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Modeling

Synthesis

INTRODUCTION

Models are helpful tools in dealing with complex systems where uncertainty is present, as is often the case for ecological systems (Patten and Jørgensen 1995). A numerical model can be considered as a series of hypotheses set into mathematical terms (Caswell 1979). Ecological models, when correctly developed, have useful predictive properties; they can help answer “what if?” questions, generate testable hypotheses, and increase our understanding of how real systems function (Jørgensen 1994). An ecological model cannot contain all the details of the complex ecosystem, but only the variables and processes thought to be of importance to the problem (Jørgensen 1986; Caswell 1988). The trend is to build more realistic models that are rich in mechanical details, and that focus on a particular system (DeAngelis 1988; Kareiva 1989; Grimm 1994). These types of models demand intensive measurements to make good parameter estimates, a basis for accurate and precise simulations of the system.

Modeling is a process of simplifying a real world system, in an attempt to understand some aspect of the system, which is important to the question or problem being posed (Caswell 1988; Kareiva 1989). A flowchart of modeling would include at least the following steps (Jørgensen 1994): Conceptual model Parameterization Calibration and

Sensitivity Analysis Validation (see Chapter 1). A conceptual model can be considered a list of state variables and mathematical formulations of importance to the system and the problem being studied (Grimm 1994). A conceptual model diagram shows how the variables are connected by flows of material and information (Jørgensen 1994) (Fig. 1). Parameterization defines the numerical values in the mathematical equations. Calibration is the fine-tuning of the model using suitable data sets. Validation is the estimation of the confidence in the model, testing fit to the observed values over a number of independent data-sets (Rykiel 1996). Further understanding can be achieved by varying one parameter at a time and observing output, a procedure called sensitivity analysis (Jørgensen 1986, 1994).

Seagrass Systems

Seagrass habitats exhibit dynamic complexity of the kind that makes ecological models difficult to validate across the entire range of real system behaviors. Seagrass meadows are highly productive and ecologically important habitats within south Florida's estuaries and coastal lagoons, as well as throughout the world (Zieman 1982; Larkum *et al.* 1989; Bortone 2000). The seagrass community of the South Florida region is structurally and functionally complex. The dominant species of seagrass is generally *Thalassia testudinum*, whereas *Halodule wrightii* and *Syringodium filiforme* may co-occur or dominate in some areas (Zieman 1982; Fong and Harwell 1994). The seagrass community also includes many species of algae that can be grouped into a few functional groups: drift algae, rhizophytic algae, attached (psammophytic) algae, and seagrass epiphytes. Each of these functional groups comprises numerous species that may be seasonally abundant. Functional-form classifications (*sensu* Littler and Littler 1980) can be used to further divide the species in each functional group according to morphological and physiological attributes (Borden 1995).

Benthic macroalgae, such as rhizophytic algae in the genera *Penicillus*, *Halimeda*, and *Caulerpa*, are important in stabilizing sediments, thereby facilitating seagrass succession (Williams 1990). In addition to these benthic species, macroalgae such as *Laurencia*, *Polysiphonia*, *Chondria*, *Hypnea*, *Dictyota*, and *Gracilaria* are present in seagrass beds as large clumps of detached drift algae (Josselyn 1977; Williams-Cowper 1978; Benz *et al.* 1979; Virnstein and Carbonara 1985; Bell and Hall 1997; McGlathery 2001). Epiphytic micro- and macroalgae, especially filamentous and sheet-like reds and greens, grow attached to the seagrass blades (Humm 1964; Jensen and Gibson 1986; Moncreiff *et al.* 1992). Epiphytes and drift algae shade light to the seagrass blades and thereby may reduce productivity of the seagrasses (Jones 1968; Bulthuis and Woelkerling 1983; Jensen and Gibson 1986). Recent attention has focused on blooms of drift algae and epiphytes, which are hypothesized to be related to eutrophication in many shallow nearshore seagrass environments (McGlathery 2001; Valiela *et al.* 1997; Hauxwell *et al.* 2001). However, they may also be a function of ecosystem-wide changes arising from deteriorating water quality that are not directly related to nutrient input, such as cascading, pervasive changes in food-web dynamics from over-harvesting pressures in a multitude of both commercial and recreational fisheries (e.g., Valiela *et al.* 1997; Ault *et al.* 1998; Miller *et al.* 1999; Heck *et al.* 2000; Szmant 2001). An alternative, and little considered implication, of rising CO₂ concentrations from global climate change indicate that an increase in free CO₂ can be expected to have a significant fertilizing effect on marine algae that can photosynthesize free CO₂ more readily than the more abundant bicarbonate ion, thereby shifting competitive balances by enhancing marine plant growth (Brouns 1994); a climate-related development that would increase the prevalence of tendencies already ascribed to anthropogenic nutrient loading in coastal waters (Buddemeier 1994).

The importance of biotic and abiotic factors controlling the distribution and abundance of the algae and seagrass components of the seagrass ecosystem is still largely unknown, although Fong and Harwell (1994) have developed a model to examine some mechanisms

controlling spatial and temporal variability in the structure of seagrass communities. Their seagrass systems-model simulates dynamic changes in biomass of the three potentially dominant seagrass species in South Florida: *Thalassia*, *Halodule*, and *Syringodium*, as well as two algal groups: epiphytes and rhizophytes. Biomass of a “population” of plants in a meter square area is simulated. Modeled changes in biomass are based primarily on literature-derived relationships among the autotrophs and environmental factors. The major changes in community composition were found to be a result of responses to salinity and disturbance stressors (Fong and Harwell 1994). This model is incomplete, however, in part because of the lack of knowledge about the dynamics of the macro-algal component of seagrass ecosystems. The purpose of the current modeling effort was to quantify the relationship between the environmental conditions, interacting with physiological processes in the algae to affect growth, and to explore how algal biomass changes with spatio-temporal differences in environmental conditions.

Aims

The Fong and Harwell (1994) seagrass model was used as a starting point for my modeling efforts. I used a similar approach and separated the three functional groups (drift, rhizophytic, and epiphytic algae) into discrete, independent models. The three algal models require quantitative parameterization for light, temperature, salinity, and nutrient responses of growth. A comprehensive literature survey found only a few useful studies pertaining to Biscayne Bay (Jones 1968; Josselyn 1977; Bach 1979; Morrison 1984) that would allow these functions to be parameterized on the basis of literature values alone. For this reason a number of experimental approaches were undertaken to provide additional needed data (Chapters 2-6). To augment the experimental data gathered to parameterize these models, data for similar seagrass systems (e.g., in the Caribbean) available from the literature were used where appropriate.

The interaction with the seagrass model is through light limitation of the seagrass in the presence of drift algae and epiphytes. This interaction was modeled as part of the output data from the separate algal models, and can be used as an input function to the seagrass-model light-function.

The aims of this chapter are to:

- develop a conceptual model for the three functional groups of algae in relation to environmental conditions found within Biscayne Bay;
- parameterize the model using literature data and experimental data collected in this dissertation;
- calibrate and validate the model to an acceptable goodness-of-fit with field data from different regimes within the Bay; and
- analyze the model construct and robustness using sensitivity analysis.

METHODS

1. Conceptual Model and Mathematical Formulation

The first step of the modeling effort is to develop a conceptual model that describes a hypothetical representation of how the system works (Hall and Day 1977). Conceptual models are used to illustrate linkages among compartments and proved the basis for developing and testing causal hypotheses (Gentile *et al.* 2001). Assumptions and proposed relationships are made explicit by delineating spatial, temporal, and ecological scale and boundaries which are essential in order to bound the problem, identify what is to be included in the formal model, and identify connectivities to factors outside the scope of the model (Gentile *et al.* 2001). A conceptual model for algal biomass must, therefore, consider variables (both abiotic and biotic) that influence production-dynamics over a range of spatio-temporal scales.

Algal biomass in the model is influenced by light (L), temperature (T), salinity (S), and nutrients (N) (both water-column and sediment-porewater nutrients). Drift algae and epiphytes are able to utilize only water-column nutrients, while rhizophytic algae can also take up nutrients in the sediment porewaters (Fig. 1). Optimal productivity of each functional group occurs within a specific range for each one of these environmental factors. Loss of biomass is currently modeled by senescence of a constant proportion of biomass, and for the drift algae, removal by hydrodynamic flows. Increased mortality of epiphytes occurs when the seagrass substrate becomes limiting, a function of seagrass-blade turnover (Fig. 1).

The mathematical construct for each functional group consists of a logistic growth equation that predicts, under optimal conditions, an expected increment in biomass over time ($\frac{dB}{dt}$) of that group within a 1m² area. Each functional group has an optimal productivity that occurs within a specific range for each of the environmental factors (L , T , S , N), and the simulated production is depreciated from the optimal value when any of the environmental factors varies outside this optimal range. This depreciation is accomplished by multiplying the maximum productivity by a series of scalars from 0-1 that represent each factor (Botkin *et al.* 1972; Lehman *et al.* 1975; Guimaraens 1999). Assumptions in the model formulation include (adapted from Lehman *et al.* 1975):

- Each species has a maximum growth rate possible during optimal growth conditions.
- Growth rate can be reduced from the maximum by suboptimal L, T, S, N conditions.
- Each functional group can be characterized by a light intensity that saturates photosynthesis.
- Each functional group can be characterized by an optimal temperature and salinity range with upper and lower lethal limits.
- Each functional group possesses a growth-limiting nutrient concentration and a finite maximum growth-capacity beyond this minimum.

- Nutrient-dependent growth can be characterized by Monod equations (Vymazal 1995) with both maximal growth rates and nutrient-specific half saturation constants (K_s).
- Physiological death and grazing losses are minimal.

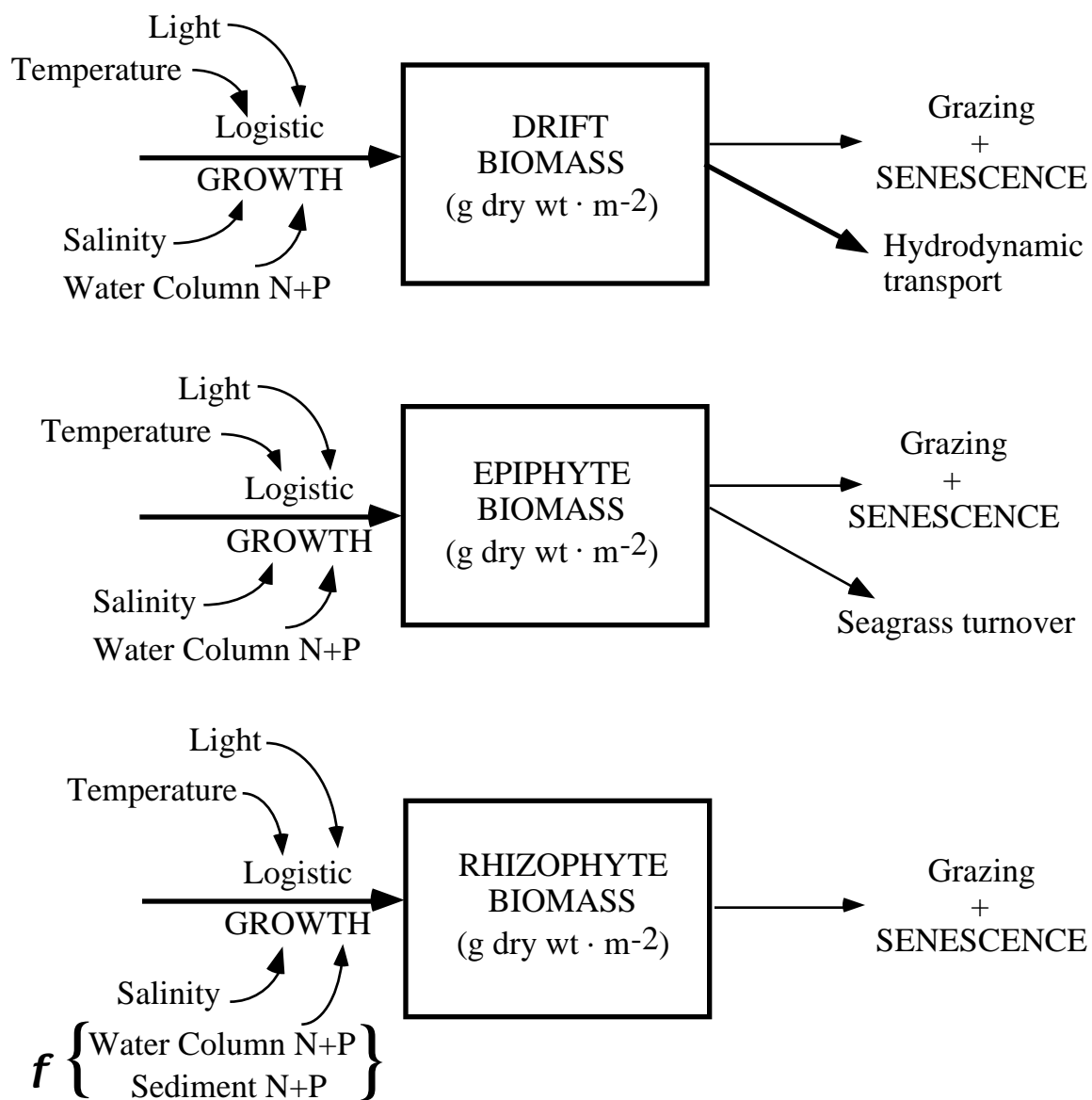


Fig. 1: Conceptual model for the three functional groups simulated, and the relation of growth to environmental variables.

