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Modeling the dynamics of three functional groups of macroalgae in tropical seagrass habitats $\stackrel{\text{\tiny{\scale}}}{\to}$

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Abstract

A model of three functional groups of macroalgae, drift algae, rhizophytic calcareous algae, and seagrass epiphytes, was developed to complement an existing seagrass production model for tropical habitats dominated by *Thalassia testudinum* (Turtle-grass). The current modeling effort simulates annual biomass dynamics for each of the three functional groups under a variety of stress regimes imposed by nutrient-laden freshwater discharges into a well-flushed coastal bay in South Florida.

The model is parameterized based on multiple years of experimental data collected from Biscayne Bay, as well as literature values reported for other Florida and Caribbean seagrass habitats. Calibration of the model yields a good fit of predicted-to-observed biomass ($r^2 > 0.85$) for sheet-flow and oceanic-influenced sites, but a poor fit ($r^2 = 0.13$) under canal-influenced conditions. This is hypothesized to be related to the lack of adequate observed data on seagrass epiphyte dynamics to parameterize the model.

Sensitivity analysis showed that the model is easily perturbed by changes in intrinsic growth parameters of the algae (daily growth rate, mortality rate, carrying capacity), while it is much less sensitive to changes in the functional form of the response curves that are used to characterize the stress tolerances of the algae to light, temperature, salinity, and nutrient conditions. This model is considered suitable for use in seagrass habitats similar to those occurring in South Florida, as these are the conditions to which the model was calibrated.

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1. Introduction

Seagrass habitats exhibit dynamic complexity of the kind that makes ecological models difficult to validate across the entire range of real-system behaviors (Patten and Jørgensen, 1995). 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* (Turtle-

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grass), whereas *Halodule wrightii* (Shoal-grass) and *Syringodium filiforme* (Manatee-grass) 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 (Biber, 2002).

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; McGlatherv, 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; Moncrieff et al., 1992). Epiphytes and drift algae potentially 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 the detrimental effects of blooms of drift algae and epiphytes, which are hypothesized to be related to eutrophication in many shallow nearshore seagrass environments (Valiela et al., 1997; Hauxwell et al., 2001; McGlathery, 2001).

The importance of biotic and abiotic factors controlling the distribution and abundance of the macroalgal components of the seagrass ecosystem is still largely unknown, although Fong and Harwell (1994) developed a model to examine some mechanisms controlling spatial and temporal variability in the structure of seagrass communities. Their seagrass system 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 macroalgal autotrophs in seagrass ecosystems. The purpose of the current modeling effort was to quantify the relationship between environmental conditions interacting with physiological processes in the algae to affect growth, and to explore how algal biomass changes with spatiotemporal differences in environmental conditions.

The Fong and Harwell (1994) seagrass model was used as a starting point for our modeling efforts. We 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 Biscavne Bay. Florida (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 (Biber, 2002). 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 (see Appendix A).

The interaction with the seagrass model of Fong and Harwell (1994) is through light limitation to 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.

2. Methods

2.1. Conceptual model and mathematical formulation

Initially, we developed a conceptual model (Hall and Day, 1977; Gentile et al., 2001) that described our hypothetical representation of critical state variables and processes. Algal biomass in the model is influenced by light (L), temperature (T), salinity (S), and nutrients (N) (both water column and sedimentporewater nutrients). Drift algae and epiphytes are able to utilize only water-column nutrients, while rhizo-



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

phytic algae can also take up nutrients in the sediment porewater (Fig. 1). Optimal productivity of each functional group occurs within a specific range for each one of these environmental factors. Loss of biomass is modeled as senescence of a constant proportion of standing-stock biomass; additionally, for the drift algae, removal of biomass by tidal currents is an important loss. 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 (dB/dt) of that group within a 1 m² 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 to 1 that represent each factor. General model equations common to each of the three functional groups are:

$$\frac{\mathrm{d}B}{\mathrm{d}t} = (g-d)B\tag{1}$$

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

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

 g_{max} : maximum growth from literature values (Table 1), (1 - 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

Table	1

Tarameter values for environ	intental foreing functions expressed as func	ge (average) at each location. eanai, si	neet now, and becan sites
	Canal	Sheet-flow	Ocean
Forcing functions	50,550 (200)	50,550,(200)	100 (00 (250)

Parameter values for environmental forcing functions expressed as range (average) at each location: canal sheet-flow and ocean sites

