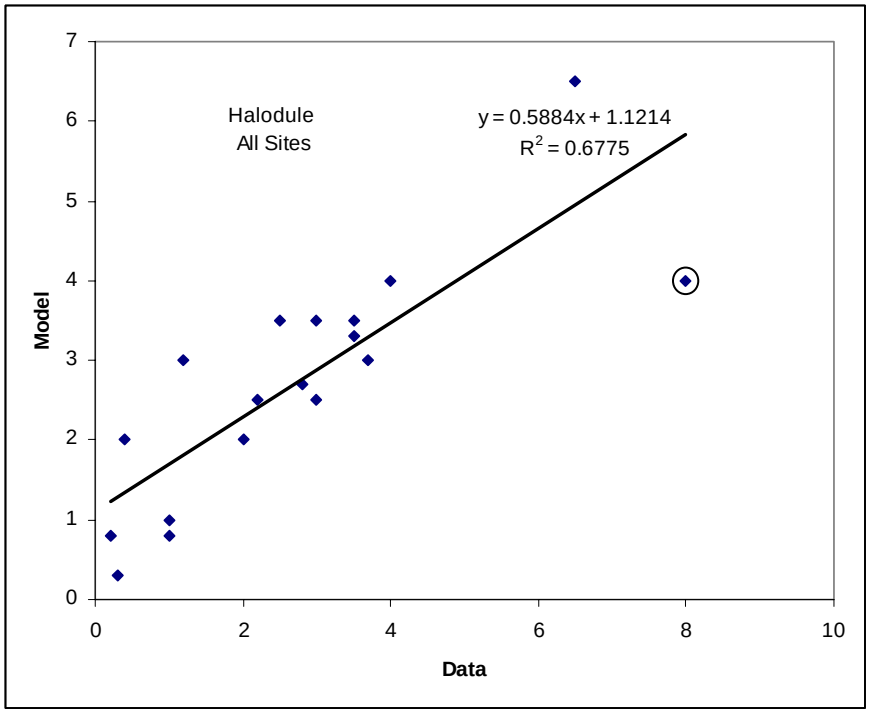


Figure 12. Regression of dual-species model output versus data for all sites.

Sensitivity Analysis

The sensitivity of the model was assessed by varying selected parameters and measuring changes in model output of biomass for both species (Tables 6 and 7). Sensitivity of response variables *Thalassia* and *Halodule* aboveground biomass were measured for the calibration period May 1997 – February 2000. The protocol for sensitivity testing of the two species running in dual-species mode involved systematic adjustment of all 56 model parameters individually by 10% and 5% in both positive and negative directions. The resulting change in the model output was compared to the baseline calibration value. The average absolute deviation from baseline was divided by the average baseline value to determine relative per cent deviation. This value was then normalized to the percent change in the input parameter (-10%, -5%, +5%, +10%), giving as a result the per cent change in output per change in input. A values that is greater than 100% (in red) indicates an amplification response, and a value in black represents a damping of the input perturbation. Parameters that produced a change less than half of the input parameter change are not presented.

The model proved to be robust and resistant to changes in most parameters, as is often the case in complex models with a large number of variables. Only eight of the 56 parameters met the threshold for significance for *Thalassia* and 16 met the threshold for *Halodule*. Changes in *Thalassia* were generally less than the input perturbation. *Thalassia* was most sensitive to the rate of translocation from the belowground to aboveground compartment and to respiration. Interestingly, increases in epiphyte growth evoked a positive response in *Thalassia*, possibly as a mechanism for increasing organic matter and nutrient input to the sediments via mortality and decay.

Halodule was far more sensitive to input perturbations, attributable to the relatively low biomass of *Halodule* and to the higher growth, respiration and mortality rates. *Halodule* was most sensitive to respiration, organic accumulation in the sediments and a number of *Thalassia* parameters. This latter effect demonstrates the importance of *Thalassia* processes in the ecosystem and the inherently dominant role of *Thalassia* in limiting *Halodule* productivity when both are present.

Table 6. Sensitivity of *Thalassia* biomass to variation in parameter values.

% CHANGE

Parameter	**-10%**	**-5%**	**+5%**	**+10%**
Epi mx Ps V_e	-69%	-70%	+73%	+75%
Thal transloc χ_{Tb}	+112%	+113%	-116%	-118%
Thal mx PsV_T	-101%	-92%	+75%	+67%
Hal resp r_{Ha}	-50%	-54%	+49%	+46%
Hal mx Ps V_H	+60%	+67%	-77%	-80%
Sed P:C δ_p	-91%	-91%	+92%	+92%
Thal P stoich δ_{uT}	+86%	+81%	-75%	-72%
Thal resp r_{Ta}	+151%	+150%	-145%	-142%

Table 7. Sensitivity of *Halodule* biomass to variation in parameter values.

% CHANGE

Parameter	**-10%**	**-5%**	**+5%**	**+10%**
Epi P sat k_{eP}	+75%	+72%	-65%	-61%
Epi mx Ps V_e	-103%	-106%	+110%	+112%
Thal transloc χ_{Tb}	-248%	-264%	+298%	+315%
Thal P sat k_{TP}	-240%	-244%	+250%	+250%
Light l_T	-169%	-172%	+177%	+179%
Thal Ps V_T	+575%	+536%	-450%	-406%
Hal transloc χ_{Hb}	+295%	+291%	-276%	-266%
Hal mortality m_H	+57%	+55%	-52%	-51%
Hal P sat k_{HP}	+295%	+280%	-251%	-237%
Hal light l_H	+163%	+159%	-151%	-147%
Hal resp r_{Ha}	+517%	+496%	-443%	-410%
Hal mx Ps V_H	-471%	-501%	+555%	+566%

Sed org accum χ_w	-585%	-584%	+581%	+580%
Sed P:C δ_p	-139%	-139%	+138%	+138%
Thal P stoich δ_{uT}	+117%	+112%	-103%	-99%
Thal resp r_{Ta}	-307%	-326%	+358%	+371%

Sensitivity to salinity averaging

Because salinity is the primary forcing function used to determine many management alternatives, we also focused an analysis on the sensitivity of the model to changes in the resolution of the salinity data used in the forcing function. This will be useful in determining how the SAV components will interact with the water quality model in the fully integrated hydrodynamic framework of the EFDC model. The baseline calibration of the SAV model interpolates instantaneous salinity from salinity data measured at 15-minute intervals. We developed alternative salinity formulations by exploring five averaging schemes: daily, 7-day moving average, 14-day moving average, 30-day moving average and a monthly average (Figure 13). Sensitivity runs were compared to baseline averages for *Thalassia* and *Halodule* biomass (Figure 14) and absolute deviations from the average were quantified as both summed squared error and root mean squared error.