General model equations common to each of the three functional groups are:

$$(1) \quad \frac{dB}{dt} = (g-d)B$$

change in biomass (B) per unit time (day) expressed as g dry weight m⁻², g = growth, d = mortality per day

$$(2) \quad g = g_{max} \cdot (1 - \frac{B}{K}) \cdot f(L) \cdot f(T) \cdot f(S) \cdot f(N)$$

g_{max} = maximum growth from literature (Table 1). $(1 - \frac{B}{K})$ = logistic growth formulation up to a 'carrying capacity' (K) characteristic for each scenario and determined from field data and calibration experiments using the model. $f(X)$ are environmental response functions. Values for these functions range from 0-1. When optimal, the function returns 1, when suboptimal <1 down to zero, when no growth can occur (= outside range of tolerance). $f(L)$ = P-I curve fitted to experimental data following the approach used by Fong and Harwell (1994). $f(T)$, $f(S)$ are curves derived from experimental data (Fig. 2). $f(N)$ is a Monod function determined experimentally for each functional group and fitted to the nutrient concentration in the ambient environments (water-column and porewater). I use Liebig's Law of the minimum to determine the limiting nutrient [nitrogen (N) or phosphate (P)] for growth: $f(N) = \min. (N, P)$.

$$(3) \quad d = (M+h)$$

where natural mortality (M) + herbivory losses (h) are estimated and the value used determined for each functional group from calibration experiments using the model (Table 1). The treatment of physiological death (M) should be regarded as a working simplification used to explain gross similarities in mortality resulting from a variety of causes (Lehman *et al.* 1975), and to simulate a phenomenon about which still little is understood. In addition, for the epiphytes and drift algae functional groups, there are additional components to g and d as follows:

$$(4) \text{ for epiphytes: } d_E = (M+h) \cdot \textit{turnover}$$

where *turnover* is a function of *Thalassia* biomass available as a suitable substrate and is defined in Fong and Harwell (1994).

After a series of preliminary model simulations, I recognized the importance of hydrodynamic transport in structuring drift algal distribution at the landscape level, and this factor was subsequently incorporated into the current model structure. For the drift algae this additional effect on biomass from hydrodynamic transport is expressed as:

$$(5) \quad dB_D/dt = (g-d)B_D + (I-E)$$

where I = biomass transported into the plot, and E = biomass transported out of the plot per time step. These are expressed as probabilities of hydrodynamic transport into or out of a plot based on prevailing hydrodynamic regime at a site and determined from field data. Biomass entering (I) is calculated as a random value between zero (no biomass) and $K - B_D$, the difference between the carrying capacity and the standing stock biomass present at that time step. This ensures that not more drift algae can enter than the maximum (K) allowable for a given scenario. Biomass leaving (E) is calculated as a random value between zero (no biomass) and B_D , the biomass present at that time step. This ensures that not more drift algae can leave than is actually present.

The simulation model was run under Stella ver. 5.1.1 (Hannon and Ruth 1994; Petersen and Richmond 1994), on a Macintosh Operating System. The model runs with a daily time step, using Runge-Kutta 4th order integration of the non-linear differential equations (Swartzman and Kaluzny 1987). All model runs were over a 3600 day period (i.e., 10 years), with stability generally occurring after about 250 days. The simulation was built up step-by-step, beginning with optimal growth for a single functional group, then the effects of less-than-optimal conditions for growth. The aim was to introduce a minimal number of assumptions and to find the simplest mathematical expression for each factor that was consistent with observation (Occam's Razor). New factors (e.g.,

hydrodynamic transport) were introduced only when it was clear that that the results of the simulation were not consistent with observation.

2. Parameterization

In this step of the modeling process, coefficients (Table 1) were inserted into the equations describing the functional relationships outlined above. The model was run initially under conditions descriptive of an oceanic environment, without stressors that occur under canal influence (Table 1). The environmental forcing-function equations are the same for all three models (oceanic, sheet-flow, and canal) but the parameter values used differ (Table 1). Light and temperature influence seasonal growth dynamics, while salinity and nutrients are important stressors from canal inputs and may modify growth of the algae; these two forcing functions vary spatially across the Bay, as well as temporally with seasonal changes in rainfall. Light, temperature, and salinity are simulated as sine functions:

$$(6) \text{ daily Env.} = \bar{X} + \{s.d. \cdot \sin[2\pi \cdot (\text{TIME} + \text{Delay})/360]\} \\ \pm \text{random (min., max.)}$$

The daily environment of L, T, or S is simulated using a mean (\bar{X}) and a standard deviation (*s.d.*) determined from environmental data at the study sites (see Chapters 3 and 4), as well as a stochastic component varying between the minimum and maximum values for that parameter seen at the study sites (see Table 1) to increase the model's realism. The *Delay* differs for each forcing function to fit the sine function closer to observed seasonal changes in L, T, and S, such that for light the maximum occurs in June and the minimum in December; for temperature the maximum is in August and minimum in February; and for salinity the maximum occurs in May, i.e., end of dry season, and minimum is in November, i.e., the end of the rainy season. Nutrients (both water-column and porewater N+P) are simulated by a mean and range determined from literature and field data (Table A1, Appendix) using a stochastic function based on a uniform random distribution:

$$(7) \text{ daily [Nutr.]} = \bar{X} \pm \text{random (min., max.)}$$

The parameters for the equations governing the biomass and growth responses of the three functional groups of algae were determined from the literature on seagrass habitats in Florida and nearby regions, experimental data, and calibration experiments using the model.

Table 1: Parameter values for environmental forcing functions expressed as range (average) at each location: canal, sheet-flow, and ocean sites. Starting conditions and parameters for each functional group. Differences in parameter values among locations are highlighted in bold text.

	Canal	Sheet-flow	Ocean
<u>Forcing Functions</u>			
Light ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	50-550 (300)	50-550 (300)	100-600 (350)
Temperature ($^{\circ}\text{C}$)	18-32 (25)	18-32 (25)	18-32 (25)
Salinity ($\text{g}\cdot\text{kg}^{-1}$)	0-40 (20)	10-35 (25)	28-38 (33)
N_{water} (μM)	5-50 (20)	5-25 (10)	2-5 (3.5)
P_{water} (μM)	0.05-0.2 (0.1)	0.05-0.2 (0.1)	0.05-0.2 (0.1)
$\text{N}_{\text{sediment}}$ (μM)	20-150 (50)	20-150 (50)	20-150 (50)
$\text{P}_{\text{sediment}}$ (μM)	1.0-2.5 (1.5)	1.0-2.5 (1.5)	0.5-1.5 (1.0)
<u>Drift</u>			
$\text{B}_{\text{initial}}$ ($\text{g}\cdot\text{m}^{-2}$)	40	40	40
K ($\text{g}\cdot\text{m}^{-2}$)	50	30	10
g_{max} (% day^{-1})	5.0-60 (10)	5.0-60 (10)	5.0-60 (10)
d (% day^{-1})	0.5-1.5 (1.0)	0.5-1.5 (1.0)	0.5-1.5 (1.0)
P (I)	0.6	0.46	0.18
P (E)	0.4	0.54	0.82
<u>Epiphytes</u>			
$\text{B}_{\text{initial}}$ ($\text{g}\cdot\text{m}^{-2}$)	50	50	50
K ($\text{g}\cdot\text{m}^{-2}$)	90	90	150
g_{max} (% day^{-1})	2.0-35 (15)	2.0-35 (15)	2.0-35 (15)
d (% day^{-1})	0.5-7.5 (1.0)	0.5-7.5 (1.0)	0.5-7.5 (1.0)
<u>Rhizophytes</u>			
$\text{B}_{\text{initial}}$ ($\text{g}\cdot\text{m}^{-2}$)	20	20	20
K ($\text{g}\cdot\text{m}^{-2}$)	25	10	60
g_{max} (% day^{-1})	2.0-9.0 (5.0)	2.0-9.0 (5.0)	2.0-9.0 (5.0)
d (% day^{-1})	0.5-1.5 (1.0)	0.5-1.5 (1.0)	0.5-1.5 (1.0)

Biomass and Growth - Drift algae are commonly found in South Florida, dominated primarily by *Laurencia poiteaui*, which can be locally abundant up to 250 g dry wt m⁻² (Josselyn 1977; Brook 1981). The initial value for drift algae biomass was set at the mean of 40 g dry wt m⁻² (Table A2). Maximum productivity of drift algae varies depending on geographic location and species present. Data for Florida and the Caribbean suggest that a value of 10% day⁻¹ is reasonable for natural populations (Table A3). Although productivity can be greater in intense culture situations (e.g., up to 60% day⁻¹ reported by Lapointe and Ryther 1978), natural populations are unlikely to ever reach this high level of productivity.

Epiphytes are a mixed group of species and functional forms (Harlin 1980). This functional group was most abundant by biomass, because of the density of *Thalassia* substrate; therefore, the initial biomass was 50 g dry wt m⁻² (Table A2). Growth rates are hard to determine for this group, but were hypothesized to be higher than for the other two groups based on functional-form considerations, and was set at 15% day⁻¹ (Table 1).

Rhizophytic algae reported from South Florida are mostly from the genera *Halimeda* and *Penicillus*. Biomass of this group was typically less than for the drift algae unless *Halimeda opuntia* was present as a dense mat within a sampling quadrat. The initial value for rhizophytic algae biomass was set at the mean of 20 g dry wt m⁻² (Table A2). Growth is slowest in this group because of investments in structural tissue and calcification (Littler and Littler 1980), with a value of 5% day⁻¹ typical in Biscayne Bay (Table A3).

Maximum biomass (K) for all three functional groups was determined from field data (see Chapter 2) and model calibration experiments to determine the best fit to the observed data.

Light - Photosynthetically active radiation (PAR) is important in determining productivity of macroalgae. The amount of available light is influenced by season, water depth, and

clarity. Several mathematical formulations of algal productivity (P) as a function of light intensity (I) have been proposed (see Duarte 1995 for a review); the formulation of Smith (1936) was reported to best fit data for marine macrophytes (Nelson and Siegrist 1987; Fourquaran and Zieman 1991).

Drift algae and epiphytes are ecologically important in seagrass ecosystems as they may reduce the amount of available light to the seagrass blades (Cambridge *et al.* 1986; Silberstein *et al.* 1986). Light-saturation values for photosynthesis in most sub-tidal species of algae lie around 150-300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Lobban *et al.* 1985). This corresponds to values found for all three functional groups (Table A4). Photo-inhibition was not reported in tropical sub-tidal drift and rhizophytic algae, even at high light levels (Littler *et al.* 1988; Dawes and Koch 1990). The saturation value for rhizophytic algae (250 $\mu\text{mol m}^{-2} \text{s}^{-1}$) lies between the I_k values for epiphytes (150 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and drift algae (300 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Fig. 2).

Temperature - Seasonal variations in temperature and light have been implicated in controlling the biomass of macroalgal components of seagrass communities (Fong and Harwell 1994). Temperature optima for drift algae and epiphytes lie in the range of 20-28°C (Table A5), which corresponds to the cooler water temperatures in November - May in shallow South Florida seagrass systems. Rhizophytic algae, in contrast, enjoy warmer summer water temperatures, with optima up to 34°C reported (O'Neal and Prince 1988), but have poor low-temperature tolerance (see Chapter 3). The temperature modifier curves (Fig. 2) show a rapid reduction in growth at high temperatures, with an upper lethal limit around 35-37°C for all three groups.

Salinity - Salinity is an important stressor in many South Florida estuaries because of numerous canals that discharge freshwater directly into these bays. Salinity can drop to

below 10 psu intermittently during the wet season (Fatt and Wang 1987) when freshwater discharge rates and volumes are high (see Chapter 4). Optimal salinity for the drift algae lies between 15-35 psu (Table A6), indicating this group is euryhaline and adapted to estuarine conditions. Epiphytes have a higher tolerance to hypersaline conditions (>35 psu) than drift algae, because of the numerous species that comprise this group (Fig. 2). The rhizophytic algae also prefer higher salinities with a sharp decline in productivity outside their optimal range of 20-35 psu (Fig. 2) indicating a stenohaline physiology in this group.

Nutrients - In general, tropical waters are characterized by low nutrient concentrations, favoring algae that can persist in low-nutrient environments, but can rapidly take up nutrients when they become available during periodic or episodic pulses from rainfall, runoff, or localized enrichment from fish excretion (D'Elia and DeBoer 1978; Fujita 1985). Water-column nutrients provide the only source of nutrients to drift algae and epiphytes, while rhizophytic algae have access to higher concentrations of sediment nutrients by translocation from the rhizomes to the fronds (Williams 1984). The relationship between nutrient concentration and growth is modeled as a Monod function (Vymazal 1995), and saturation coefficients (K_s) reflect the affinity of different groups to low nutrient concentrations (Fig. 2). Epiphytes are hypothesized to have the highest growth rates at low nutrients, because of rapid uptake and little structural tissues ($K_s = 5 \mu\text{M}$), drift algae are intermediate ($K_s = 10 \mu\text{M}$), and rhizophytic algae have the lowest K_s ($= 20 \mu\text{M}$) because of their ability to utilize high porewater nutrient concentrations (Fig. 2, Table A7).