Forcing functions			
Light $(\mu mol m^{-2} s^{-1})$	50-550 (300)	50-550 (300)	100-600 (350)
Temperature (°C)	18–32 (25)	18-32 (25)	18-32 (25)
Salinity $(g kg^{-1})$	0-40 (20)	10-35 (25)	28-38 (33)
N _{water} (µM)	5-50 (20)	5–25 (10)	2–5 (3.5)
Pwater (µM)	0.05-0.2 (0.1)	0.05-0.2 (0.1)	0.05-0.2 (0.1)
N _{sediment} (µM)	20-150 (50)	20-150 (50)	20-150 (50)
P _{sediment} (µM)	1.0–2.5 (1.5)	1.0–2.5 (1.5)	0.5 - 1.5 (1.0)
Drift			
$B_{\text{initial}} \text{ (g m}^{-2}\text{)}$	40	40	40
$K ({\rm g}{\rm m}^{-2})$	50	30	10
g_{max} (percent per day)	5.0-60 (10)	5.0-60 (10)	5.0-60 (10)
d (percent per day)	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
Epiphytes			
$B_{\text{initial}} \text{ (g m}^{-2}\text{)}$	50	50	50
$K ({\rm g}{\rm m}^{-2})$	90	90	150
g_{max} (percent per day)	2.0-35 (15)	2.0-35 (15)	2.0-35 (15)
d (percent per day)	0.5–7.5 (1.0)	0.5–7.5 (1.0)	0.5–7.5 (1.0)
Rhizophytes			
$B_{\text{initial}} \text{ (g m}^{-2}\text{)}$	20	20	20
$K (g m^{-2})$	25	10	60
$g_{\rm max}$ (percent per day)	2.0-9.0 (5.0)	2.0-9.0 (5.0)	2.0-9.0 (5.0)
d (percent per day)	0.5–1.5 (1.0)	0.5–1.5 (1.0)	0.5–1.5 (1.0)

Starting conditions and parameters for each functional group. Differences in parameter values among locations are highlighted in bold text.

range from 0 to 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) and 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). We use Liebig's Law of the minimum to determine the limiting nutrient [nitrogen (N) or phosphate (P)] for growth: $f(N) = \min(N, P)$.

$$d = (M+h) \tag{3}$$

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). In addition, for the epiphytes and drift algae functional groups, there are additional components to g and d as follows:

for epiphytes : $d_{\rm E} = (M + h) \times \text{turnover}$ (4)

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, we recognized the importance of hydrodynamic transport in structuring drift algal distribution at the landscape level, and this factor was subsequently incorporated into the model structure. For the drift algae this additional influence on biomass from hydrodynamic transport is expressed as:

$$\frac{\mathrm{d}B_{\mathrm{D}}}{\mathrm{d}t} = (g-d)B_{\mathrm{D}} + (I-E) \tag{5}$$



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*.

where *I* is biomass transported into the plot, and *E* is 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 standingstock 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), on a Macintosh Operating System. The model runs with a daily time step, using Runge-Kutta fourth order integration of the non-linear differential equations (Swartzman and Kaluzny, 1987). All model runs were over a 3650-day period (i.e. 10 years), with convergence 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-thanoptimal 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. New factors (e.g. hydrodynamic transport) were introduced only when it was clear that the results of the simulation were not consistent with observation.

2.2. Parameterization

The model was run initially under conditions descriptive of an oceanic environment, i.e. 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: Daily environment

$$= \bar{X} + \left\{ \text{S.D.} \times \sin\left[2\pi \times \left(\frac{\text{time} + \text{delay}}{360}\right)\right] \right\}$$
(6)

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 (Biber, 2002). 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 (see Appendix, Table A.1) using a stochastic function based on a uniform random distribution:

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

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.

2.2.1. 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 dw m^{-2} (Josselyn, 1977; Brook, 1981). The initial value for drift algae biomass was set at the mean of 40 g dw m^{-2} (Table A.2). 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% per day is reasonable for natural populations (Table A.3). Although productivity can be greater in intense culture situations (e.g. up to 60% per day reported by Lapointe and Ryther, 1978), natural populations are unlikely ever to 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 dw m^{-2} (Table A.2). 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 were set at 15% per day (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 dw m^{-2} (Table A.2). Growth is slowest in this group because of investments in structural tissue and calcification (Littler and Littler, 1980), with a value of 5% per day typical in Biscayne Bay (Table A.3).

Maximum biomass (K) for all three functional groups was determined from field data (Biber, 2002) and model calibration experiments to determine the best fit to the observed data.