All of the alternatives degraded model performance for *Thalassia* based on SSE and RMSE (Table 8) by increasing *Thalassia* productivity above the base case. Monthly running averaging reduced variability by about 14% (salinity standard deviation) and allows modeled plants to grow at more constant salinity, which particularly favors *Thalassia* at the expense of *Halodule*. Monthly averaging actually slightly improved the fit for *Halodule* by a very small margin compared to 15-minute empirical data, although other smoothing schemes reduced both model fit and *Halodule* production. Lengthening the averaging period has two effects on the salinity input data: it increases salinity, and it diminishes variability, notably the frequency of extreme salinity spikes. Both of these factors increase *Thalassia* growth, accounting for an enhancement of biomass relative to the base case. Smoothing has a net effect of slightly raising the average, minimum and maximum salinity. By smoothing the data, salinity values are centered more within the optimal salinity envelope for *Thalassia*. The 30-day moving average resulted in a maximum daily increase in *Thalassia* of 1.5 g, or 12.4 % of the mean *Thalassia* baseline biomass

of 12.4 g and reducing *Halodule* by 0.27 g, which is 27 % of the mean baseline biomass of 0.99 g. Long-term, 30-day smoothing elevated the *Thalassia* standing crop by about 80 mg C yr^{-1} and reduced *Halodule* by 25 mg C y^{-1}.

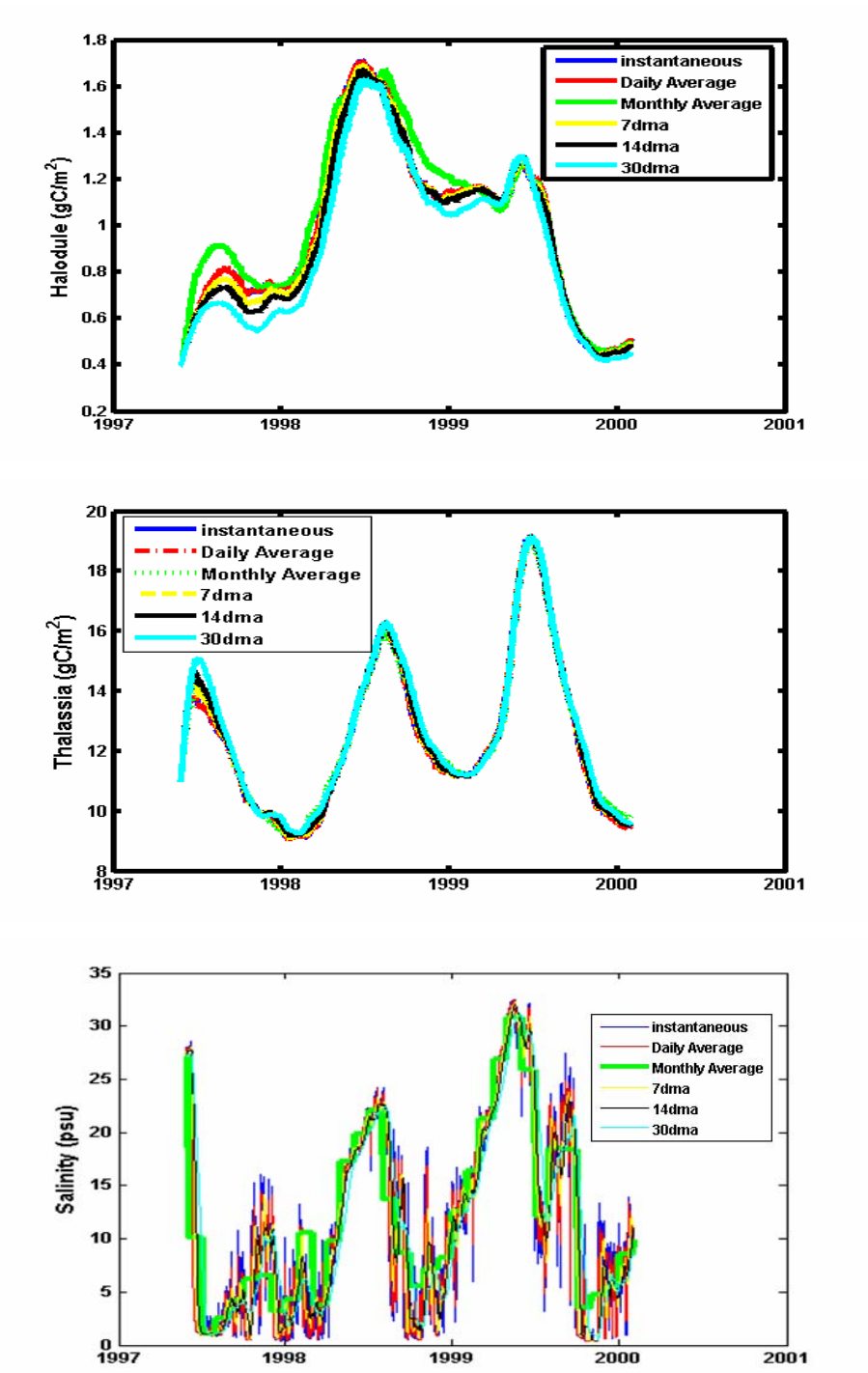


Figure 13. Salinity smoothing analysis and influence on seagrass biomass calculations.