Interactions between algae and seagrass - The linkage between this model and the Fong and Harwell (1994) seagrass model is provided by a light-attenuation function driven by epiphyte and drift biomass. Fong and Harwell (1994) hypothesized that increasing water-column nutrients, especially in high-irradiance shallow-water zones, results in increased

epiphytism, causing a decline in seagrass productivity and possibly an increase in the turnover of seagrass blades. Drift algae are hypothesized to act in a similar role to seagrass epiphytes, by reducing available light to the blades. Increased nutrient loading to estuaries and bays has been shown to increase drift algal biomass (Hauxwell *et al.* 2001; McGlathery 2001), which, coupled with increased epiphytism (Cambridge *et al.* 1986; Silberstein *et al.* 1986), could decrease seagrass productivity.

The light-reduction function proposed by Fong and Harwell (1994) was modified by incorporating drift biomass:

$$(8) \text{ Light attenuation} = L \cdot f(B_E + B_D)$$

where $B_D = 1 - B_D/K$ and is a function of percent cover of drift algae. If biomass = K, then 100% cover of drift algae occurs and no light penetrates through to the seagrass. If biomass < K, then light is available to the seagrass in some reduced quantity.

Epiphyte biomass is driven by the availability of *Thalassia* blades as a suitable substrate. Output of the Fong and Harwell (1994) seagrass model was used as an input for the epiphyte component. Epiphyte mortality is increased when *Thalassia* biomass declines:

$$(9) \ d = (d_E \cdot d_{substr})$$

where:

$$d_{substr} = f(B_{Thal})$$

$$B_{Thal} = B_{Thal} + B_{Thal} \cdot turnover$$

$$turnover = g_{Thal}/d_{Thal}$$

Turnover increases when growth of *Thalassia* declines, either from seasonal changes or environmental stressors. Substrate-dependent death rate of epiphytes (d_{substr}) increases up to 5 times normal levels as *Thalassia* biomass (i.e., suitable substrate) declines. This can be a result of reduced biomass (senescence), or increased turnover making the substrate more ephemeral.

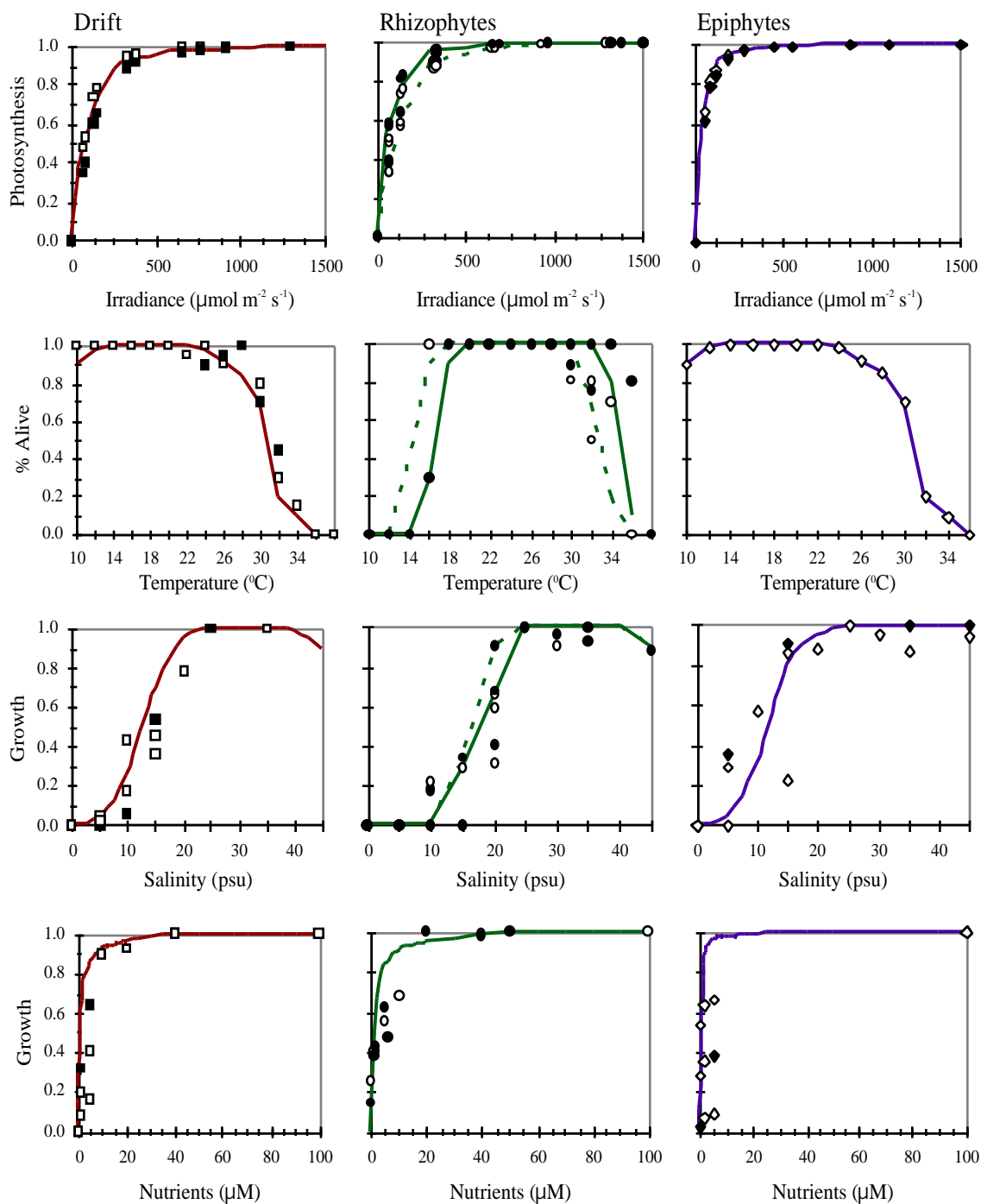


Fig. 2: Response functions of three functional groups of algae (drift algae, rhizophytic algae, and epiphytes) to light, water temperature, salinity, and water-column nutrient levels. All functions are expressed as scalar ratios from zero (= no growth) to one (= optimal conditions for growth). Filled and open symbols denote two separate experiments from which the response functions were determined. The light response curve is fitted using the P-I model of Smith (1936), and the nutrient response is fitted with a Monod function. Temperature and salinity responses use a line of best fit. For the rhizophytic group, the dashed line indicates data for *Penicillus*, and the solid line is *Halimeda*.

RESULTS

3. Calibration

Calibration is the estimation and adjustment of model parameters and constants to improve the agreement between model output and a data set (Jørgensen 1994; Rykiel 1996). Model calibration is in essence the step of making a model as consistent as possible with the data from which parameters are estimated. As this model was designed to simulate different regimes within Biscayne Bay, the first series of calibration experiments was done under oceanic conditions, and subsequently canal and sheet-flow environments were investigated (see Table 1).

Field and literature data were used to determine initial biomass and K at each site, with the values adjusted until a good visual agreement between field data and model output was obtained (Fig. 3). Experimental and literature data were used to parameterize the environmental responses (see Chapters 3-6) and to define the scalars for each functional group (Fig. 2). To make the model stochastic, the growth and death parameters for each functional group were defined as a mean and a random distribution between a minimum and maximum value determined from the literature (Table A3). Some parameters that were not measured (e.g., senescence, seagrass turnover) were estimated and varied to better the observed fit of the model with the field data. Finally, a delay was added to the growth of the drift algae of 60 days, and 90 days for rhizophytic algae, while the epiphytes showed no delay in growth; this is a reflection of the time between exposure of individuals to a stimulus and the response of the 'population' at the spatial scale (1m^2) being modeled, i.e., a lag induced by physiological processes within the plants and the resultant turnover to biomass at this spatial scale.

The model was run with all three functional groups simultaneously, using the formulations from Fong and Harwell (1994) for *Thalassia*. Model output for each functional group in each regime (total of nine plots) is shown in Fig. 3. The simulated data

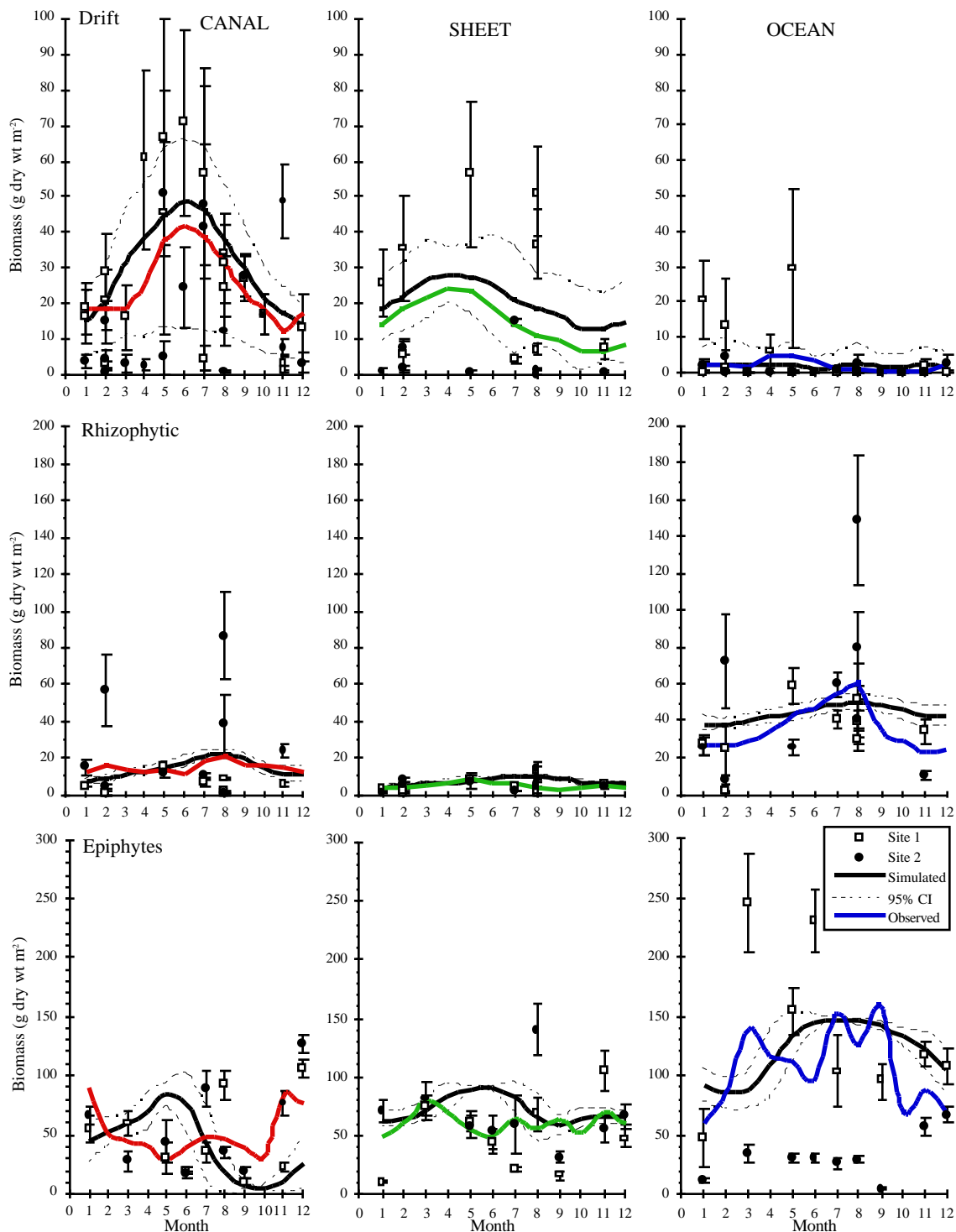


Fig. 3: Plots of simulated (black line) vs. observed (colored line) biomass at two sites in three salinity regimes (ocean, sheet-flow, canal) for three functional groups of algae (drift, rhizophytes, epiphytes). Observed data points are mean \pm S.E. of biomass data from 1m² quadrats collected at 2 sites per regime (n=24-40) from 1996-99 (see Fig. 8, Chapter 2). Simulated (mean \pm 95% CI) biomass is from 27 years of model output.

trace is compared with observed field biomass measures obtained over a number of years for two sites in each regime (see Chapter 2).

Drift: For drift algae, the modeled biomass declines from canal ($45 \text{ g dw}\cdot\text{m}^{-2}$) to oceanic sites ($<5 \text{ g dw}\cdot\text{m}^{-2}$). The highest average biomass is simulated in June at the canal sites, and May in sheet-flow sites, while the oceanic site is dominated by random variation arising from hydrodynamic removal of biomass (Fig. 3). The seasonality predicted by the model and shown by the field data indicates that drift algae in nearshore freshwater-influenced regimes (canal, sheet-flow) are most abundant in the late spring, early summer, and then decline because of higher water temperatures and possibly reduced salinities (Fig. 3). The population lags behind seasonal changes by about 60 days.