2.2.2. 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; Fourqueran 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 are around 150–300 μ mol m⁻² s⁻¹ (Dring, 1982; Lobban et al., 1985). This corresponds to values found for all three functional groups (Table A.4). 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 μ mol m⁻² s⁻¹) is between the I_k values for epiphytes (150 μ mol m⁻² s⁻¹) and drift algae (300 μ mol m⁻² s⁻¹) (Fig. 2).

2.2.3. 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 are in the range of 20–28 °C (Table A.5), 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. 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.

2.2.4. 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 practical salinity units (psu) intermittently during the wet season (Fatt and Wang, 1987) when freshwater discharge rates and volumes are high. Optimal salinity for the drift algae is between 15 and 35 psu (Table A.6), 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).

2.2.5. 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 or bird excretion (D'Elia and DeBoer, 1978; DeBoer et al., 1978). 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, 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 ($K_s = 5 \mu M$), drift algae are intermediate ($K_s = 10 \mu M$), and rhizophytic algae have the lowest K_s (20 μM) because of their ability to utilize high porewater nutrient concentrations (Fig. 2; Table A.7).

2.2.6. 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 highirradiance 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), which, coupled with increased epiphytism, could decrease seagrass productivity.

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

$$Light attenuation = L \times f(B_{\rm E} + B_{\rm D})$$
(8)

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:

$$d = (d_{\rm E} \times d_{\rm substr}) \tag{9}$$

where:

 $d_{\text{substr}} = f(B_{\text{Thal}})$ $B_{\text{Thal}} = B_{\text{Thal}} + (B_{\text{Thal}} \times \text{turnover})$ $\text{turnover} = \frac{g_{\text{Thal}}}{d_{\text{Thal}}}$

Turnover decreases when growth of *Thalassia* declines, either from seasonal changes or environmental stressors. Substrate-dependent death rate of epiphytes (d_{substr}) increases up to five 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.

3. Results

3.1. Calibration

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 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 A.3). Some parameters that were not measured (e.g. senescence, seagrass turnover) were estimated and adjusted 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 (1 m²) 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 trace is compared with observed field biomass measures obtained over a



Fig. 3. Plots of simulated (black line) vs. observed (grey 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 1 m² quadrats collected at two sites per regime (n = 24-40) from 1996 to 1999. Simulated (mean \pm 95% CI) biomass is from 27 years of model output.

number of years for two sites in each regime (Biber, 2002).

For drift algae, the modeled biomass declines from canal (45 g dw m⁻²) to oceanic sites (<5 g dw m⁻²). The highest average biomass is simulated in June at the canal sites, and in May at 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 and 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 (10–15 g dw) of the three functional groups (Fig. 3). The oceanic site has the highest biomass of rhizophytic algae (50 g dw m⁻²), followed by the canal (25 g dw m⁻²), while the sheet-flow sites have the least (<10 g dw m⁻²). In all three regimes, simulated biomass is highest in the summer (August), and lowest in the winter (January), 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 g dw m^{-2} at the oceanic site, and about 100 g dw 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 in 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 salinity 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 qualitatively 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.

3.2. Validation

In the validation stage the model predictions are compared to independent field observations (Jørgensen, 1994). A number of statistics measure how well model-generated and real-system data compare (van Horn, 1971; Harrison, 1990; 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; Rykiel, 1996), i.e. determining if the model mimics the real world sufficiently for its stated purpose.

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.

Often validation is determined subjectively by a statement that extols the visual goodness-of-fit (Law and Kelton, 1991; Mayer and Butler, 1993). 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 days 366 to 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) versus 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.

The modeled data fit the observed points well ($r^2 > 0.85$) 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



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. Symbols on the plot of All Locations are: open squares = canal sites; triangles = sheet-flow sites; dots = oceanic sites.

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 and 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).

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 versus predicted values. Modeling efficiency 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 = Xline (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).

Statistic	All sites	Canal	Sheet	Ocean	Drift	Rhizophytes	Epiphytes
MAE	11.636	14.358	7.245	13.306	4.420	5.364	25.124
MSE	360.004	526.165	121.946	431.902	29.342	55.639	995.032
RMSE	18.974	22.938	11.043	20.782	5.417	7.459	31.544
MAE/\bar{y}	0.334	0.476	0.273	0.278	0.320	0.294	0.346
RMSE/y	0.544	0.760	0.416	0.434	0.393	0.409	0.434
U	0.350	0.657	0.252	0.276	0.242	0.278	0.362
EF	0.697	0.350	0.808	0.810	0.984	0.967	0.722
r^2	0.7599	0.1283	0.9103	0.8548	0.9397	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

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.