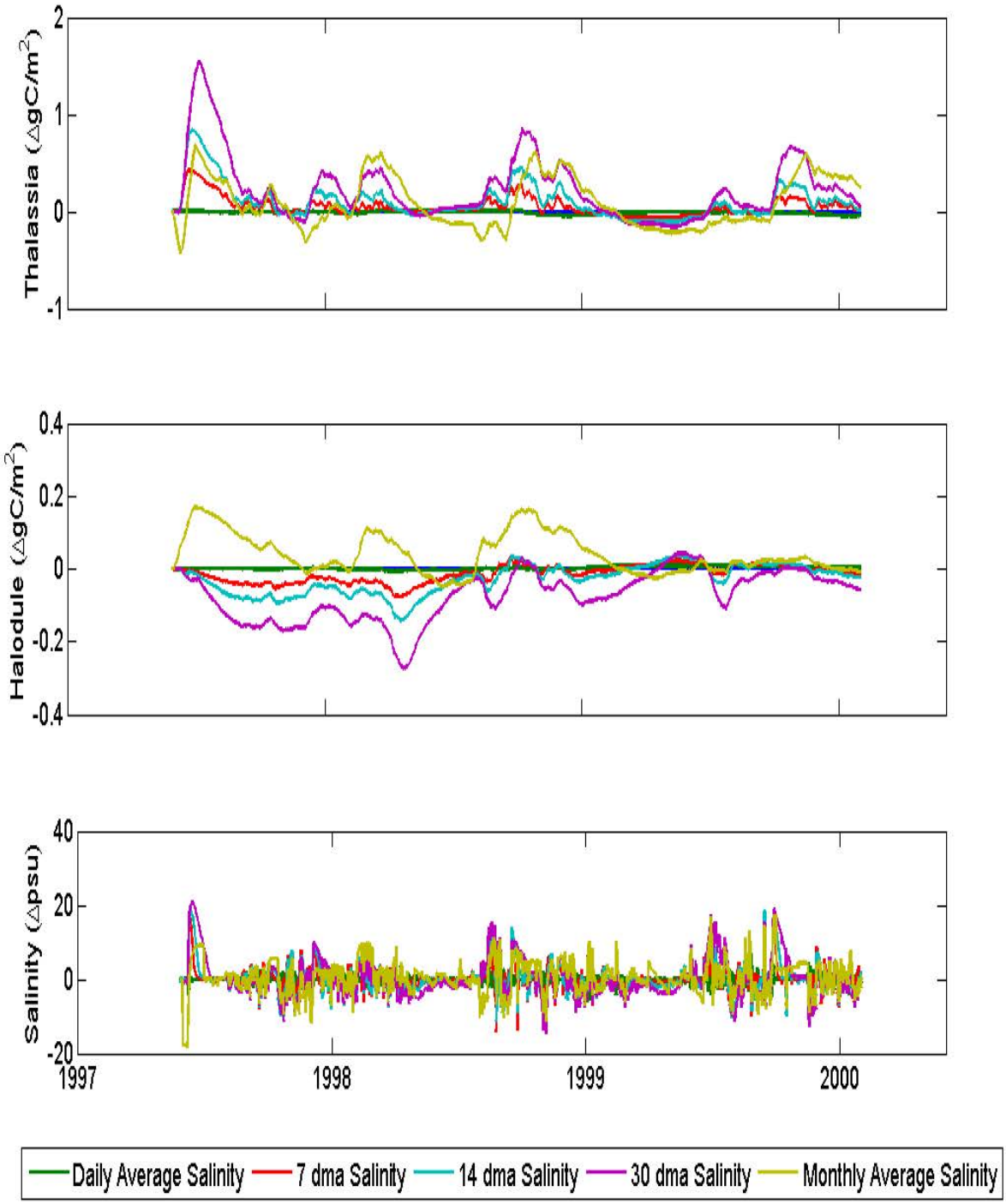


Figure 14. Deviations of SAV biomass and salinity from the baseline calibration values caused by differential smoothing of the salinity input function.

Table 8. Model fit to data with the smoothed salinity inputs. All numbers are reported in gC m^{-2}. DMA = day moving average, SSE = summed squared error, RMSE = root mean squared error.

Smoothing Applied	Thalassia SSE	Thalassia RMSE	Halodule SSE	Halodule RMSE
Instantaneous	311	7.89	17.8	1.89
Daily Average	311	7.89	17.9	1.89
7 DMA	313	7.91	18.9	1.94
14 DMA	316	7.94	19.7	1.99
30 DMA	323	8.04	21.8	2.09
Monthly Average	328	8.10	17.7	1.88

Table 9. Net effects of different smoothing in the salinity input function. Values are the integrated difference from the calibration baseline using instantaneous data across the entire calibration period.

Smoothing Applied	Thalassia (mg C m^{-2})	Halodule (mg C m^{-2})	Salinity (psu)	Std Dev Salinity
Instantaneous	n/a	n/a	n/a	9.2
Daily Average	-11	3	0.00	9.1
7 DMA	46	-13	0.06	8.9
14 DMA	100	-29	0.12	8.8
30 DMA	224	-73	0.26	8.5
Monthly Average	92	39	0.34	7.9

Model System Physiology

Several key physiological indicator variables were monitored to assess realism of model processes and to diagnose mechanisms by which environmental perturbations effect changes in the plant community. We are careful to assess carbon flows in the model, because it is possible to generate apparently reasonable output for state variables that integrate several underlying processes with offsetting errors. For example, seagrass biomass integrates flows of production, mortality, translocation and respiration and an overestimate of respiration could be offset by an overestimate of production. By routinely monitoring carbon dynamics in this model, such spurious results are identified and avoided.

Indicator variables were also used to track key model processes, which were responsible for observed patterns of seagrass and epiphyte biomass. By quantifying the flow and fate of carbon on a normalized basis, assessment of the velocity of carbon and nutrient movement through state variables could be made. Carbon flows showed that under baseline conditions, seagrass

photosynthesis was highest in the mid growing season (Figure 15), and gross photosynthetic rates peaked at above 400 mg C m^{-2} d^{-1} during summer of each year. The respiration term, which is expressed as a negative carbon flow, combines active and basal metabolism and ranged from about 20-25 of gross photosynthesis throughout the year, peaking at about 75 mg C $m^{-2}d^{-1}$ during mid-summer. Losses to leaf mortality were slightly greater than respiratory losses and similarly expressed as a negative. Together, both loss terms combine to represent about 45 mg C^{-1} $m^{-2}d^{-1}$ in winter to 160 in summer or about 30%-50% of the gross normalized production. As an example, this corresponds to a complete biomass turnover time of about 150 d in summer for the average square meter of bay bottom containing 30 g *Thalassia* plant material.

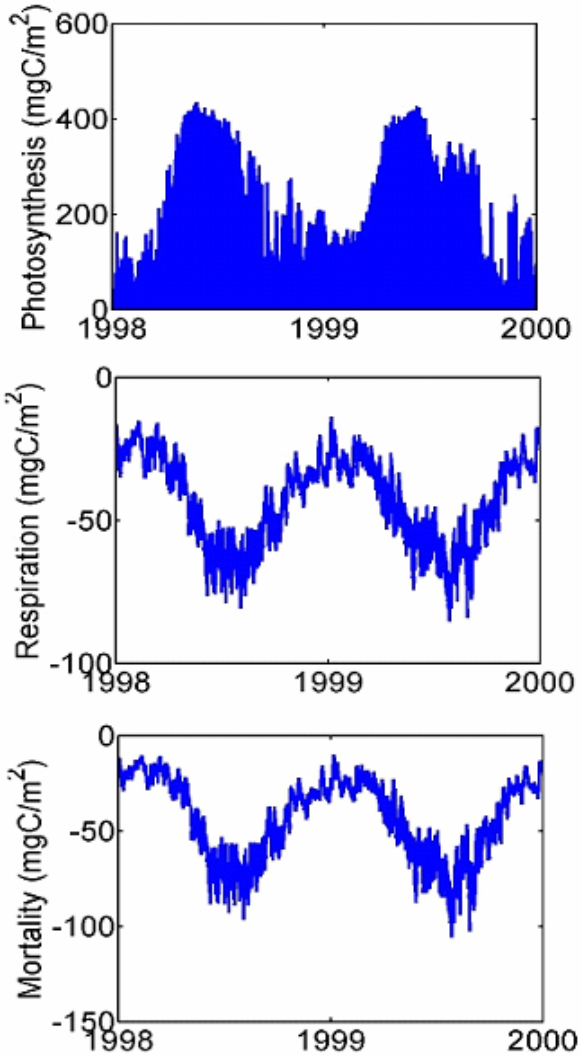


Figure 15. Internal carbon flow in a *Thalassia* bed permitting calculation of turnover time for biomass.

Model Applications

A multitude of major management and research questions can be addressed using the model. The following issues are being actively investigated for Florida Bay using the seagrass model:

- What is the appropriate salinity level, range and timing of salinity for a healthy seagrass community?
- What are the recovery periods to differential levels of seagrass loss or community change, and what salinity conditions are optimal for recovery?
- How does salinity regime affect species composition, reproduction and plant vigor?
- How will strong pulses of low-salinity water affect plant health?
- What is the effect of differential schedules of fresh water input on plant health?
- How is sediment sulfide implicated in seagrass health?
- How does the light regime affect seagrass health and species composition? Which species dominates under low and high light regimes?
- How does the nutrient regime affect seagrass health and species composition? Which species dominates under low and high nutrient regimes?
- What are the responses of epiphytes, and what are the tolerances of seagrasses to nutrient enrichment?
- How does the oxygen regime contribute to die-off?
- How might sea level rise affect the interaction of environmental factors and seagrass community health?
- What are the effects of multiple stressors: hypersalinity, hyposalinity, thermal stress, hypoxia, hydrogen sulfide, low light and interspecific competition on seagrass community health and species composition?

Two applications of the model are presented here as examples of its utility as a tool for retrospective data exploration and hypothesis testing.