Rhizophytic: biomass shows the smallest seasonal change ($10\text{-}15 \text{ g dw}$) of the three functional groups (Fig. 3). The oceanic site has the highest biomass of rhizophytic algae ($50 \text{ g dw}\cdot\text{m}^{-2}$), followed by the canal ($25 \text{ g dw}\cdot\text{m}^{-2}$), while the sheet-flow sites have the least ($<10 \text{ g dw}\cdot\text{m}^{-2}$). In all three regimes, simulated biomass is highest in the summer (Aug.), and lowest in the winter (Jan.), a seasonal response that has been reported previously for this functional group (Bach 1979; Wefer 1980; Garrigue 1991)

Epiphytes: are the most abundant functional group by weight, with $150 \text{ g dw}\cdot\text{m}^{-2}$ at the oceanic site, and about $100 \text{ g dw}\cdot\text{m}^{-2}$ in both the canal and sheet-flow sites (Fig. 3). The seasonal response of this group was determined in large part by the tolerance of its substrate *Thalassia* to environmental stressors, particularly reduced salinity. At the oceanic sites, epiphyte biomass is highest summer when *Thalassia* standing stock is highest (Fig. 3). In the sheet-flow and canal sites, biomass of *Thalassia* is reduced during the summer because of low salinities from freshwater runoff during the summer rainy season. The lack of suitable substrate results in reduced biomass of epiphytes during this period (Fig. 3). Epiphyte biomass in these two regimes is highest during the spring, when turnover of *Thalassia* blades is high, resulting in an abundance of suitable substrate.

From the visual assessment of the observed points with the predicted time-series, it appears that the model does a good job of simulating the drift and rhizophytic functional groups, but less so for the epiphytes; however, this needs to be addressed more rigorously using validation procedures (Botkin *et al.* 1972; Jørgensen 1994).

4. Validation

In the validation stage the model predictions are compared to independent field observations (Jørgensen 1986, 1994). A number of statistics measure how well model-generated and real-system data compare (Naylor *et al.* 1966; van Horn 1971; Power 1993). A model is considered to be valid if it matches data measured from a real system and reproduces behavior in a way that can be construed as being reflective of the operating characteristics of the real system (Ziegler 1976; Shugart 1984; Rykiel 1996), i.e., does the model mimic the real world well enough for its stated purpose (Giere 1991)? Models are generally validated for the normal circumstances in which they are expected to be applied, and such validation is presumed inapplicable if the model is run outside this domain (Rykiel 1996). The validation process is analogous to the normal scientific process, where hypotheses are subjected to more and more rigorous tests (Popper 1959, 1962). Accordingly, validation increases model utility by increasing user confidence (Power 1993). It is, however, a perilous myth to believe that validation can unquestioningly establish the truth of a model; at best models can be shown to be credible (Holling 1978; Harrison 1990; Power 1993). Validation indicates the model is acceptable for use, not that it embodies any absolute truth, nor even that it is the best model available.

For the model to be validated the purpose, criteria for acceptable use, and context for operation of the model need to be stated (Rykiel 1996). The purpose of this model is to synthesize the knowledge of algal autotrophs in tropical seagrass systems by simulating biomass change with seasonal and stressor inputs. The model is currently deemed

acceptable for use over the domain in which it has been tested, i.e., conditions similar to those present within Biscayne Bay.

Often validation is determined subjectively by a statement that extols the visual goodness-of-fit (Law and Kelton 1991; Mayer and Butler 1993; Rykiel 1996; Giordano et al. 1997). Increasingly statistical metrics are employed to determine rigorously the fit between modeled output and observed data (Mayer and Butler 1993; Power 1993; Smith and Rose 1995). To compare observed with predicted values for validation, the output data were sub-sampled by randomly picking a day in each month from day 366-3650 of the output. This was assumed to be a “sampling” date, and so the same day was used in each model output across the three regimes. These simulated monthly biomass values ($n=27$) were compared with biomass data collected from the field in observed (Y) vs. predicted (X) plots (Fig 4). Both the $Y = X$ line of perfect correspondence and the fitted regression line to the data points are shown to compare model fit with a perfect fit (Mayer and Butler 1993).

The modeled data fit the observed points well ($r^2 > 0.80$) for the sheet-flow and oceanic site, but poorly at the canal site ($r^2 < 0.13$) (Fig. 4, Table 2). This is because of the scatter of the epiphytes at the canal site, compared to the other two regimes (Fig. 4). When simulated data from the three sites are plotted simultaneously against observed values, both drift algae and rhizophytes fit the regression line well, and this regression has an $r^2 = 0.76$ (Fig. 4, Table 2). In the canal and sheet-flow sites, drift algae were more abundant than rhizophytic algae, whereas in the oceanic site the opposite was true. In contrast, the epiphytes were always the most abundant functional group in all three sites (Figs. 3&4). However, the simulated epiphyte biomass fit the field data poorly, probably because of the underlying seasonal response of *Thalassia* in the model. Seasonal changes in epiphyte substrate occur with reductions in *Thalassia* biomass in winter as a response to lower water temperatures, and in summer at canal and sheet-flow sites as a response to lowered salinities present during the wet season (Fig. 3).

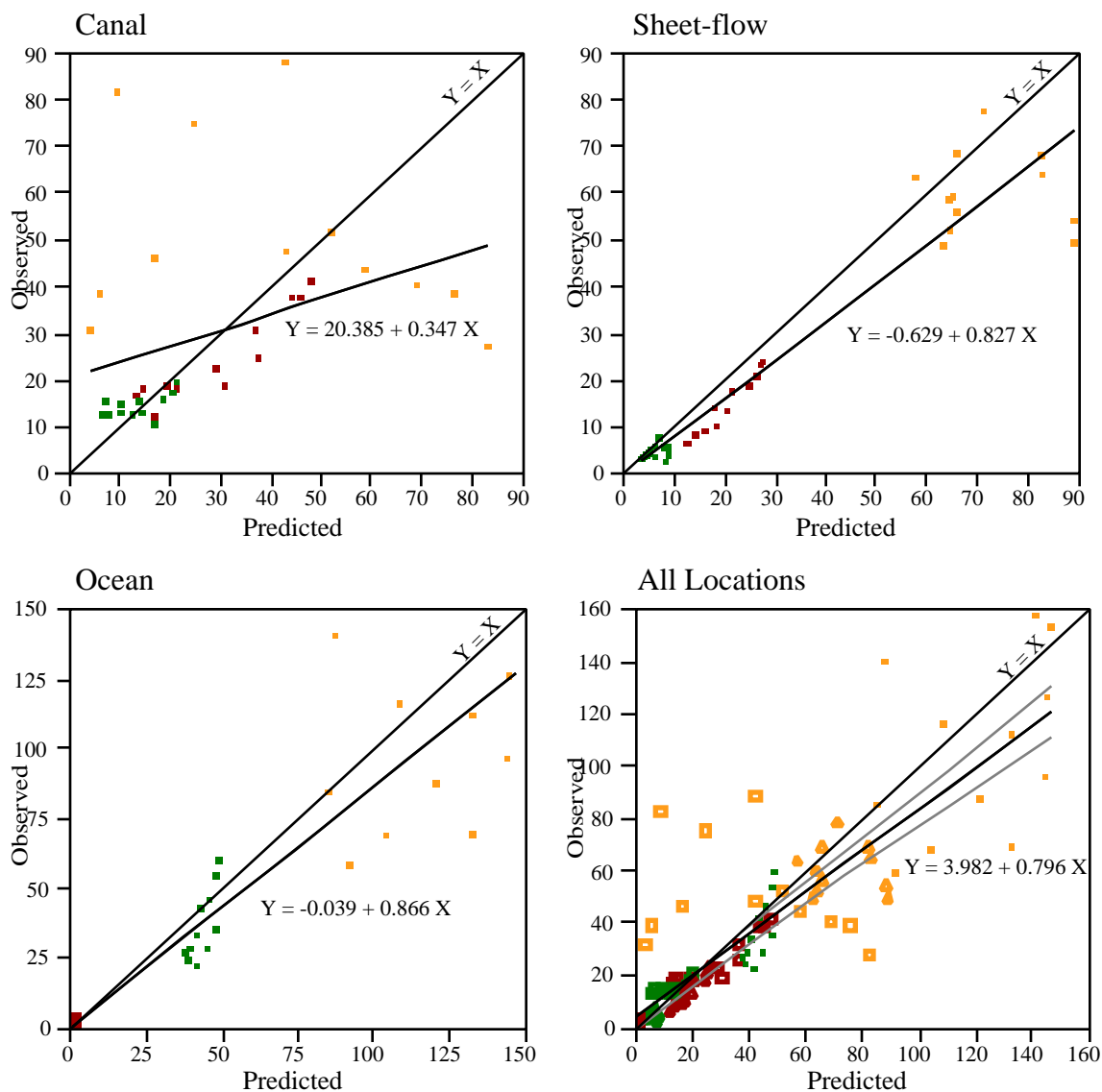


Fig. 4: Observed vs. Predicted plots of model output for the three locations. For reference a perfect fit would be indicated by all the points falling on the line $Y=X$. Linear regressions performed on the same data to show the line of best fit to the points. Brown points = drift algae, green points = rhizophytic algae, yellow points = epiphytes. Symbols on the plot of All Locations are: open squares = canal sites, triangles = sheet-flow sites, dots = oceanic sites.

We cannot always assume that the data accurately represent the real system and therefore constitute the best test of the model (Rykiel 1996). The relative inaccuracy and imprecision of ecological data place limits on model testability. Obviously computer simulation programs cannot be expected to provide results that are more accurate and precise than the data that are available. Conversely, it can be argued that the model may be a

better representation of reality than the data that are limited by our ability to measure and are subjectively biased by our perceptions of the system (Rykiel 1996). Practically all simulation models contain unobservable quantities, quantities that can only be observed with significant error, and calculations that cannot be compared with data because no data exist (Rykiel 1996).

Simulated data were paired with the observed biomass measures and differences between these values and their relationship were examined statistically using deviance measures. The following deviance measures were calculated for each model (Mayer and Butler 1993; Power 1993): mean absolute error (MAE), mean square error (MSE), root mean square error (RMSE), mean absolute error relative to the observed mean (MAE/\bar{y}), root mean square error relative to the observed mean ($RMSE/\bar{y}$), as well as the statistical metrics: Theil's inequality coefficient (U), and the modeling efficiency (EF). Theil's U (Theil 1958) is based on prediction error, the difference between matched pairs of observed vs. predicted values. Modeling efficiency (EF) is a dimensionless statistic that directly relates model predictions to observed values, and is interpreted as a proportion of the variance explained by the fit of the simulated data to the $Y=X$ line (Loague and Green 1991). For a perfect fit $EF = 1.0$, and the degree of fit declines as the statistic falls away from unity (Mayer and Butler 1993).

The metrics EF, MSE and RMSE indicate differences in the ability of a model to fit the observed data Elliot *et al.* (2000). Theil's U is heavily influenced by real data values that tend towards zero when combined with a few values of higher magnitude (Elliot *et al.* 2000). MSE and RMSE are ostensibly the same; MSE is easier to use as its values are larger, and thus differences among models are easier to identify. Of all the statistics, EF is both simple to understand and powerful in providing information upon the relationship between the model output and the real data Elliot *et al.* (2000). EF is preferred over the other metrics because of the similarities of EF to r^2 (correlation coefficient).

Based on the reported statistics, the model fit the sheet-flow observations best (Table 2). The exception was modeling efficiency, which was highest at the oceanic site (Table 2). Looking at the output by functional group, i.e., across models, it is apparent that the simulations performed best for the drift algae functional group (Table 2). Rhizophytes were more favored by the MAE/\bar{y} statistic; however, the value of this statistic varies very little among models, and so may not be as sensitive as other measures to the fit of the model (Table 2).

Table 2: Summary validation statistics^a and linear regression statistics^b applied to the plots in Fig. 4 as well as the three functional groups. For the validation statistics, the value that is closest to a “perfect fit” by location and functional group is in italics. For the regression statistics, significant results at $\alpha = 0.05$ are highlighted in bold.

Statistic	All Loc.	Canal	Sheet	Ocean	drift	rhizoph.	epiphytes
MAE	11.636	14.358	<i>7.245</i>	13.306	<i>4.420</i>	5.364	25.124
MSE	360.004	526.165	<i>121.946</i>	431.902	<i>29.342</i>	55.639	995.032
RMSE	18.974	22.938	<i>11.043</i>	20.782	<i>5.417</i>	7.459	31.544
MAE/ \bar{y}	0.334	0.476	<i>0.273</i>	0.278	0.320	<i>0.294</i>	0.346
RMSE/ \bar{y}	0.544	0.760	<i>0.416</i>	0.434	<i>0.393</i>	0.409	0.434
U	0.350	0.657	<i>0.252</i>	0.276	<i>0.242</i>	0.278	0.362
EF	0.697	0.350	0.808	<i>0.810</i>	<i>0.984</i>	0.967	0.722
r^2	0.7599	0.1283	<i>0.9103</i>	0.8548	<i>0.9397</i>	0.8272	0.4053
a (P> t)	0.0935	0.0006	0.7497	0.9933	0.8748	0.6011	0.0027
b (P>F)	<0.0001	0.0319	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

^aMAE = $(\sum |y_i - \hat{y}_i|) / n$, mean absolute error; MSE = $(\sum (y_i - \hat{y}_i)^2) / n$, mean square error; RMSE = $(MSE)^{0.5}$, root mean square error; RMSE/ \bar{y} , general standard deviation; U, Theil's inequality coefficient; and EF, the modeling efficiency; where y = observed data, \hat{y} = predicted/ simulated data, and $\bar{y} = (\sum y_i) / n$.

^b r^2 , correlation coefficient; a, probability of t-test of intercept = 0; b, probability of simultaneous F-statistic for intercept = 0 and slope = 1.