^a MAE = $(\sum |y_i - \hat{y}_i|)/n$, mean absolute error; MSE = $(\sum y_i - \hat{y}_i)/n$, 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 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 by Elliot et al. (2000) 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).

The regression line fitted to the data points indicated agreement between observed versus 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; in both cases, 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 versus predicted plots, this is because of the simulated seasonal dynamics of the epiphytes not agreeing closely with the observed time trace (Fig. 3). As the field data do not show any of the underlying Thalassia dynamic, we 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 $\alpha = 0.05$ (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 macro-algae within *Thalassia* habitats in Biscayne Bay and similar systems.

3.3. Sensitivity analysis

Sensitivity analysis is the process of varying model parameters and comparing the results against a reference simulation (Miller, 1974, 1979; Fong et al., 1997). This process identifies the model parameters,

Table 2

structures, empirically derived input information, and initial conditions that cause the greatest change in model predictions. 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 of this model 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 epiphytesubstrate-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 $\pm 3 \,^{\circ}$ 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 two of the 3-year simulations was summed, and 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:

relative change X = $\frac{100 \times (\text{rerun } X - \text{baseline } X)}{\text{baseline } X}$ (10) where baseline X is the statistic for predicted productivity for algal group X in the baseline model, and rerun X is 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 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 (Fig. 5).

3.3.1. Biomass and growth

The results of the sensitivity analysis on the intrinsic growth parameters (Fig. 5) showed increasing growth and reducing death rates resulted in increased biomass of all three functional groups in both the oceanic and canal sites (Fig. 5). 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, whereas it remained 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 less than 20% increase in the canal model (Fig. 5). 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, export probability (P(E)), and for the epiphytes, turnover, were parameters with a consequential effect on predicted biomass. The drift algae were more heavily influenced by the P(E) parameter in the oceanic site, reflecting the importance of water motion in local biomass dynamics. An in-



Fig. 5. Relative change (percent) in predicted productivity 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. The productivity parameters: initial biomass, carrying capacity (*K*), growth rate, death rate, were altered by $\pm 10\%$. In the final panel the drift algae export-probability, and the epiphyte-substrate turnover-rate, were altered by $\pm 25\%$

crease in P(E) resulted in increased removal of drift algae, while a reduction caused the model to predict increases in drift abundance at the oceanic site (Fig. 5). There were no changes greater than $\pm 10\%$ biomass with changes in P(E) at the canal site (Fig. 5). For instance, 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. 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 (Fig. 5).

3.3.2. Light

The sensitivity of the three functional groups to changes in their environmental response functions at both sites is plotted in Fig. 6. 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. 6). 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. 6). 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.

3.3.3. Temperature and salinity

Changes to the temperature optima resulted in <24% change in the mean biomass of any of the functional groups at either site (Fig. 6). However, the range was reduced for both the drift and rhizophytic algae at the canal site, whereas 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. 6). 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. 6). 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 alter the modeled productivities significantly under the low salinities encountered in the canal sites.

3.3.4. 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 significantly alter the mean biomass of any of the three functional groups in the highnutrient 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. 6).

Phosphorus is often touted as being the limiting nutrient in tropical waters (Lapointe, 1987a,b; Lapointe et al., 1992), and the increased biomass of all three groups simulated in both canal and oceanic conditions



Fig. 6. 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.

with a lower P optimum lends some support to this hypothesis. P-limitation is apparently more severe in the nitrogen-rich canal site, as evidenced by the greater increase in simulated mean productivity compared to the oceanic site for the same downward shift in Puptake optima (Fig. 6). The reduction in simulated rhizophytic 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 rhizophytic 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. 6).

The sensitivity analysis highlighted the importance of intrinsic growth parameters, the functional groupspecific 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.

4. Discussion

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 1960s (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,b; Ang and de Wreede, 1990, 1993), and physiological models that represent the relationship between productivity and different physical and chemical factors (e.g. Pregnall and Rudy, 1985; Jørgensen, 1986; Ferreira and Ramos, 1989; Gordon and McComb, 1989; Bendoricchio et al., 1993, 1994; Fong et al., 1994; Guimaraens, 1999). Models that have used a multiplicative formulation to parameterize the physiological responses to multiple limiting factors include papers by Lehman et al. (1975) on 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. 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. 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 we 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, unpublished manuscript). 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.