<u>Case #1: Long-Term Historical Retrospective Model Analysis</u>

We applied the model to do 30- year retrospective simulations of seagrass trends using the calibrated model combined with salinity input from the FATHOM model's base case. FATHOM salinity output for Basin #14 (Little Madeira Bay) and Basin #15 (Eagle Key Basin) was used for the two simulation runs in the downstream reach of Taylor River outflow. FATHOM output from Basin #34, Whipray Basin, was used to run the model for an area that is relatively isolated from freshwater inflow in the central bay. Output from FATHOM Basin # 47, Trout Cove, was used to reconstruct plant dynamics for an area that receives a large volume of freshwater input from Trout Creek, but that is extremely P-limited (Fourqurean et al. 1992). This reconstructive analysis enabled the evaluation of probable effects of droughts and other low flow conditions on the

seagrass community in different parts of the bay over long periods and during a time when no seagrass or salinity data were collected. The analysis enables us to provide a best estimate of seagrass biomass and composition response to historically high salinity conditions.

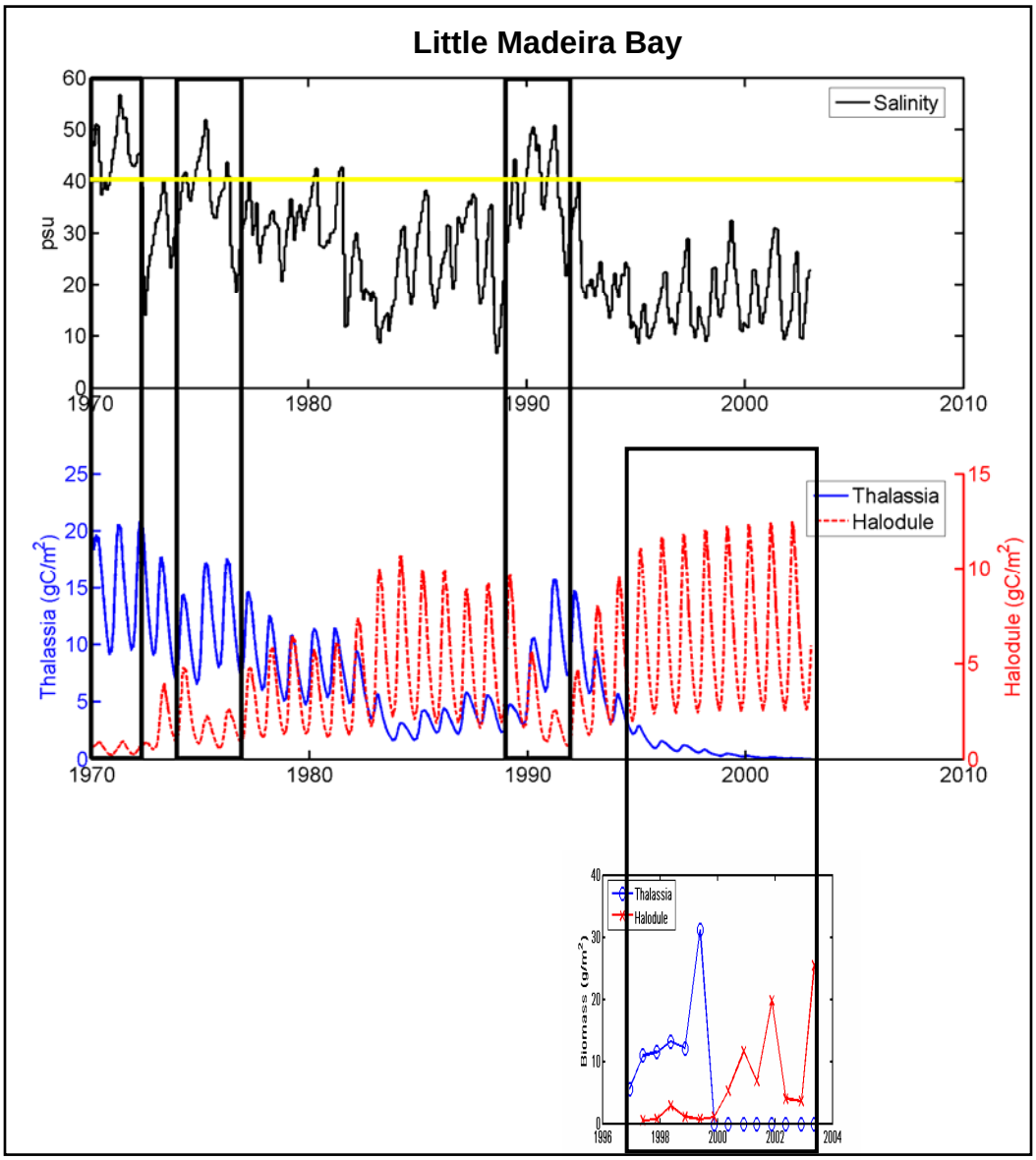


Figure 16. 30-year retrospective simulation of *Thalassia* (blue) and *Halodule* (red) using modeled salinity reconstruction from FATHOM in Little Madeira Bay. Inset: Data (M-DDERM 2004) from field measurements south of Taylor River.