The regression line fitted to the data points indicated agreement between observed vs. predicted at $r^2 > 0.75$, except for the epiphytes and the canal site (Table 2). The highest agreement between the model and the field data was at the sheet-flow sites and for the drift algae, with both the variation explained is greater than 90% (Table 2). The canal site has the poorest prediction, with less than 13% of the variability explained (Table 2). As is

evident from the observed vs. predicted plots, this is due to the seasonal dynamics of the epiphytes not agreeing closely with the observed time trace (Chapter 2, Fig. 6). As the field data does not show any of the underlying *Thalassia* dynamic, I suggest that the poor fit of the model may occur because of the high variability in the epiphyte field data, leading to a less robust observed time trace than for the other functional groups. In all the regression models, the slope is significantly different from zero ($P < 0.03$). The intercept is not significantly different from zero, except for the canal site at $= 0.05$ (Table 2).

These results suggest that the model is a useful tool to aid in understanding the effects of seasonal and stress-related effects from freshwater inputs on the dynamics of macroalgae within *Thalassia* habitats in Biscayne Bay and similar systems. The model fits observed data closely for most regimes, and where it does not (canal) is likely due to the low confidence in the observed data points, rather than the model simulation.

5. Sensitivity analysis

Sensitivity analysis is the process of varying model parameters and comparing the results against another simulation in which all other variables are the same, except for the sensitivity parameter (Miller 1974; Fong and Harwell 1994). This process identifies the model parameters, structures, empirically derived input information, and initial conditions that cause the greatest change in model predictions (Miller 1979; Fong *et al.* 1997). Those parameters that cause significant changes in the model's behavior should be estimated with the greatest accuracy.

Sensitivity analysis of eutrophication models have shown that maximum growth of algae is an important parameter to assess with high accuracy (Jørgensen 1986). Other parameters with a high degree of uncertainty, because of a lack of knowledge, include: mortality estimates, seagrass turnover function on epiphyte mortality, and K (the maximum biomass, which was found to be important in the calibration phase).

The sensitivity analysis was conducted in four parts. First, model predictions under oceanic conditions were analyzed for sensitivity to a 10% change in initial biomass, maximum biomass (K), maximum growth rate, and senescence rates for each functional group. Second, sensitivities to the functional group-specific terms, namely epiphyte substrate-dependent mortality (a function of *Thalassia* biomass), and drift algal hydrodynamic-transport removal, were investigated by altering the magnitude (by 10%) of each function in successive runs. Third, the sensitivities of each functional group to changes in their environmental response functions to light, temperature, salinity, nitrogen and phosphorus were tested by shifting the response curve optimum to the left (lower optimum range) or the right (higher optimum range) by approximately 10% of the range (for temperature this equals a $\pm 3^\circ\text{C}$ shift); this varied somewhat depending on the interval and range of each environmental parameter. Fourth, the entire suite of 60 sensitivity runs was repeated under canal conditions, to assess the impact of the altered environmental conditions on model output.

To assess the effects of changes over an entire year, the daily productivity predicted by the model for each algal group for year 2 of the three-year simulations was summed, also the range (max.-min.) and mean were calculated. These statistics were then used to calculate the relative change in the model output. Sensitivity for each group was calculated as percent relative change from the baseline (Jørgensen 1986; Fong *et al.* 1997):

$$(10) \text{ rel. change } X = 100 \cdot (\text{rerun } X - \text{baseline } X) / \text{baseline } X$$

where *baseline* X = the statistic for predicted productivity for algal group X in the baseline model, and *rerun* X = the statistic for predicted productivity for algal group X when a model parameter was changed by 10%. The summed daily productivity reflects the cumulative change in biomass over a year, mean indicates any systematic change and the magnitude between the baseline and the sensitivity rerun, and finally, the range is

Table 3: For the oceanic model, change in three statistics related to predicted productivity for changes in each of the three functional groups, with the sensitivity parameter that was altered. A change of >10% +, >25% ++, >100% +++, and 0 indicates no change in the model output from the baseline scenario.

	SUM = MEAN			RANGE		
	Drift	Epi	Rhizo	Drift	Epi	Rhizo
<u>Drift</u>						
Ib x1.1	+			+		
Ib x0.9	0			0		
K x1.1	++			++		
K x0.9	-			-		
gr x1.1	+			++		
gr x0.9	0			-		
dr x1.1	0			+		
dr x0.9	+			++		
P(E) = 100	--			-		
P(E) = 82	0			0		
P(E) = 61	+			+		
P(E) = 41	+++			+++		
<u>Epiphytes</u>						
Ib x1.1		0			0	
Ib x0.9		0			0	
K x1.1		++			++	
K x0.9		--			-	
gr x1.1		+			-	
gr x0.9		-			0	
dr x1.1		-			+	
dr x0.9		+			-	
turnover x1.1		+			+	
turnover x0.9		-			0	
<u>Rhizophytes</u>						
Ib x1.1			0			+
Ib x0.9			0			-
K x1.1			++			++
K x0.9			-			--
gr x1.1			+			++
gr x0.9			-			-
dr x1.1			-			-
dr x0.9			+			+

Ib = initial biomass, K = “carrying capacity”, gr = max. growth rate, dr = mortality, P(E) = probability of drift removal, turnover = seagrass blade substrate-dependent mortality for epiphytes.

Table 4: For the canal model, change in three statistics related to predicted productivity for intrinsic changes in each of the three functional groups, with the sensitivity parameter that was altered. A change of >10% +, >25% ++, >100% +++, and 0 indicates no change in the model output from the baseline scenario.

	SUM = MEAN			RANGE		
	Drift	Epi	Rhizo	Drift	Epi	Rhizo
<u>Drift</u>						
Ib x1.1	0			0		
Ib x0.9	0			-		
K x1.1	+			+		
K x0.9	-			-		
gr x1.1	+			0		
gr x0.9	0			0		
dr x1.1	-			+		
dr x0.9	0			0		
P(E) = 0	0			0		
P(E) = 20	0			0		
P(E) = 40	0			0		
P(E) = 70	0			0		
<u>Epiphytes</u>						
Ib x1.1		0			0	
Ib x0.9		0			0	
K x1.1		+			+	
K x0.9		-			-	
gr x1.1		+			0	
gr x0.9		-			0	
dr x1.1		-			+	
dr x0.9		+			0	
turnover x1.1		++			+	
turnover x0.9		--			-	
<u>Rhizophytes</u>						
Ib x1.1			0			0
Ib x0.9			0			0
K x1.1			+			+
K x0.9			-			-
gr x1.1			+			+
gr x0.9			-			-
dr x1.1			-			-
dr x0.9			+			+

Ib = initial biomass, K = “carrying capacity”, gr = max. growth rate, dr = mortality, P(E) = probability of drift removal, turnover = seagrass blade substrate-dependent mortality for epiphytes.

indicative of changes in the seasonal amplitude (max.-min.) over the course of the year simulated. The relative (%) change in the sum and mean are identical, as mean is a scalar of sum (by a factor of n^{-1}); therefore, only the mean and range were reported for the two regimes (Tables 3&4).

Biomass and Growth - The results of the sensitivity analysis on the intrinsic growth parameters (Tables 3&4) showed increasing growth and reducing death rates resulted in increased biomass of all three functional groups in both the oceanic and canal sites (Tables 3&4). The range (seasonal changes) for the drift algae increased in the oceanic model, but not in the canal model; the range for the epiphytes decreased in the oceanic model while it stayed the same in the canal model; the range for the rhizophytic algae increased with increasing mean and decreased with decreasing mean in both models, indicating that the mean and range were not independent. The maximum biomass (K) affected both the mean and the range in all three functional groups in both the oceanic and canal models. This factor was determined from calibration runs for each group at each site, so it is important to determine the sensitivity of this parameter on model performance. Changes in K of a factor of 10% resulted in a greater than 25% increase in the simulated output for the three groups in the oceanic model, but only a 10% increase in the canal model (Table 4). An increase in K caused an increase in both the mean and the range, while reducing K resulted in a decrease in both parameters, indicating a change in both magnitude and amplitude of the simulated daily productivity.

For the drift algae, hydrodynamic transport, P(E), and for the epiphytes, turnover, were parameters with a consequential effect on predicted biomass. The drift algae were highly influenced by the P(E) parameter in the oceanic site, reflecting the importance of water motion in local biomass dynamics. An increase in the probability of removal, P(E), resulted in increased removal of drift algae, while successive reductions in P(E) caused the model to predict large increases in drift abundance at the oceanic site (Table 3). There were

no changes greater than $\pm 10\%$ biomass with changes in $P(E)$ at the canal site. A simulation that predicted no net removal of drift ($P(E) = 0$) predicted the same relative change in model output as the simulation where $P(E) = 70\%$ of the biomass was removed (Table 4). Also, the magnitude of the changes with variations in $P(E)$ were less than $\pm 10\%$, indicative of the lesser importance of hydrodynamic transport at the canal site, relative to seasonal changes, in predicting drift algal biomass dynamics.

The turnover parameter influences the epiphyte death rate, already shown to be an important parameter, by increasing mortality when *Thalassia* is less abundant. Not surprisingly, the turnover parameter (mean and range) was more sensitive at the canal site, because of the sensitivity of *Thalassia* to environmental conditions (salinity) at this site. The same magnitude change in the turnover parameter caused less of a change in epiphyte biomass at the oceanic site compared to the canal site (Tables 3&4).

Light - The sensitivity of the three functional groups to changes in their environmental response functions at both sites is plotted in Figure 5. Altering the response to ambient PAR resulted in no notable change in the ocean model, but did result in changes in the canal model. The canal site typically experiences lower light levels than the oceanic site; shifting the optimal tolerance curve for light to the left (-10%) resulted in increased drift biomass (43.7%), as well as epiphyte and rhizophytic biomass, whereas an increase in the optimum to the right ($+10\%$) resulted in a reduction in biomass of all three groups, with epiphytes reduced by 46.6% (Fig. 5). Concomitant changes in the range were only evident in the drift algae at the canal site, with a higher range corresponding to the higher mean, or a reduced seasonal range in biomass with a reduction in the mean annual biomass present (Fig. 5). While the rhizophytic algae at the oceanic site did not show any significant change in the mean, the range declined 34.3%, indicating a reduction in the amplitude of the seasonal biomass dynamic with a shift to higher light requirements.

Temperature and Salinity - Changes to the temperature optima did not cause much of a difference (<24%) to the mean biomass of any of the functional groups at either site (Fig. 5). However, the range was reduced for both the drift and rhizophytic algae at the canal site, while it was increased in both groups at the oceanic site. Salinity is an environmental factor that differed greatly between oceanic and canal models and was hypothesized to be one of the major factors influencing community structure. Shifts in the optimal salinity range did not affect biomass under oceanic conditions, where salinity remains high. In contrast, algal biomass of all three groups in the canal site was positively influenced when salinity tolerance was shifted to simulate better tolerance to lower salinity (-10%), especially in the drift algae, resulting in an increase in mean annual biomass of 32.5% for this functional group (Fig. 5). Corresponding to these changes in mean drift biomass at the canal site were larger magnitude changes in the seasonal range, but in opposing directions, i.e., as mean biomass increased, the range declined, and vice versa (Fig. 5). This systematic shift resulted in higher simulated productivity for the drift algae when they were more tolerant of reduced salinity, while the opposite was true if poorer tolerance to low salinity levels were considered. The rhizophytic algae, which are considered stenohaline, did not show any increase in biomass under improved low salinity tolerance, possibly because the 10% change was not enough to significantly alter the modeled productivities under the low salinities encountered in the canal sites.

Nutrients - The two nutrients, N and P, are present in higher concentrations at the low-salinity canal site as a result of increased terrestrial loadings. Changes in N responses did not alter the mean biomass of any of the three functional groups in the high nutrient canal site. In the low-nutrient oceanic site, the epiphytes completely disappeared, reflected in the 89.6% reduction in the range, after the nitrogen-uptake function was shifted to higher nitrogen requirements (Fig. 5).