Development of 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-dynamic formulation of Michaelis-Menten uptake kinetics, coupled with a Droop formulation for growth (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 luxury uptake and starvation-induced changes in nutrient cell quotas, resulting in time lags between water-column nutrient availability and biomass production. 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; 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 our 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 nonetheless 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 these coefficients were 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 (Bendoricchio 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 was more important in structuring Ulva biomass than 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 wellinvestigated 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; Lirman and Cropper, 2003). 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 cooccurrence 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 versus direct grazing.

Many of the limitations of the current model construct could be abolished using a structural dynamic modeling approach. Structural dynamic models are ecological models that describe both quantitative and qualitative changes occurring to a system using some type of ecological goal function, e.g. exergy, or optimization algorithm (Nielsen, 1995; Jørgensen, 2001; Zhang et al., 2003). The advantage of this "fifth generation" model construct (Jørgensen, 1995) is the ability of a model to simulate ecosystem properties that are structurally or qualitatively dynamic, such as shifts in species composition that often occur during eutrophication, a property which deterministic, steady-state models do not possess or simulate poorly (Marques et al., 1997; Nielsen, 1997). Like many structural dynamic models, our approach was optimized to the pertinent forcing functions with the implicit goal of reducing model complexity by only including additional variables once they became necessary to realistically simulate the observed system dynamics, e.g. hydrodynamic transport of drifting macroalgae. However, the inability of the mathematical formulations used to incorporate variability, such as intrinsic growth rates and carrying capacity, limited the model to a reduced range of dynamic behaviors. We suggest that the current algal production model should be linked with the existing seagrass

production model of Fong and Harwell (1994) to yield a total benthic autotroph model, and that using a structural dynamic approach would allow this nextiteration model to capture a broader range of possible ecosystem behaviors. This approach will result in a policy-relevant tool that aims to aid in the management of Biscayne Bay under various proposed South Florida restoration scenarios (Harwell et al., 1996).

5. Conclusion

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 was 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 time lag was introduced in the model construct. There was no time lag 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 epiphytesubstrate-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.

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Appendix A

Range of parameter values used to calibrate the model, based on literature reports from South Florida and Caribbean seagrass systems (see Tables A.1–A.7).

Table A.1

Range of water-column nutrient concentrations and porewater nutrient concentrations (units = μM) reported from the literature for seagrass habitats similar to those studied (TiN = NH₄⁺ + NO₃⁻)

Location	NH4 ⁺	NO ₃ -	TiN	PO4 ³⁻	Reference
Water column					
Biscayne Bay	0.4-2.8	0.5-6.5	0.75-10.0	0.3-1.8	Irlandi (unpublished 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	Fourqurean et al. (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 et al. (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 et al. (unpublished data)
Fla Keys	1.86-5.48	0.26-1.38		0.07 - 0.49	Lapointe and Matzie (1996)
Jamaica	0.19-0.49	4.25-27.86		0.11-0.33	Lapointe (1997)
Western Caribbean			3.16	0.04	Lapointe et al. (unpublished data)
Belize	0.38-1.4		0.08-0.1		Lapointe et al. (1987)
Bermuda			<1.0	< 0.15	Lapointe and Connell (1989)
Porewaters					
Biscayne Bay	25-180	0.75-2.5	40-200	0.7-2.4	Irlandi (unpublished data)
Fla Bay	400-1100			5.0-30	Rosenfeld (1979)
Fla Keys			470-1035	4.0-10.3	Lapointe et al. (1990)
Bermuda			23.0-40.0	0.3-0.5	Lapointe and Connell (1989)
Bermuda			60.4-107.0	17.9-23.8	McGlathery et al. (1992)
U.S. Virgin Isl.	10.0-79.0	2.78-39.8			Williams et al. (1985)
Puerto Rico	5.0-60.0	0.1–4.2			Corredor and Capone (1985)

Table A.2

Maximum and average biomass values $(g \, dw \, m^{-2})$ of the three functional groups of macroalgae modeled, from reported literature on seagrass habitats in Florida and nearby regions