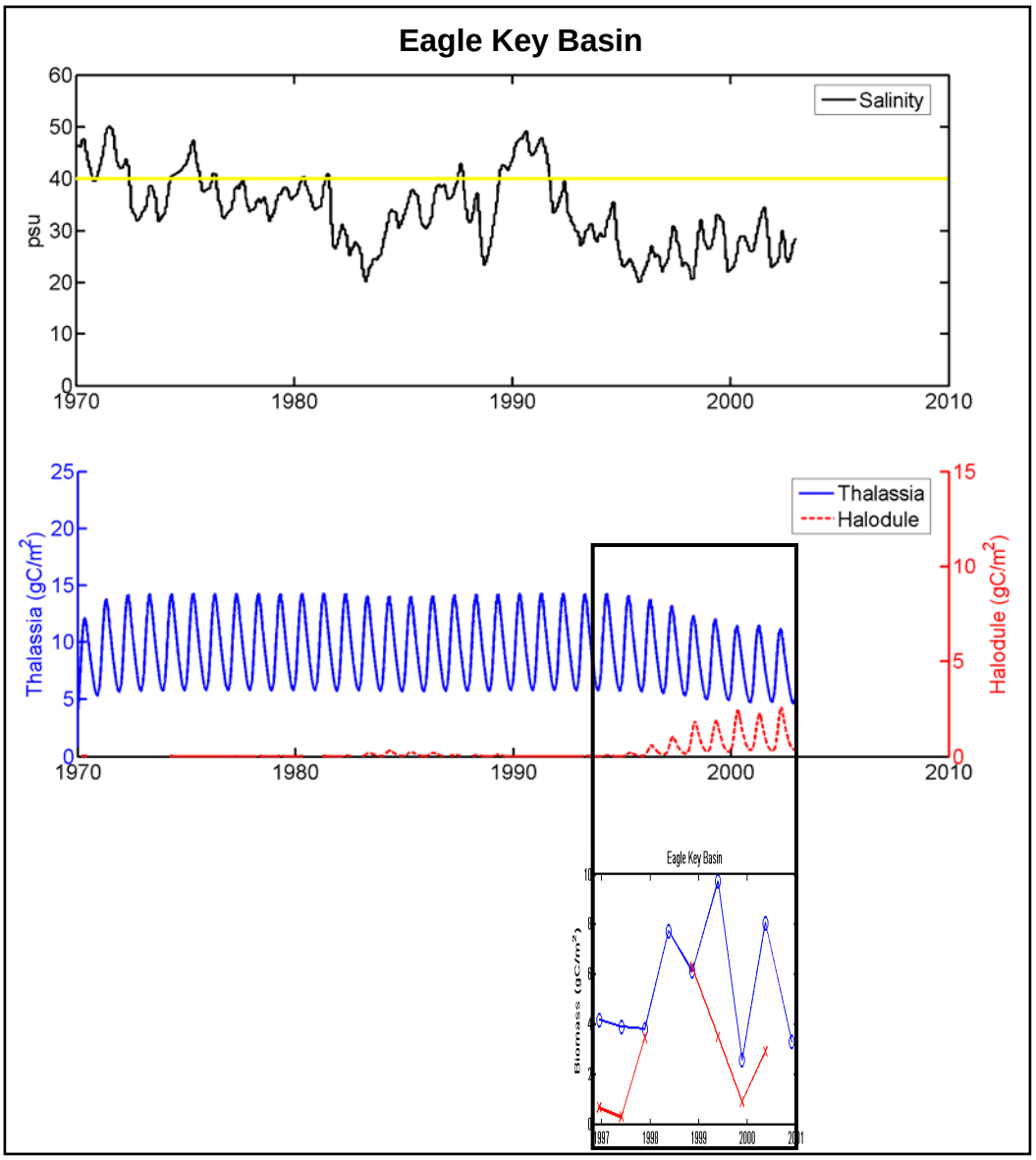


Figure 17. 30-year retrospective simulation of *Thalassia* (blue) and *Halodule* (red) using modeled salinity reconstruction from FATHOM in Eagle Key Basin. Inset: Data (M-DDERM 2004) from field measurements in Eagle Key Basin south of Little Madeira Bay.

The Florida Bay seagrass model was initially used to reconstruct Little Madeira Bay (Figure 16) and Eagle Key Basin (Figure 17) SAV populations using FATHOM predictions as input salinity datafiles. Values for other environmental variables (nutrients, temperature, light) throughout the 30-year simulation were from data from 1995-2001, averaged monthly to produce a standard annual curve and repeated for each year of the 30-year simulation. The time series for salinity from the FATHOM model and biomass for *Thalassia* and *Halodule* are shown for the period

1970-2000. In Little Madeira Bay (Figure 16), three periods correspond to loss of *H. wrightii* at the inner site shown in the boxed area: (1) 1970-1971 drought, (2) mid 1970s and (3) 1989-1990 drought. In all cases, marine to hypersaline conditions prevailed for > 1 year. Note the development of monospecific *Thalassia* beds in the early 1990s at the inner site in the early 1990s and then decline in wetter years mid 1990s. At the outer site in Eagle Key Basin (Figure 17), *Thalassia* dominated the seagrass community from 1970 through the mid 1990s when a mixed bed appears during wetter period in the mid 1990s. During the simulation period, the same drought and hypersalinity conditions were evident in Eagle Key Basin, but the salinity peaks were not as extreme (none above 50 psu) nor as persistent as in the Little Madeira Bay simulation.

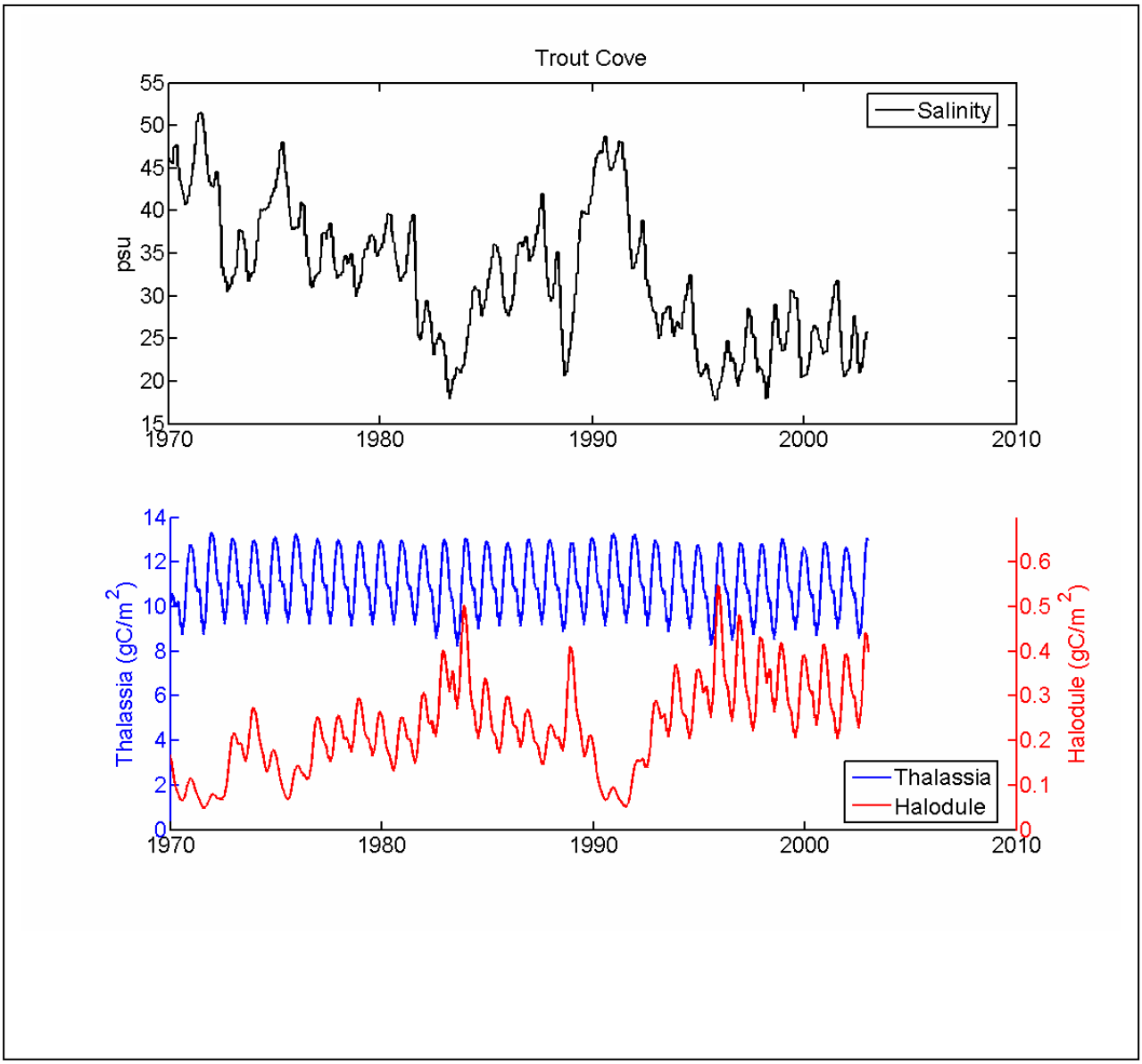


Figure 18. 30-year retrospective simulation of *Thalassia* (blue) and *Halodule* (red) using modeled salinity reconstruction from FATHOM in Trout Cove.