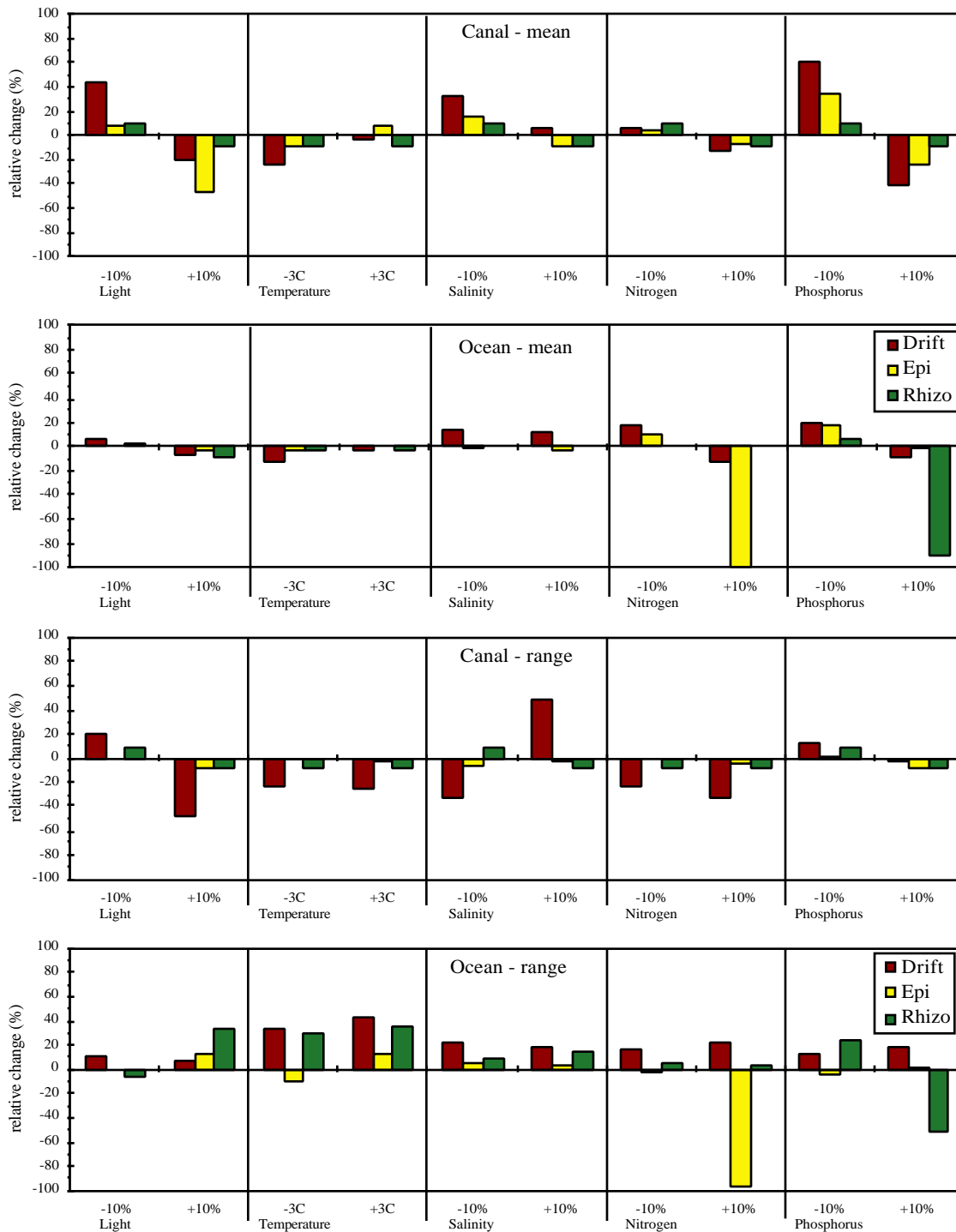


Fig. 5: Relative change (percent) in environmental response-functions for three functional groups of algae in two salinity regimes. For both regimes the relative change from the baseline condition in the mean predicted annual biomass and the range (an indicator of seasonal changes) are plotted. Response functions were shifted to the left (-10%) to create a lower optimum, and to the right (+10%) for a higher optimal zone of tolerance to a particular environmental parameter.

Phosphorus is often touted as being the limiting nutrient in tropical waters (Lapointe 1987b; Lapointe *et al.* 1992), and the increased biomass of all three groups in both canal and oceanic conditions with a lower P optimum lends some support to this observation. P-limitation is apparently more severe in the nitrogen-rich canal site, as evidenced by the greater increase in mean productivity compared to the oceanic site for the same downward shift in P-uptake optima (Fig. 5). The reduction in rhiziphytic algal biomass in the oceanic site, where P is low, when the optimum is shifted upward, also indicates that this group is dependent on its ability to take up P at very low environmental concentrations. Changes in the seasonal range are negligible for the canal site, and most affect the rhiziphytic group in the oceanic site. Shifting the P uptake to lower concentrations (-10%) increases the range 23.9%, while reducing the ability to take up P at low concentrations (+10%) results in a decline in the seasonal range of 52.8%, mirroring the results for the reduction in mean annual biomass of 91.1% (Fig. 5).

The sensitivity analysis highlighted the importance of intrinsic growth parameters, the functional group-specific terms of drift hydrodynamic transport and epiphyte-substrate turnover rates, and the optimal response range towards environmental parameters on model performance under two extremes found in Biscayne Bay. The results are complex, but the assessment of the magnitude of the change in model output compared to baseline conditions agrees with what is known about the system, and highlights the need for high-quality data to simulate adequately some of the interactions occurring among environmental forcing functions and algal physiological and population responses, which determine community and landscape characteristics evident in different regions of the Bay.

DISCUSSION

Algal Simulation Models

Algal growth is one of the most intensely modeled aquatic biological processes, as it is the most important submodel in eutrophication models (Jørgensen 1986). Concern with

the environment has prompted the development of ecological models for environmental management since the 1960's (Jørgensen 1986; Schnoor 1996). Algal models in the literature are of two basic types: matrix models that represents processes at the population level (e.g., Åberg 1992a, 1992b; Ang and de Wreede 1990, 1993), and physiological models that represent the relationship between productivity and different physical and chemical factors (Pregnall and Rudy 1985; Jørgensen 1986; Ferreira and Ramos 1989; Gordon and McComb 1989; Bendoricchio *et al.* 1993; Fong *et al.* 1994b; Guimaraens 1999).

One successful early model formulation based partly on physiological parameterization are gap-phase models (Botkin *et al.* 1972; Shugart 1984, 1998), which have spawned a multitude of similar formulations in all ecosystem types. Gap-phase models feature simple protocols for estimating model parameters (Botkin *et al.* 1972, Shugart 1984). The models have simple rules for interactions among individuals (e.g., shading, nutrient competition), and equally simple rules for birth, death, and growth resulting in an ease of estimating model parameters (Shugart 1998). Applications that have used this type of physiological parameterization approach to simulating marine macrophytes include Lehman *et al.* (1975) paper on modeling phytoplankton dynamics, a seagrass model by Fong and Harwell (1994), and a recent suite of studies on *Ulva* (Bendoricchio *et al.* 1994; Coffaro and Sfriso 1997; Solidoro *et al.* 1997), as well as this study.

Many macrophyte models treat autotrophs as a single unit (e.g., Fong and Harwell 1994; Kemp *et al.* 1995; Madden and Kemp 1996), without regard for differences among species in their relationship between maximum photosynthesis and light intensity, or species-specific differences in nutrient-uptake efficiencies (Lehman *et al.* 1975). Alternatively, in some models only a single species is simulated (e.g., Bendoricchio *et al.* 1994; Coffaro and Sfriso 1997; Solidoro *et al.* 1997; Guimaraens 1999; da Silva and Asmus 2001), and community-level changes in composition are not considered. In this study I have applied aspects of both approaches, by aggregating species of macroalgae with

similar physiology into functional groups, while parameterizing the component models from data on one, or a few closely related species. One test of the similarity among species within a functional group in this model could be applied by separating the experimental data obtained for *Penicillus* and *Halimeda*, both representatives of the rhizophytic algae functional group. Also, enough literature data exist to parameterize a separate drift model using data for *Gracilaria* (P. Biber, unpubl. manu.). However, there has been little effort to date to simulate the numerous individual species in a community and little attempt to model changes in species composition during cultural eutrophication (but see Coffaro *et al.* 1997), which is addressed in this model.

Aggregation

The aggregation often found in ecosystem models is necessary to avoid cumulative errors associated with the estimation of a large number of parameters, and to reduce model complexity (Rastetter *et al.* 1992). Because of the impracticality of handling large numbers of fine-scale components individually, they are generally lumped into aggregated components (e.g., functional groups) and treated collectively (Rykiel 1996). The problem with this is that the aggregated group does not generally behave the same way as the fine-scale components (e.g., species) from which it is constituted (O'Neill 1979; Rastetter *et al.* 1992). Further, fine-scale mechanisms such as photosynthesis and nutrient-uptake kinetics in different species, tend to have high-frequency, transient behaviors that are damped in the aggregate (Caughley 1982; Cale and Odell 1980), in this case algal production per unit area. However, the loss of accuracy introduced by aggregation must be balanced against a loss in precision through the accumulation of errors associated with the estimation of large numbers of parameters in complex models, and the loss of model transparency and understanding when many equations are incorporated to describe the fine-scale processes (O'Neill 1973, 1979; Rastetter *et al.* 1992).

Aggregation was a necessary approach in this study because there are over 200 species of algae that are present in Biscayne Bay (Humm 1963, 1964), including approximately 70 species of drift and rhizophytic algae. With this large number of species, it is impossible to model separately the dynamics of each, especially as the ecology of most remains yet to be investigated. Furthermore, many of the species have similar ecological roles in the seagrass ecosystem and can be placed into the three functional groups described in the model.

Model Limitations and Suggested Refinements

This model has also made obvious areas for which information on tropical macroalgal ecology is lacking, particularly factors involved with population demographics such as: birth and recruitment (no data available), and physiological death (little data, but estimable by model calibration). In the literature only a few studies to date have addressed the importance of recruitment to algal dynamics (Clifton and Clifton 1999; Lotze 1998; Lotze *et al.* 2000). The senescence or decay process and other factors contributing to loss rates, e.g., grazing and sporulation, have also been less studied than production (Lehman *et al.* 1975; Coffaro and Bocci 1997; Salomonsen *et al.* 1997). This may be a methodological problem, as growth is an intrinsic property of an organism, and therefore more easily isolated and measured under controlled laboratory conditions, while loss rates are often controlled by external, habitat-specific factors that may be difficult to reproduce under controlled conditions (Salomonsen *et al.* 1997).

The Monod nutrient-response formulation was used in this model because of the lack of information on uptake kinetics and nutrient cell-quotas for most tropical macroalgal species. The generally accepted two-step nutrient-dynamics formulation of Michaelis-Menten uptake kinetics, coupled with a Droop formulation for growth (Dring 1982; Vymazal 1995; Borchart 1996), is widely used in temperate models of algal dynamics where seasonal nutrient inputs with spring and summer blooms in biomass are prevalent (e.g.,

Bendoricchio *et al.* 1994; Kemp *et al.* 1995; Solidoro *et al.* 1997) as well as in a recent model for tropical species under upwelling conditions (Guimaraens 1999). The incorporation of a two-step nutrient dynamic allows these models to mimic such subtle observations as luxury uptake and starvation-induced changes in nutrient cell quotas, resulting in time lags between water-column nutrient availability and biomass production (Lehman *et al.* 1975; Fong *et al.* 2001). This can be important for enclosed bodies of water where introduced N and P can disappear from the water column from the rapid uptake by algae, and the subsequent bloom formation of drift and epiphytic species (Madden and Kemp 1996; Coffaro and Bocci 1997; Coffaro and Sfriso 1997; Valiela *et al.* 1997). Further, this type of mathematical formulation is important for models that attempt to simulate resource competition among groups of species, because it mimics physiological processes important in nutrient uptake and growth dynamics (Fong *et al.* 1994; Tilman 1977, 1982). Unfortunately, the lack of data precluded the use of this type of approach in my model.

Coefficients in the algal response-functions to light and nutrient uptake, such as I_k and K_s , are treated as constants, even though they are not strictly so in nature (Lehman *et al.* 1975). Although this treatment is simplistic compared to the real-world situation, they are none-the-less basic to a predictive model of algal dynamics (Lehman *et al.* 1975; Cloern 1977; Keller 1989; Fasham *et al.* 1990; Duarte 1995). The experimental measurement of these parameters is complicated by the fact that they may change through time as algae adapt to varying environmental conditions. For instance, light intensity, temperature, and nutrient concentration are all known to influence the photosynthetic responses in algae (Davison 1991; Falkowski and LaRoche 1991; Turpin 1991). Seasonal changes in the functional responses to salinity were observed in the drift algae collected from the canal site, with better low-salinity tolerance during the wet season.

The consequence of these hypotheses can be tested by the model formulation being altered, such as during sensitivity analyses when the formulations were altered by

increasing or decreasing the optimal range, a change similar to altering the magnitude of the physiological coefficients. The changes in these parameters indicated that for many of the formulations, the magnitude of these coefficients was not very sensitive over the range of conditions that the algae would normally experience in the Bay. The coefficients that did cause significant changes were not unexpected from previous knowledge about the system being investigated, e.g., nutrient limitation. This insensitivity of a functional response, compared to the range of environmental conditions present, has been reported previously for nutrient-uptake rates and algal growth under eutrophic conditions (Coffaro and Sfriso 1997), even though this was the major process under investigation for the model being developed (Bendorichio *et al.* 1994; Coffaro and Bocci 1997; Coffaro and Sfriso 1997; Solidoro *et al.* 1997). In that project it was found that spatial variation arising from flow regimes were important in structuring *Ulva* biomass followed by local nutrient variation, which generally was non-limiting to productivity (Coffaro and Sfriso 1997; Flindt *et al.* 1997).

Hydrodynamic transport of unattached biomass was important in simulating drift dynamics accurately in this model. It was found to be a very important process in describing the temporal change in biomass at locales with different intensities of tidal flow, resulting in sharply reduced persistence times in areas subject to high tidal flushing. Recent modeling efforts have indicated that the flow regime can be a major environmental process in balancing the biomass budget for a variety of macrophytes (Coffaro and Bocci 1997; Flindt *et al.* 1997; Salomonsen *et al.* 1997; da Silva and Asmus 2001). This process has not been well investigated in many macrophyte models, presumably because of the attached nature of many aquatic plants.