Group/species	Location	Maximum biomass	Mean biomass	Reference
Drift				
Drift	Biscayne Bay	408.0	12.6	Biber (2002)
Drift	Black Pt, Bisc B.	12.7	6.8	Brook (1981)
Drift	Fender Pt, Bisc B.	251.7	148.2	Brook (1981)
Laurencia	Card Sound	29.2	6.1	Josselyn (1977)
Laurencia	Card Sound	176.0	7.0	Thorhaug (1971)
Laurencia	Card Sound	40.5	20.8	Thorhaug (1976)
Laurencia	Card Sound	10.0	2.8	Thorhaug et al. (1979)
Laurencia	Florida Bay		24.1	Zieman et al. (1989)
Dicytota	N. Fla Reef Tract	20.4	10.4	Lirman and Biber (2000)
Chondria	Indian River	405.3	4.5	Benz et al. (1979)
Drift	Indian River	219.0	40.0	Kulczycki et al. (1981)
Drift	Indian River	4860	164.0	Virnstein and Carbonara (1985)
Drift	Indian River	191.2	75.0	Virnstein and Howard (1987)
Drift	Tampa Bay	150.0	25.0	Bell and Hall (1997)
Rhizophytes				
Halimeda	Biscayne Bay	360.0	41.5	Biber (2002)
Halimeda	Fender Point		0.9	Brook (1981)
H. incrassata	Card Sound	21.7	5.8	Bach (1979)
H. monile	Card Sound	7.1	1.5	Bach (1979)

Group/species	Location	Maximum biomass	Mean biomass	Reference
Halimeda	Card Sound	199.0	14.8	Thorhaug (1971)
Halimeda	Florida Bay	112.0	7.6	Bosence (1989)
Halimeda	N. Fla Reef Tract	258.6	99.6	Lirman and Biber (2000)
Halimeda	Bermuda	504.0	12-156.0	South (1983)
Halimeda	Bermuda	350.0	7.5	Wefer (1980)
Penicillus	Biscayne Bay	422.0	20.7	Biber (2002)
Penicillus	Fender Point	12.6	8.2	Brook (1981)
Penicillus	Card Sound	455.0	8.3	Thorhaug (1971)
Penicillus	Card Sound	6.1	1.2	Bach (1979)
Penicillus	Florida Bay	80.0	3.5	Bosence (1989)
Penicillus	Florida Bay	377.0	65.0	Montague and Ley (1993)
Penicillus	Florida Bay	56.0	2.5	Stockman et al. (1967)
Penicillus	Florida Bay		6.7	Zieman et al. (1989)
Penicillus	Bermuda	56.0	10.0	South (1983)
Penicillus	Bermuda		11.2	Wefer (1980)
Epiphytes				
Thalassia	Biscayne Bay	869.0	73.0	Biber (2002)
Thalassia	Biscayne Bay	315.0	45.0	Irlandi (unpublished data)
Thalassia	Florida Bay	2.6	2.0	Bosence (1989)
Thalassia	Bimini	88.0	54.0	Capone et al. (1979)
Thalassia	Bahamas		11.3	Jensen and Gibson (1986)
Thalassia	Indian River		106.3	Heffernan and Gibson (1983)
Thalassia	Indian River		21.9	Jensen and Gibson (1986)
Thalassia	Tampa Bay		18.7	Jensen and Gibson (1986)
Thalassia	N. Florida	130.0	78.0	Sullivan and Wear (1996)

Table A.3

Range or maximum, and average growth rates (percent per day) of the three functional groups of macroalgae modeled, from reported literature on seagrass habitats in Florida and nearby regions

Group/species	Location	Range/maximum	Mean	Reference
Drift				
Drift	Biscayne Bay	7.0	2.5	Biber (2002)
Laurencia	Biscayne Bay	4.0-8.0	5.5	Thorhaug and Marcus (1981)
Laurencia	Card Sound	2.0-10.0	4.0	Thorhaug et al. (1979)
Laurencia	Card Sound	1.0-7.0	3.5	Josselyn (1977)
Laurencia	N. Fla Reef Tract	1.7–3.4	2.8	Lirman and Biber (2000)
Hypnea	N. Fla Reef Tract		0.8	Lirman and Biber (2000)
Gracilaria	N. Fla Reef Tract	4.0-8.0	6.0	Thorhaug and Marcus (1981)
Laurencia	Florida Bay		2.0	Lapointe (1989)
Gracilaria	Florida Bay	14.0	2.0	Lapointe (1989)
Laurencia	Florida Keys	2.8-5.5	4.0	Delgado and Lapointe (1994)
Gracilaria	Florida Keys	2.0-12.0	7.0	Lapointe (1985)
Gracilaria	Florida Keys	0.1-12.0	5.0	Lapointe (1987a)
Hypnea	Florida Keys		20.0	Guist et al. (1982)
Gracilaria	Indian River	11.2–23.1	17.0	Hanisak et al. (1988)
Gracilaria	Indian River		1.5	Hwang et al. (1987)
Gracilaria	Indian River	60.0		Lapointe and Ryther (1978)
Rhizophytes				
Halimeda	Biscayne Bay	1.3	0.5	Biber (2002)
Halimeda	Biscayne Bay	1.5	1.3	Lirman and Biber (2000)
Halimeda	Card Sound	0.01-8.5	1.4 ^a	Bach (1979)
Halimeda	Florida Bay	1.0	0.5 ^a	Bosence (1989)