In the Trout Cove historical reconstruction (Figure 18), higher freshwater input maintained salinities generally in the range supportive of healthy populations of both *Thalassia* and *Halodule*, resulting in a mixed community throughout the simulation. The oligotrophic nature of the water and sediments at this site is reflected in the generally lower productivity of both species. In Whipray Basin (Figure 19), salinity was generally high and more constant than in other basins. Levels of salinity were above 40 psu for prolonged periods during the 30-year simulation. This mean salinity level may be erroneously lower than the true salinities experienced in this part of the bay, as based on the data available and anecdotal information. The result was a very productive and stable mixed seagrass community.

Results from the first three of these model runs, which had highly variable salinity patterns, showed clear responses of seagrasses to salinity (boxes) as *Thalassia* became dominant during periods when salinity was elevated above 40 psu for extended periods. This dynamic differs from what would be expected based on the mesocosm experiments previously described, which indicated that *Halodule* is at least as tolerant of high salinity as *Thalassia*. This pattern was reflected in the fourth simulation, reconstructing a stable salinity regime in Whipray Basin. During the periods when salinity remained above 40 psu for two or more consecutive years at the inner Little Madeira site, *Thalassia* growth was favored at the expense of *Halodule.* Immediately following extended periods of elevated salinity, increased freshwater flow from Taylor River resulted in lowered salinities, and by the late 1990's, *Thalassia* was nearly eliminated from the Little Madeira Bay site. At the Eagle Key Basin site, about 5 km from Taylor River mouth, salinity was less variable and remained at higher levels, favoring *Thalassia* and suppressing *Halodule* growth throughout the period 1970 - 1997. Briefly during the mid 1980s, and then persistently beginning in the mid 1990s, the onset of reduced salinities corresponded with increased *Halodule* biomass at Eagle Key, resulting in the development of a mixed *Thalassia-Halodule* assemblage. The results discussed here and earlier have pointed to the importance of competitive interaction for nutrients and light between plants *in situ* and that a competitive advantage appears to be strongly influenced by salinity.

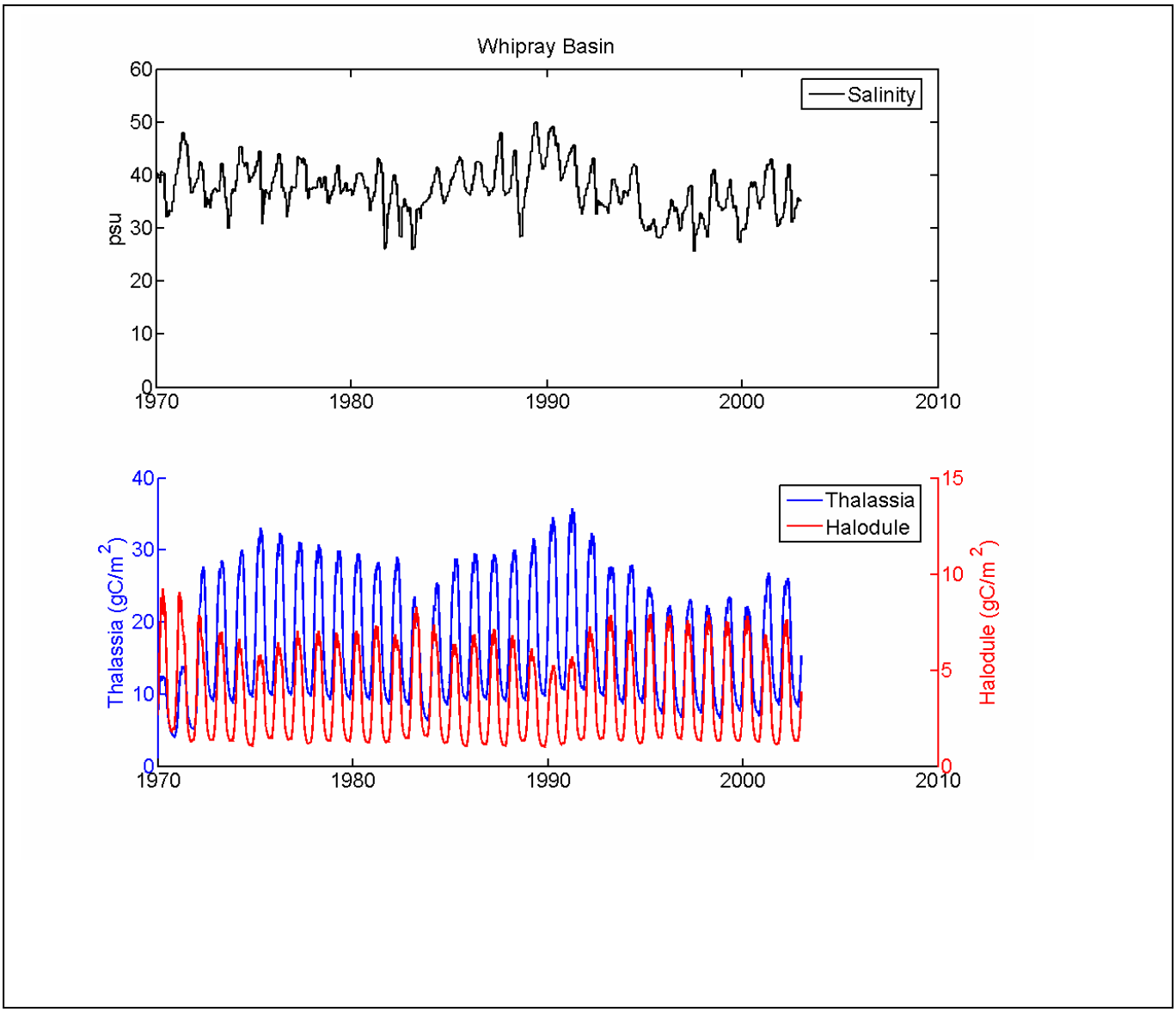


Figure 19. 30-year retrospective simulation of *Thalassia* (blue) and *Halodule* (red) using modeled salinity reconstruction from FATHOM in Whipray Basin.

Because mesocosm studies demonstrated that elevated salinities alone caused internal, physiological stress in the seagrass plants- even though growth continued in the otherwise ideal conditions of light, nutrient, oxygen- we suspect that the dynamics of interspecific competition are shifted by high salinity *in situ* (and in the model), where *Thalassia* could out-compete *Halodule*, particularly for nutrients, but also for light and space. In the bay, sulfide-rich sediments and interspecific competition appear to result in cumulative stresses that could provoke a decline in the vigor of both species at elevated salinity levels (Madden et al. 2003). The model prediction is due

to the reduced ability of *Halodule* to compensate for hypersalinity in the face of such multiple environmental stresses and to successfully compete with *Thalassia* for limited resources.

These modeling results reflect species composition changes of *Thalassia* and *Halodule* that have been observed in Little Madeira Bay and Eagle Key Basin. It is instructive to look at the longer term field dataset for the two calibration sites above. Empirical data for biomass, shown in the inset for both species was collected from 1997-2004 (Figures 16-17), extending three years beyond the calibration period of the model. The 30-year model run does not incorporate these data in its calibration dataset meaning that these data can be considered a validation dataset. The changes in biomass in the field, though delayed, are consistent with the model prediction at both sites. As flow increased in the late 1990s, *Thalassia* declined to zero, and *Halodule* became the dominant species in the Little Madeira site, while at Eagle Key Basin, a mixed assemblage develops.