This current study is also one of the first models that investigates the importance of salinity differences in structuring community dynamics, a continuation of work published on South Florida seagrass systems (Fong and Harwell 1994; Fong *et al.* 1997). Salinity is an under-investigated process in eutrophication models, although it has the potential to

influence community structure by the exclusion of intolerant species. Because of the co-occurrence of nutrient inputs with salinity reductions, this process should be more completely investigated.

The linkage of the algal models presented here to the seagrass model of Fong and Harwell (1994) occurs primarily via reduction of irradiance available to the seagrasses from shading by epiphyte and drift algal biomass. The second linkage occurs between seagrass biomass and epiphyte substrate availability. Sensitivity analysis and validation statistics demonstrated the importance of this parameter on epiphyte dynamics, especially in canal conditions that are stressful to the simulated *Thalassia* based on the Fong and Harwell (1994) model. The current formulation reduces epiphyte biomass, if substrate becomes limiting, by increasing the epiphyte mortality rate. This may not be reflective of the real-world situation, where epiphytes can continue to persist even after seagrass blade detachment. It has been proposed that numerous species of drift algae originate as epiphytes that continue to flourish after the seagrass blade senesces (Humm 1964; Benz *et al.* 1979). A number of alternative formulations exist for epiphyte biomass as a function of macrophyte (seagrass) substrate (Madden and Kemp 1996; da Silva and Asmus 2001), which could be adapted to the current model.

The present model does not currently allow for spatially explicit functions such as drift transport distance over different substrate-types, and source-sink relationships that may be important for understanding Bay-wide distributions of this functional group. These spatially discrete processes can be of fundamental importance to understanding community dynamics over time (Tilman 1994; Turchin 1998). The rhizophytic algae are not dynamically linked to the other two functional groups in this version of the model. Feedbacks on rhizophytic biomass could occur through light limitation from drift algae and possibly epiphytes, analogous to the seagrass. Also, competition with seagrasses for nutrients and space, and the facilitation of succession of the seagrass community via substrate stabilization and nutrient enrichment of the sediments by the rhizophytes (Zieman

1982; Williams 1990), should be addressed in a coupled version of the seagrass and algal models. The importance of grazing on the loss rates of the three different functional groups was not addressed here because of the lack of adequate data from the Bay. Some initial experiments indicated that drift algae are preferentially consumed over the calcareous and chemically defended rhizophytic algae (Paul and Hay 1986; Paul and Fenical 1987; Hay *et al.* 1994;). Further, drift algae exposed to high-nutrient, low-salinity regimes (canal conditions) were preferentially consumed over those grown under oceanic conditions, indicating the importance of investigating grazing responses in future studies, because of the potential links to higher consumers via the different trophic paths of detrital export vs. direct grazing. Furthermore, the current algal production model should be linked with the existing seagrass production model of Fong and Harwell (1994) and incorporated into the Seascape model, to complete the benthic autotroph component of this policy relevant tool that aims to aid in the management of Biscayne Bay under various proposed South Florida restoration scenarios (Harwell *et al.* 1994).

Importance of System History

Finally, almost all mathematical models of the dynamics of populations or communities assume that a system's future depends solely on its present state, and that even its immediate past is irrelevant (Tanner *et al.* 1996). Studies of the effects of history at the community level have generally focused on the role of chance events in structuring assemblages (Sutherland 1974; May 1977; Lubchenco 1978; Hubbell and Foster 1986). For instance, the order of arrival (or subsequent establishment) of species can strongly influence community structure (Sale 1977; Chesson and Case 1986; Robinson and Dickerson 1987; Butler and Chesson 1990). Some mechanistic models of succession implicitly address the importance of sequences of interactions (e.g., facilitation and inhibition, *sensu* Connell and Slatyer 1977). Similarly the history of unpredictable disturbances may also play a role in changing the trajectory of an assemblage (Lewontin

1969; Law and Morton 1993). If a community has a single stable point that exhibits global attraction, then history is important only in that it determines where on the road to recovery the community is. However, if multiple stable points exist, the community may be perturbed into a new domain of attraction (Lewontin 1969; Holling 1973; Peterman *et al.* 1979). In this case, the community's history must be known in order to elucidate both its current configuration and trajectory (Hughes 1989, 1994; Law and Morton 1993).

SUMMARY

A seasonal trend in biomass was evident in all three functional groups of algae in this model and was caused by seasonal changes in simulated light and water temperature, although salinity was also important, especially in the canal simulation. The most abundant group by biomass were the epiphytes at all sites, with drift algae the next most abundant in the canal simulation, while the rhizophytic algae ranked second in the oceanic simulation. Both drift algae and epiphytes were euryhaline in their salinity tolerance. The stenohaline rhizophytes were excluded under low salinity conditions. Drift algae had higher biomass under high nutrient conditions (chiefly nitrogen). Rhizophytic algae were simulated to do better under low-nutrient conditions, provided P concentrations were not limiting in the simulation. Both predicted drift and rhizophytic algal productivity agreed with observed data better when a lag time was introduced in the model construct. There was no lag time for the epiphytes, although this functional group was found to be strongly influenced by the ability of its *Thalassia* substrate to tolerate salinity stress through feedback provided on the epiphyte mortality rate. This was the one instance where the model performed poorly at matching the observed data, indicating a possible admonition on relying too heavily on ecological field data.

Model sensitivity was high to changes in algal intrinsic growth and death rates, as well as the maximum biomass, which was site-specific. Furthermore, functional-group specific interactions including drift removal by currents, and epiphyte substrate-dependent mortality

were also important in determining the biomass dynamics. Drift algae were found to be heavily influenced by local hydrodynamic conditions, with the removal of a large percentage of standing stock biomass under conditions of strong tidal flows. Of the environmental variables, light and temperature were not found to alter model predictions considerably, whereas salinity and nutrients did cause changes in the composition of the simulated algal community. Salinity negatively affected both epiphyte (via a reduction in *Thalassia*) and rhizophytic algal abundance under canal conditions. Nutrient limitation was both functional group- and condition-specific. Nitrogen-limited epiphyte production occurred under oceanic conditions, whereas phosphorus appeared to be limiting all three functional groups in the canal scenario.

The stated purpose of this model was to synthesize the knowledge about algal autotrophs in seagrass systems within Biscayne Bay by simulating changes in biomass with seasonal and stressor inputs. The model can currently be deemed acceptable for use over this domain by the user community, with a number of future improvements and additions suggested. These include investigating the formulation of the epiphyte substrate-dependent mortality function, determining the importance of grazing losses, and linking the algal model to a pre-existing seagrass model, which could then be made spatially explicit.

APPENDIX: Tables of Parameter Values

Table A1: Range of water column nutrient concentrations and porewater nutrient concentrations (units = μM) reported from the literature for seagrass habitats similar to those studied. $\text{TiN} = \text{NH}_4^+ + \text{NO}_3^-$.

Location	NH_4^+	NO_3^-	TiN	PO_4^{4-}	Reference
<u>WATER COLUMN</u>					
Biscayne Bay	0.4-2.8	0.5-6.5	0.75-10.0	0.3-1.8	Irlandi (unpubl. data)
Big Pine Key			1.14-2.42	0.08-0.14	Lapointe 1987b
Fla Bay	2.0-3.0			0.1	Rosenfeld 1979
Fla Bay	0.02-11.03	0-6.13.0	7.0-123.2	0-0.33	Fourqrean <i>et al.</i> 1993
Key Largo			0.75-1.71	0.04-0.09	O'Neal and Prince 1988
Fla Keys	0.04-0.29	0.29-0.3		0.07-0.11	Delgado and Lapointe 1994
Fla Keys	0.3-1.2	0.25-2.1		<0.12	Lapointe 1989
Fla Keys	0.15-6.92	0.27-49	2.5-5.0	0.03-1.6	Lapointe <i>et al.</i> 1990
Fla Keys	1.0-1.5	0.6-1.0		0.1-0.3	Lapointe and Clark 1992
Fla Keys			3.11	0.19	Lapointe <i>et al.</i> (unpubl.)
Fla Keys	1.86-5.48	0.26-1.38		0.07-0.49	Lapointe and Matzie 1996
Fla Keys					Szmant and Forrester 1996
Jamaica	0.19-0.49	4.25-27.86		0.11-0.33	Lapointe 1997
Western Caribbean			3.16	0.04	Lapointe <i>et al.</i> (unpubl.)
Belize	0.38-1.4		0.08-0.1		Lapointe <i>et al.</i> 1987
Bermuda			<1.0	<0.15	Lapointe and Connell 1989
<u>POREWATERS</u>					
Biscayne Bay	25-180	0.75-2.5	40-200	0.7-2.4	CMEA, Univ. Miami
Fla Bay	400-1100			5.0-30	Rosenfeld 1979
Fla Keys			470-1035	4.0-10.3	Lapointe <i>et al.</i> 1990
Bermuda			23.0-40.0	0.3-0.5	Lapointe and Connell 1989
Bermuda			60.4-107.0	17.9-23.8	McGlathery <i>et al.</i> 1992
U.S. Virgin Isl.	10.0-79.0	2.78-39.8			Williams <i>et al.</i> 1985
Puerto Rico	5.0-60.0	0.1-4.2			Corredor and Capone 1985

Table A2: Maximum and average biomass values (g dry wt·m⁻²) of the three functional groups of macroalgae modeled, from reported literature on seagrass habitats in Florida and nearby regions.

Group/Spp.	Location	Max B.	Mean B.	Reference
		(g dry wt·m⁻²)		
<u>DRIFT</u>				
drift	Biscayne Bay	408.0	12.6	Biber 2002
drift	Black Pt, Bisc B.	12.7	6.8	Brook 1982
drift	Fender Pt, Bisc B.	251.7	148.2	Brook 1982
<i>Laurencia</i>	Black Pt, Bisc B.	12.7	6.3	Brook 1982
<i>Laurencia</i>	Fender Pt, Bisc B.	184.5	125.3	Brook 1982
<i>Laurencia</i>	Card Sound	29.2	6.1	Josselyn 1977
<i>Laurencia</i>	Card Sound	176.0	7.0	Thorhaug 1971
<i>Laurencia</i>	Card Sound	40.5	20.8	Thorhaug 1976
<i>Laurencia</i>	Card Sound	10.0	2.8	Thorhaug <i>et al.</i> 1979
<i>Laurencia</i>	Florida Bay		24.1	Zieman <i>et al.</i> 1989
<i>Dicytota</i>	N. Fla Reef Tract	20.4	10.4	Lirman and Biber 2000
<i>Chondria</i>	Indian River	405.3	4.5	Benz <i>et al.</i> 1979
<i>Dictyota</i>	Indian River	260.2	1.5	Benz <i>et al.</i> 1979
drift	Indian River	219.0	40.0	Kulczycki <i>et al.</i> 1981
drift	Indian River	4860	164.0	Virnstein and Carbonara '85
drift	Indian River	191.2	75.0	Virnstein and Howard 1987
drift	Tampa Bay	150.0	25.0	Bell and Hall 1997
		max. =	mean =	min. =
		4860.0	40.0	1.5
Group/Spp.	Location	Max B.	Mean B.	Reference
		(g dry wt·m⁻²)		
<u>RHIZOPHYTES</u>				
<i>Halimeda</i>	Biscayne Bay	360.0	41.5	Biber 2002
<i>Halimeda</i>	Fender Point		0.9	Brook 1982
<i>H. incrassata</i>	Card Sound	21.7	5.8	Bach 1979
<i>H. monile</i>	Card Sound	7.1	1.5	Bach 1979
<i>Halimeda</i>	Card Sound	199.0	14.8	Thorhaug 1971
<i>Halimeda</i>	Florida Bay	112.0	7.6	Bosence 1989
<i>Halimeda</i>	N. Fla Reef Tract	258.6	99.6	Lirman and Biber 2000
<i>Halimeda</i>	Bermuda	504.0	12-156.0	South 1983
<i>Halimeda</i>	Bermuda	350.0	7.5	Wefer 1980
<i>Penicillus</i>	Biscayne Bay	422.0	20.7	Biber 2002
<i>Penicillus</i>	Fender Point	12.6	8.2	Brook 1981
<i>Penicillus</i>	Card Sound	455.0	8.3	Thorhaug 1971
<i>Penicillus</i>	Card Sound	6.1	1.2	Bach 1979
<i>Penicillus</i>	Florida Bay	80.0	3.5	Bosence 1989
<i>Penicillus</i>	Florida Bay	377.0	65.0	Montague and Ley 1993
<i>Penicillus</i>	Florida Bay	56.0	2.5	Stockman <i>et al.</i> 1967
<i>Penicillus</i>	Florida Bay		6.7	Zieman <i>et al.</i> 1989
<i>Penicillus</i>	Bermuda	56.0	10.0	South 1983
<i>Penicillus</i>	Bermuda		11.2	Wefer 1980
		max. =	mean =	min. =
		504.0	19.3	0.9

Group/Spp.	Location	Max B.	Mean B.	Reference
		(g dry wt·m⁻²)		
<u>EPIPHYTES</u>				
<i>Thalassia</i>	Biscayne Bay	869.0	73.0	Biber 2002
<i>Thalassia</i>	Biscayne Bay	315.0	45.0	Irlandi (unpubl. data)
<i>Thalassia</i>	Florida Bay	2.6	2.0	Bosence 1989
<i>Thalassia</i>	Bimini	88.0	54.0	Capone <i>et al.</i> 1979
<i>Thalassia</i>	Bahamas		11.3	Jensen and Gibson 1986
<i>Thalassia</i>	Indian River		106.3	Heffernan and Gibson 1983
<i>Thalassia</i>	Indian River		21.9	Jensen and Gibson 1986
<i>Thalassia</i>	Tampa Bay		18.7	Jensen and Gibson 1986
<i>Thalassia</i>	N. Florida	130.0	78.0	Sullivan and Wear 1996
		max. =	mean =	min. =
		869.0	45.6	1.98

Table A3: Range or maximum, and average growth rates (% day⁻¹) of the three functional groups of macroalgae modeled, from reported literature on seagrass habitats in Florida and nearby regions.