Group/species	Location	Range/maximum	Mean	Reference
Halimeda	Florida Bay	1.6–2.7	2.1	Stockman et al. (1967)
Halimeda	Florida Keys	1.0-3.5	1.8	Delgado and Lapointe (1994)
Halimeda	Marquesas Keys	0.04-1.0	0.6	Hudson (1985)
Halimeda	Bahama Banks	8.0-9.0		Freile et al. (1995)
Halimeda	Bermuda		3.3	Wefer (1980)
Penicillus	Biscayne Bay	1.5	0.2	Biber (2002)
Penicillus	Card Sound	0.04-6.2	8.5 ^a	Bach (1979)
Penicillus	Florida Bay		1.5 ^a	Bosence (1989)
Penicillus	Florida Keys	0.7–2.2	2.0	Delgado and Lapointe (1994)
Penicillus	Bermuda		2.0	Wefer (1980)
Epiphytes				
Thalassia	Biscayne Bay	1.0-35.0	5	Biber (2002)
Thalassia	Florida Bay	0.9–1.6	1.0	Frankovich and Zieman (1995)
Thalassia	Bahamas	0.16-4.7	0.3	Jensen and Gibson (1986)
Thalassia	Indian River	0.09-3.4	1.3	Heffernan and Gibson (1983)
Thalassia	Indian River	0.15-5.6	1.6	Jensen and Gibson (1986)
Thalassia	Tampa Bay	0.1-1.5	0.5	Jensen and Gibson (1986)
Thalassia	N. Florida	0.05-5.4	2.7	Sullivan and Wear (1996)

^a Production estimated from CaCO₃ production, underestimates true production.

Table A.4

Light-saturation values (I_k) from P-I curves for the three functional groups of macroalgae modeled, from reported literature on seagrass habitats in Florida and nearby regions

Group/species	Location	$I_{\rm k}~(\mu{ m mol}{ m m}^{-2}{ m s}^{-1})$	Reference
Drift			
Drift	Biscayne Bay	300	Biber (2002)
Laurencia	Biscayne Bay	40–174	Marcus and Thorhaug (1980)
Laurencia	Biscayne Bay	76.4–90.3 ^c	Josselyn (1977)
Gracilaria	Florida Keys	1000-1100	Lapointe (1987)
Laurencia	Florida Keys	600 ^a	Mathieson and Dawes (1986)
Hypnea	Florida Keys	850 ^a	Mathieson and Dawes (1986)
Gracilaria	Florida Keys	600 ^a	Mathieson and Dawes (1986)
Gracilaria	Indian River	100	Hanisak and Samuel (1983)
Drift	Indian River	344-431 ^b	Benz et al. (1979)
Gracilaria	Tampa Bay	1200^{+}	Dawes and Koch (1990)
Gracilaria	Tampa Bay	65	Friedlander and Dawes (1984a,b)
Hypnea	Tampa Bay	500 ^a	Dawes et al. (1976)
Acanthophora	Tampa Bay	1000^{a}	Dawes et al. (1978)
Gracilaria	Tampa Bay	500 ^a	Dawes et al. (1978)
Rhizophytes			
Halimeda	Biscayne Bay	250-300	Biber (2002)
Halimeda	Florida Keys	80^{a}	Mathieson and Dawes (1986)
Halimeda	Bahamas	60–103	Littler et al. (1988)
Penicillus	Biscayne Bay	250-300	Biber (2002)
Caulerpa	Florida Keys	80	Mathieson and Dawes (1986)
Caulerpa	Florida Keys	38–111	O'Neal and Prince (1988)
Epiphytes			
Thalassia	Biscayne Bay	150	Biber (2002)
Thalassia	Bimini	105-630	Capone et al. (1979)

Table A	4 (C	ontinued)
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Group/species	Location	$I_{\rm k} ~(\mu {\rm mol} ~{\rm m}^{-2} ~{\rm s}^{-1})$	Reference
Halodule	Mississippi	300	Moncrieff et al. (1992)
Halodule	Mississippi	<400	Sullivan et al. (1991)
Halodule	Texas	300-400	Morgan and Kitting (1984)
Zostera	N. Carolina	60–300	Penhale (1977)

 μ mol m⁻² s⁻¹ = ^aft candles × 3.3; ^bLy × 0.86; ^cg cal × 0.28.