Case #2: Multiple Stressor Evaluation

The model has been effectively used to test the response of plant biomass to individual stress and simultaneous multiple stressors, as more realistically occurs *in situ*. Simulations were performed to investigate influences of different stresses common to plants in Florida Bay on the performance of *Thalassia*: high salinity, high sulfide concentrations and elevated nutrient levels (Figure 20). For this application, stresses were applied in combination at the levels they had been applied individually. Interestingly, whereas individually neither salinity nor nutrient increases alone caused much response in the *Thalassia* growth profile, together these stresses caused a strong reduction in spring initial growth rate and the spring-summer biomass level. The model community did recover to ‘normal’ peak biomass levels by fall, but overall, annual production was reduced by half in response to elevated nutrients and salinity.

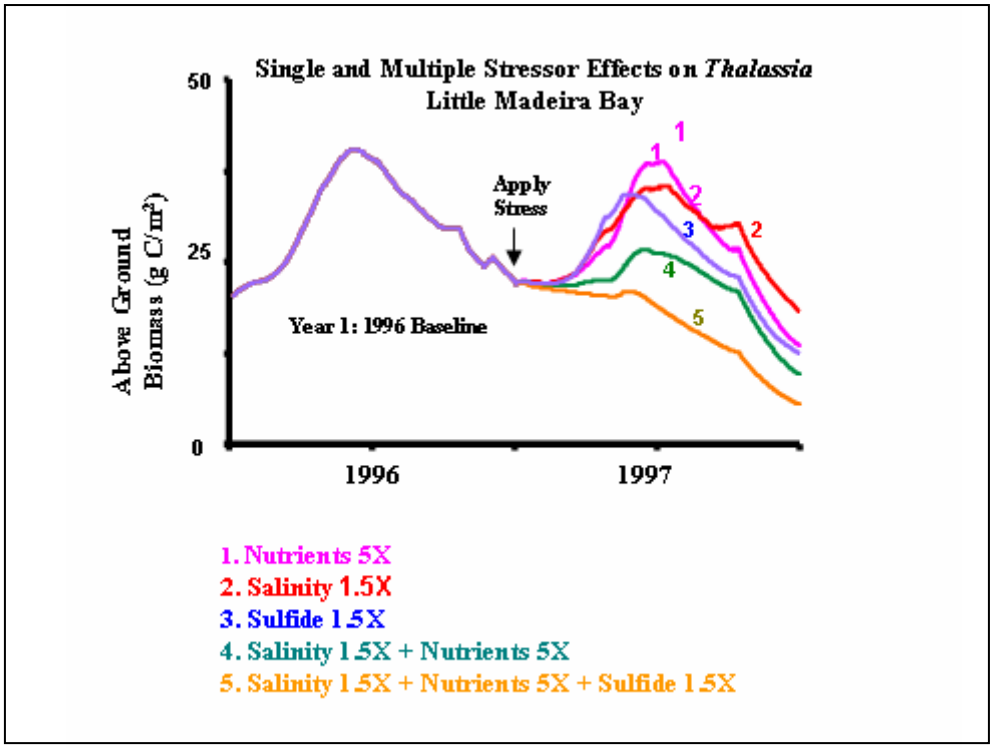


Figure 20. Single-species model scenario test of individual and simultaneous stressors on *Thalassia* growth. See text for explanation.

Application of a multiple stress condition involving elevated nutrients, salinity and elevated sulfide concentrations produced more dramatic results in the *Thalassia* growth profile. The level of nutrient 'stress' (inorganic N and P) applied in the model, a quintupling of baseline observed levels, has not been observed in Florida Bay. However, given the low concentrations of each of these nutrients currently measured, an increase by a factor of five is not very extreme and still places the modeled concentrations of these nutrients well below the levels commonly observed in many estuaries, and within the range that could occur under certain conditions in the bay. In fact, the nutrient treatment increased seagrass biomass slightly.

When three relatively benign stresses were applied simultaneously (run #5), biomass declined continuously from the point of stress application in January throughout the growing season, as *Thalassia* rapidly died off. Examination of processes underlying this model behavior revealed that photosynthesis, though operational, was impaired and functioning at such a low level that the net daily production was negative throughout the growing season. Interaction of the above- and belowground compartments plays a strong role in the trajectory of the seasonal biomass

curve in the model. Exchanges of organic carbon and nutrients between leaf and root compartments are seasonally variable and critical for survival of submersed plants. The modeled plants can mobilize belowground resources to supplement carbon input to the aboveground compartment, should autotrophic assimilation become deficient. The amount of carbon in the root/rhizome material available for growth supplementation can control the outcome of plants subjected to stress conditions. Therefore, the status of the belowground compartment can determine the survival of the entire plant. Conversely, when conditions are unfavorable to growth, and belowground resources are depleted, the existence of aboveground plant material can mask a plant community in fragile condition. We believe that this model conceptualization is realistic and is likely close to the physiological and community behavior that occurs in the real system, emphasizing the importance of thresholds and non-linear behaviors, which can be tracked and revealed by model analysis.

Data sources and description

A large and varied set of data sources were used in developing this model, reflecting the synthetic nature of the process and the importance of creating linkages among the various research programs (Table 10). The ongoing acquisition of data will continue to require collaboration with research scientists and managers active in Florida Bay. One of the benefits of this model is its emerging role as a tool for synthesis of the myriad data types, formats and scales being sampled in Florida Bay. By continuing to locate new data sources and updating current data sources, the resolution and range of the calibration data set increases, allowing for increasingly greater confidence and accuracy in model predictions. Data included in the calibration data set are: bathymetry, salinity pattern, nutrient inputs, water column light dynamics, sediment characteristics and depth, chemistry conditions, hydrology and seagrass distributions. This database will enable calculation of conditions and seagrass distributions across representative areas of the bay.

Table 10. Data sources utilized directly or in development of the conceptual understanding and model of the bay. Sources marked by an asterisk (*) were not used directly in the model but did provide background and supporting information during model development.

Data Type and Org.	Comments and Source
Seagrass biomass and cover monitoring program. Miami-Dade DERM	As part of a monitoring program from 1996 to 2005, bimonthly assessments of seagrass cover were conducted using a modified Braun-Blanquet index as well as measurements of short shoot density and compartmentalized biomass for Biscayne Bay and northeast Florida Bay. From 2005, sampling was reduced to twice a year. Biomass data is used as calibration data for northeastern Florida Bay while the Braun-Blanquet and short shoot density data were used to determine regional differences in biomass per shoot and to develop relationships between biomass and cover.
Seagrass biomass and cover monitoring program. Seagrass cover monitoring and change analysis FHAP (Fish Habitat Assessment Program)	Sampling was done in spring and fall of every year from 1996 to 2004 of Braun-Blanquet cover analysis and short shoot density. Cores for compartmentalized biomass were taken during spring sampling. The spatial extent of this sampling is distinct from the DERM sampling with most of the sampling in central and western Florida Bay. Beginning 2005, sampling was reduced to once a year Braun-Blanquet and short shoot density, but spatial extent was increased from Biscayne Bay to the Southwest Florida coast. Coring was discontinued. Biomass data is used as calibration data for central and western Florida Bay while the Braun-Blanquet and short shoot density data were used to determine regional differences in biomass per shoot and to develop relationships between biomass and cover.
FATHOM model output of salinity distributions	The Fathom mass balance model for Florida Bay provides monthly salinity distributions for 42 basins in the bay (Cosby et al. 1999).
*PHAST Model	Fresh water flow calculations were used as inputs for the FATHOM