Group/Spp	Location	Range/Max.	Mean (% day⁻¹)	Reference
DRIFT				
drift	Biscayne Bay	7.0	2.5	Biber 2002
<i>Laurencia</i>	Biscayne Bay	4.0-8.0	5.5	Thorhaug and Marcus 1981
<i>Laurencia</i>	Card Sound	2.0-10.0	4.0	Thorhaug <i>et al.</i> 1979
<i>Laurencia</i>	Card Sound	1.0-7.0	3.5	Josselyn 1977
<i>Laurencia</i>	N. Fla Reef Tract	1.7-3.4	2.8	Lirman and Biber 2000
<i>Dictyota</i>	N. Fla Reef Tract	3.1-4.9	4.0	Lirman and Biber 2000
<i>Hypnea</i>	N. Fla Reef Tract		0.8	Lirman and Biber 2000
<i>Gracilaria</i>	N. Fla Reef Tract	4.0-8.0	6.0	Thorhaug and Marcus 1981
<i>Laurencia</i>	Florida Bay		2.0	Lapointe 1989
<i>Gracilaria</i>	Florida Bay	14.0	2.0	Lapointe 1989
<i>Laurencia</i>	Florida Keys	2.8-5.5	4.0	Delgado and Lapointe 1994
<i>Dictyota</i>	Florida Keys	3.5-11.0	7.0	Delgado and Lapointe 1994
<i>Gracilaria</i>	Florida Keys	2.0-12.0	7.0	Lapointe 1985
<i>Gracilaria</i>	Florida Keys	0.1-12.0	5.0	Lapointe 1987
<i>Hypnea</i>	Florida Keys		20.0	Guist <i>et al.</i> 1982
<i>Gracilaria</i>	Indian River	11.2-23.1	17.0	Hanisak <i>et al.</i> 1988
<i>Gracilaria</i>	Indian River		1.5	Hwang <i>et al.</i> 1987
<i>Gracilaria</i>	Indian River	60.0		Lapointe and Ryther 1978
		max. =	mean =	min. =
		60	5.56	0.8
Group/Spp	Location	Range/Max.	Mean (% day⁻¹)	Reference
RHIZOPHYTES				
<i>Halimeda</i>	Biscayne Bay	1.3	0.5	Biber 2002
<i>Halimeda</i>	Biscayne Bay	1.5	1.3	Lirman and Biber 2000
<i>Halimeda</i>	Card Sound	0.01-8.5	1.4 ¹	Bach 1979
<i>Halimeda</i>	Florida Bay	1.0	0.5 ¹	Bosence 1989
<i>Halimeda</i>	Florida Bay	1.6-2.7	2.1	Stockman <i>et al.</i> 1967
<i>Halimeda</i>	Florida Keys	1.0-3.5	1.8	Delgado and Lapointe 1994
<i>Halimeda</i>	Marquesas Keys	0.04-1.0	0.6	Hudson 1985
<i>Halimeda</i>	Bahama Banks	8.0-9.0		Freile <i>et al.</i> 1995
<i>Halimeda</i>	Bermuda		3.3	Wefer 1980
<i>Penicillus</i>	Biscayne Bay	1.5	0.2	Biber 2001
<i>Penicillus</i>	Card Sound	0.04-6.2	8.5 ¹	Bach 1979
<i>Penicillus</i>	Florida Bay		1.5 ¹	Bosence 1989
<i>Penicillus</i>	Florida Keys	0.7-2.2	2.0	Delgado and Lapointe 1994
<i>Penicillus</i>	Bermuda		2.0	Wefer 1980
		max. =	mean =	min. =
		9.0	1.98	0.15

Group/Spp	Location	Range/Max.	Mean (% day⁻¹)	Reference
<u>EPIPHYTES</u>				
<i>Thalassia</i>	Biscayne Bay	1.0-35.0	5	Biber 2002
<i>Thalassia</i>	Florida Bay	0.9-1.6	1.0	Frankovich and Ziemann '94
<i>Thalassia</i>	Bahamas	0.16-4.7	0.3	Jensen and Gibson 1986
<i>Thalassia</i>	Indian River	0.09-3.4	1.3	Heffernan and Gibson 1983
<i>Thalassia</i>	Indian River	0.15-5.6	1.6	Jensen and Gibson 1986
<i>Thalassia</i>	Tampa Bay	0.1-1.5	0.5	Jensen and Gibson 1986
<i>Thalassia</i>	N. Florida	0.05-5.4	2.7	Sullivan and Wear 1996
		max. =	mean =	min. =
		35.0	1.78	0.32

¹production estimated from CaCO₃ production, underestimates true production.

Table A4: Light saturation values ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) from P-I curves of the three functional groups of macroalgae modeled, from reported literature on seagrass habitats in Florida and nearby regions.

Group/Spp	Location	Optimum/Saturatn I_k ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Reference
<u>DRIFT</u>			
drift	Biscayne Bay	300	Biber 2002
<i>Laurencia</i>	Biscayne Bay	40-174	Marcus and Thorhaug 1980
<i>Laurencia</i>	Biscayne Bay	76.4-90.3 ³	Josselyn 1977
<i>Gracilaria</i>	Florida Keys	1000-1100	Lapointe 1987
<i>Laurencia</i>	Florida Keys	600 ¹	Mathieson and Dawes 1986
<i>Hypnea</i>	Florida Keys	850 ¹	Mathieson and Dawes 1986
<i>Gracilaria</i>	Florida Keys	600 ¹	Mathieson and Dawes 1986
<i>Gracilaria</i>	Indian River	100	Hanisak and Samuel 1983
drift	Indian River	344-431 ²	Benz <i>et al.</i> 1979
<i>Gracilaria</i>	Tampa Bay	1200+	Dawes and Koch 1990
<i>Gracilaria</i>	Tampa Bay	65	Friedlander and Dawes 1984a+b
<i>Hypnea</i>	Tampa Bay	500 ¹	Dawes <i>et al.</i> 1976
<i>Acanthophora</i>	Tampa Bay	1000 ¹	Dawes <i>et al.</i> 1978
<i>Gracilaria</i>	Tampa Bay	500 ¹	Dawes <i>et al.</i> 1978
<u>RHIZOPHYTES</u>			
<i>Halimeda</i>	Biscayne Bay	250-300	Biber 2002
<i>Halimeda</i>	Florida Keys	80 ¹	Mathieson and Dawes 1986
<i>Halimeda</i>	Bahamas	60-103	Littler <i>et al.</i> 1988
<i>Penicillus</i>	Biscayne Bay	250-300	Biber 2001
<i>Caulerpa</i>	Florida Keys	80	Mathieson and Dawes 1986
<i>Caulerpa</i>	Florida Keys	38-111	O'Neal and Prince 1988
<u>EPIPHYTES</u>			
<i>Thalassia</i>	Biscayne Bay	150	Biber 2002
<i>Thalassia</i>	Bimini	105-630	Capone <i>et al.</i> 1979
<i>Halodule</i>	Mississippi	300	Moncreiff <i>et al.</i> 1992
<i>Halodule</i>	Mississippi	<400	Sullivan <i>et al.</i> 1991
<i>Halodule</i>	Texas	300-400	Morgan and Kitting 1984.
<i>Zostera</i>	N. Carolina	60-300	Penhale 1977
<i>Syringodium</i>	Fiji	240	Pollard and Kogure 1993

$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} = {}^1\text{ft candles} \times 3.3; {}^2\text{Ly} \times 0.86; {}^3\text{g cal} \times 0.28$

Table A5: Temperature ranges and optima of the three functional groups of macroalgae modeled, from reported literature on seagrass habitats in Florida and nearby regions, for epiphytes responses were assumed to be identical to drift algae.

Group/Spp	Location	Range	Optimum (°C)	Reference
<u>DRIFT</u>				
<i>Laurencia</i>	Biscayne Bay	7-35	10.0-28	Biber 2002
<i>Laurencia</i>	Biscayne Bay	18-30	23-26	Josselyn 1977
<i>Laurencia</i>	Biscayne Bay	19-32	30	Thorhaug 1976
<i>Laurencia</i>	Biscayne Bay		20-29	Marcus and Thorhaug 1980
<i>Laurencia</i>	Card Sound	15-30	32-35 lethal	Bader and Roessler 1971
<i>Hypnea</i>	Florida Keys		18-24	Guist <i>et al.</i> 1982
drift	Indian River		23-27	Benz <i>et al.</i> 1979
<i>Gracilaria</i>	Indian River		24-30	Hanisak and Samuel 1983
<i>Gracilaria</i>	Indian River		22	Lapointe 1982
<i>Hypnea</i>	Tampa Bay	15-35	28-32	Dawes <i>et al.</i> 1976
<i>Acanthophora</i>	Tampa Bay	15-36	30-36	Dawes <i>et al.</i> 1978
<i>Gracilaria</i>	Tampa Bay	18-36	30	Dawes <i>et al.</i> 1978
<i>Hypnea</i>	Tampa Bay		24-32	Durako and Dawes 1980
<i>Gracilaria</i>	Tampa Bay		25-28	Friedlander and Dawes 1984a+b
<u>RHIZOPHYTES</u>				
<i>Halimeda</i>	Biscayne Bay	17-36	30-31	Biber 2002
<i>Halimeda</i>	Biscayne Bay	19-34	30-32	Thorhaug 1976
<i>Halimeda</i>	Card Sound	15-36	30	Bader and Roessler 1971
<i>Penicillus</i>	Biscayne Bay	15-35	27-29	Biber 2001
<i>Penicillus</i>	Biscayne Bay	19-34	29-31	Thorhaug 1976
<i>Penicillus</i>	Card Sound	15-36	30	Bader and Roessler 1971
<i>Caulerpa</i>	Florida Keys	15-34	30-34	O'Neal and Prince 1988

Table A6: Salinity ranges and optima of the three functional groups of macroalgae modeled, from reported literature on seagrass habitats in Florida and nearby regions.

Group/Spp	Location	Range	Optimum (psu)	Reference
<u>DRIFT</u>				
drift	Biscayne Bay	7.0-35	15-35	Biber 2002
<i>Hypnea</i>	Tampa Bay	15-45	20	Dawes <i>et al.</i> 1976
<i>Acanthophora</i>	Tampa Bay			Dawes <i>et al.</i> 1978
<i>Acanthophora</i>	Tampa Bay	10.0-50	15-20	Dawes <i>et al.</i> 1978
<i>Gracilaria</i>	Tampa Bay	10.0-50	30	Dawes <i>et al.</i> 1978
<i>Gracilaria</i>	Tampa Bay		30	Friedlander and Dawes 1984b
<i>Gracilaria</i>	Indian River		24-36	Hanisak and Samuel 1983
drift	Indian River		33-34	Benz <i>et al.</i> 1979
<i>Chondria</i>	South Texas	20-40	25-30	Conover 1964
<i>Dictyota</i>	South Texas	25-35	30	Conover 1964
<i>Laurencia</i>	South Texas	10.0-30	25-35	Conover 1964
<u>RHIZOPHYTES</u>				
<i>Halimeda</i>	Biscayne Bay	15-45	20-35	Biber 2002
<i>Penicillus</i>	Biscayne Bay	15-40	20-35	Biber 2002
<i>Penicillus</i>	South Texas	15-45	30-40	Conover 1964
<i>Caulerpa</i>	Florida Keys	27-35	32	O'Neal and Prince 1988
<i>Caulerpa</i>	South Texas	25-35	30	Conover 1964
<u>EPIPHYTES</u>				
<i>Thalassia</i>	Biscayne Bay	15-55	30-45	Biber 2001
<i>Thalassia - Spirulina</i>	Tampa Bay		20-25	Phillips 1964
<i>Thalassia - Lyngbya</i>	Tampa Bay		>27.5	Phillips 1964

Table A7: Monod saturation coefficient (K_s) of the three functional groups of macroalgae modeled, from reported literature on seagrass habitats in Florida and nearby regions.

Group/Spp	Location	N	P	Reference
		K_s (μM)		
<u>DRIFT</u>				
drift	Biscayne Bay	10	1	Biber 2002
<i>Gracilaria</i>	Indian River	8-9		Hwang <i>et al.</i> 1987
<i>Gracilaria</i>	Tampa Bay	<600 ¹	<12 ¹	Friedlander and Dawes 1985
<i>Gracilaria</i>	Massachusetts	1-2		DeBoer <i>et al.</i> 1978
<i>Gracilaria</i>	Massachusetts	17-37		Fujita 1985
<u>RHIZOPHYTES</u>				
<i>Halimeda</i>	Biscayne Bay	40	4	Biber 2002
<i>Halimeda</i>	GBR	12.5		Abel and Drew 1985
<i>Penicillus</i>	Biscayne Bay	20	2	Biber 2001
<i>Caulerpa</i>	West Indies	107		Williams 1984

¹growth not saturated.