Table A.5

Temperature ranges and optima (°C) 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/species	Location	Range	Optima	Reference
Drift				
Laurencia	Biscayne Bay	7–35	10-28	Biber (2002)
Laurencia	Biscayne Bay	18-30	23-26	Josselyn (1977)
Laurencia	Biscayne Bay	19-32	30	Thorhaug (1976)
Laurencia	Biscayne Bay		20-29	Marcus and Thorhaug (1980)
Laurencia	Card Sound	15-30	32-35 lethal	Bader and Roessler (1971)
Hypnea	Florida Keys		18-24	Guist et al. (1982)
Drift	Indian River		23–27	Benz et al. (1979)
Gracilaria	Indian River		24-30	Hanisak and Samuel (1983)
Gracilaria	Indian River		22	Lapointe (1982)
Hypnea	Tampa Bay	15-35	28-32	Dawes et al. (1976)
Acanthophora	Tampa Bay	15-36	30-36	Dawes et al. (1978)
Gracilaria	Tampa Bay	18-36	30	Dawes et al. (1978)
Hypnea	Tampa Bay		24-32	Durako and Dawes (1980)
Gracilaria	Tampa Bay		25–28	Friedlander and Dawes (1984a,b)
Rhizophytes				
Halimeda	Biscayne Bay	17-36	30-31	Biber (2002)
Halimeda	Biscayne Bay	19–34	30-32	Thorhaug (1976)
Halimeda	Card Sound	15-36	30	Bader and Roessler (1971)
Penicillus	Biscayne Bay	15-35	27-29	Biber (2002)
Penicillus	Biscayne Bay	19–34	29-31	Thorhaug (1976)
Penicillus	Card Sound	15-36	30	Bader and Roessler (1971)
Caulerpa	Florida Keys	15–34	30–34	O'Neal and Prince (1988)

Table A.6

Salinity ranges and optima (practical salinity units, psu) of the three functional groups of macroalgae modeled, from reported literature on seagrass habitats in Florida and nearby regions

Group/species	Location	Range	Optima	Reference
Drift				
Drift	Biscayne Bay	7.0–35	15-35	Biber (2002)
Hypnea	Tampa Bay	15-45	20	Dawes et al. (1976)
Acanthophora	Tampa Bay			Dawes et al. (1978)
Acanthophora	Tampa Bay	10.0-50	15-20	Dawes et al. (1978)
Gracilaria	Tampa Bay	10.0-50	30	Dawes et al. (1978)
Gracilaria	Tampa Bay		30	Friedlander and Dawes (1984b)
Gracilaria	Indian River		24-36	Hanisak and Samuel (1983)
Drift	Indian River		33–34	Benz et al. (1979)

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Table A.6 (Continued)

Group/species	Location	Range	Optima	Reference
Chondria	South Texas	20-40	25-30	Conover (1964)
Dictyota	South Texas	25-35	30	Conover (1964)
Laurencia	South Texas	10.0-30	25-35	Conover (1964)
Rhizophytes				
Halimeda	Biscayne Bay	15-45	20-35	Biber (2002)
Penicillus	Biscayne Bay	15-40	20-35	Biber (2002)
Penicillus	South Texas	15-45	30-40	Conover (1964)
Caulerpa	Florida Keys	27-35	32	O'Neal and Prince (1988)
Caulerpa	South Texas	25-35	30	Conover (1964)
Epiphytes				
Thalassia	Biscayne Bay	15-55	30-45	Biber (2002)
Thalassia—Spirulina	Tampa Bay		20-25	Phillips (1964)
Thalassia—Lyngbya	Tampa Bay		>27.5	Phillips (1964)

Table A.7

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/species	Location	Ν (μΜ)	Ρ (μΜ)	Reference
Drift				
Drift	Biscayne Bay	10	1	Biber (2002)
Gracilaria	Indian River	8–9		Hwang et al. (1987)
Gracilaria	Tampa Bay	<600 ^a	<12 ^a	Friedlander and Dawes (1985)
Gracilaria	Massachusetts	1–2		DeBoer et al. (1978)
Gracilaria	Massachusetts	17–37		Fujita (1985)
Rhizophytes				
Halimeda	Biscayne Bay	40	4	Biber (2002)
Halimeda	GBR	12.5		Abel and Drew (1985)
Penicillus	Biscayne Bay	20	2	Biber (2002)
Caulerpa	West Indies	107		Williams (1984)

^a Growth not saturated.

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