	hydrologic model. (Marshall et al. 2004a, b).
DERM seagrass monitoring	As part of a monitoring program from 1996 to 2005, bimonthly assessments of seagrass cover were conducted using a modified Braun-Blanquet index as well as measurements of short shoot density and compartmentalized biomass for Biscayne Bay and northeast Florida Bay. From 2005, sampling was reduced to twice a year. Biomass data is used as calibration data for northeastern Florida Bay while the Braun-Blanquet and short shoot density data were used to determine regional differences in biomass per shoot and to develop relationships between biomass and cover. (M-D DERM 2004)
Seagrass monitoring, nutrient status	Collection of seagrass nutrient composition in 2002 at FCE-LTER sites. Used to calculate C:P ratios for phosphorus uptake in model. (Fourqurean et al. 2002, 2005). LTER
Subsurface light regime data.	Measurements of photosynthetically active radiation (PAR) using spherical (4pi) sensors for bottom reading (submerged to just above substrate) and flat (2pi) sensors above water surface at 15 minute intervals from 1998-2002. Sensors are established near water quality platforms in seven basins. Light – Paul Carlson (FWCC) – daily average light on bottom (Julian day average that includes nighttime 0's) Carlson 2003. Florida Marine Research Institute.
Seagrass and epiphyte monitoring	Seagrasses were monitored for biomass and morphology and epiphyte load during the period from 1989 to 2001 for several basins across Florida Bay. This data is used in calibration of the model development and calculation of biomass to surface area ratio for *Thalassia*. Frankovich, Zieman, Bricker, Schwarzschild Univ. of VA. Frankovich and Zieman (2005).
Water quality monitoring network	Since 1990, multiple point stations throughout the bay have been sampled monthly for water quality, including salinity, temperature,

	turbidity, chlorophyll a concentration, and inorganic macronutrients. This data is used as the water column nutrient forcing for the calibration of the model. J. Boyer et al. FIU, under SFWMD contract. http://serc.fiu.edu/wqmnetwork/
*Salinity and temperature – USGS.	Mouth of Taylor River and ENP for the mouth of Little Madeira Bay platform data at 15 minute intervals which is linearly interpolated to provide instantaneous salinity. http://www.evergladesplan.org/facts_info/science_maps.cfm
Water column nutrient inputs	Mouth of Taylor River and Joe Boyer (FIU) for the mouth of Little Madeira Bay. (monthly grab samples that serve as anchor points for linear interpolation of a daily time series.)
*Water column nutrient concentrations in north and central bay	Quarterly to monthly synoptic sampling was performed by SFWMD using a high-speed mapping platform (Madden and Day 1993) to develop snapshots of salinity distributions in the bay. Madden SFWMD
Salinity at inflows	Monitoring of salinity and nutrient inputs at major flow points using permanent instrument deployments. USGS Hittle & Zucker
*Organic and inorganic nutrients	Measured from grab samples taken on a monthly basis at the platforms for monitoring salinity and flow during the time period of 1996 to 2000. After 2000, nutrient sampling at the northeastern Florida Bay sites was continued by a team from. Childers FIU
Total nutrients at inflow points	Automatic samplers at major input flows. Childers FIU
Thalassia growth	In situ chamber studies of nutrients and sediment effects on growth. Koch FAU
*Photosynthetic efficiency and stress	PAM fluorometery: in situ measurements of plant stress, efficiency, P vs I. Durako UNC-W
Thalassia biomass and growth	In situ measurements of growth, leaf elongation, tissue content Fourqurean- tissue content relative to environmental N:P, respiration rates. Madden SFWMD
*Multiple stress effects	Mesocosm studies of 3 seagrass species responses to multiple

	stresses. Koch and Durako 2005
*Seed survival	Seed germination and seedling growth and survival. Durako FMRI
Plant metabolism	Incubation of plant and community components. Madden SFWMD
*Sediment profiles of H2S, and oxygen metabolism	O2 measured the micro structure of oxygen and sulfide distribution vertically in the sediments using micro electrodes. The study was conducted at one site on two occasions. Borum et al. 2005
Epiphyte loading and light absorption	Data on the distribution of epiphyte species on Thalassia leaves and density and light absorption. Frankovich and Zieman (2005) UVA
Tissue N and P in Thalassia. Limiting nutrients.	a survey of tissue content, limiting nutrients, sediment depth, seagrass distribution, seagrass health, photosynthesis and respiration rates. Fourqurean 1992

The seagrass modeling effort is linked to, and part of, the overall Scientific Program for the Restoration of Florida Bay (Table 11), and this Program is organized around five central research and modeling areas. The importance of model linkages within the program is presented in the following tabular organization showing how the various models being developed might be integrated.

Table 11. Linkage of the seagrass model with other models to be developed for Florida Bay.

Linked Model	**Linked model output to Seagrass Model**	**Seagrass Model output to linked model:**
PHYSICAL MODEL	Velocity Turbulence & Wave energy Water depth Salinity Temperature Fetch Sediment resuspension Residence Time	Total Leaf Area Specific Growth Biomass Canopy height Shoot Density/m^2
	Light Penetration N and P	N and P uptake Productivity and turnover

WATER QUALITY MODEL	Chl *a* Light quality Turbidity Color	Stabilized sediments Sedimentation
SEDIMENT MODEL	Depth Characteristics - texture N and P Organic content	Cover Shoot Density/m^2 Below-ground biomass Redox (H_2S) Deposition OM and $CaCO_3$ Resuspension
CONSUMER MODELS	Herbivory Decreased standing crop Recruitment Migration Bioturbation Filtration	Species Composition LAI, ss/m^2 Canopy height Litter Epiphytes

Conclusion

The seagrass model project has produced an operational mechanistic dual-species unit model of the *Thalassia-Halodule* community distribution, calibrated for six representative basins in Florida Bay. Under this proposed project expansion, the model code for phytoplankton will be initially developed in STELLA, running on a desktop PC, then ported to MATLAB so as to be compatible with, and to facilitate incorporation into the existing Florida Bay Seagrass Model. Code has been ported to a FORTRAN platform for compatibility with the emerging 3-D hydrodynamic water quality model at a landscape scale to be developed for Florida Bay (Hamrick and Moustafa 2003; Cerco 2000).

The seagrass model is a proven tool in active use in the development of management strategies of the state-mandated Florida Bay Minimum Flows and Levels program (Madden and McDonald 2005; Hunt et al. 2005). The integrated seagrass-phytoplankton model will provide a powerfully upgraded tool for addressing community health and restoration issues involving water column processes and Harmful Algal Blooms (HAB). It will incorporate mechanisms for nutrient inputs and community transformations into the model and predict their outcome under a variety of natural and management scenarios. The model is actively being used to test hypotheses and alternative management strategies for Everglades and Florida Bay restoration.

Linkage of the seagrass model to a hydrodynamic transport framework, landscape model based on a geospatial platform is currently planned under an existing SFWMD project. This proposed project will leverage the incorporation of the phytoplankton module into the water quality model as well. The seagrass unit model has already been successfully integrated with higher trophic General Additive Models (GAM) to produce predictions of the density of important fish species and pink shrimp in response to habitat type and quality (Bennett et al. 2005). By integrating these bottom-up components into the model, the predictive capability of the GAM models supported by the seagrass parameters of species composition and density will be enhanced (Johnson et al. 2005).

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