

# Monitoring and Modeling of *Syringodium filiforme* (Manatee Grass) in Southern Indian River Lagoon

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Received: 4 January 2012 / Revised: 2 July 2012 / Accepted: 2 July 2012 / Published online: 2 August 2012  
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**Abstract** Decreased salinity and submarine light associated with hurricanes of 2004–2005 impacted seagrass habitats in the Florida coastal zone. A combination of salinities  $\leq 20$  and light attenuation  $\geq 1.5 \text{ m}^{-1}$  resulting from the freshwater discharge in 2005 were among the drivers for a widespread decrease in the coverage and biomass of *Syringodium filiforme* (manatee grass) in 2006. These observations provided an opportunity to develop and apply a modeling framework to simulate responses of *S. filiforme* to variable water quality. The framework connects water column variables to field monitoring of seagrass abundance and salinity growth response experiments. The base model was calibrated with macrophyte abundance observed in southern Indian River Lagoon (IRL) from 2002 to 2007 and tested against shoot data from a different time (1997–2002) and nearby location in the IRL. Model shoot biomass ( $\text{gC m}^{-2}$ ) was similar to field observations ( $r^2=0.70$ ) while responding to monthly seasonal fluctuations in salinity and light throughout the 6-year simulations. Field and model results indicated that *S. filiforme* growth and survival were sensitive to, and increased with, rising salinity throughout 2007. This modeling study emphasizes that discharge, salinity, and submarine light are inter-dependent variables affecting South Florida seagrass habitats on seasonal to inter-annual time scales.

**Keywords** Seagrass · Model · *Syringodium* · Hurricane · Salinity · Irradiance

## Introduction

The Florida estuaries experienced extreme freshwater input following hurricane passages in 2004 and 2005 (Sallenger et al. 2006; Greening et al. 2006; Castenada-Moya et al. 2010). These discharge events greatly decreased salinity and increased dissolved and suspended material in many coastal basins (Steward et al. 2006; Hagy et al. 2006). In some instances, sediment scouring greatly impacted subtidal habitat composition including seagrass meadows (van Tussenbroek et al. 2008). The cumulative effects of these events included widespread loss and/or changes in seagrass community composition, distribution, and density (Ridler et al. 2006; Steward et al. 2006).

In the northern Indian River Lagoon (NIRL) along the east coast of Florida, the aerial extent of the dominant seagrass *Halodule wrightii* (shoal grass) decreased by 50 % cover after the hurricanes of 2004 and 2005 (Steward et al. 2006). Following the storms, the abundance of *Ruppia maritima* (widgeon grass) in the NIRL fluctuated greatly with discharge induced changes in salinity and light. In another area to the south (Loxahatchee River Estuary or LRE), *Syringodium filiforme* (manatee grass) was abundant until September 2004 but less evident during the post-hurricane period (Ridler et al. 2006). A final example occurred in the Southern Indian River Lagoon (SIRL) near the mouth of the St. Lucie Estuary (SLE) in southeastern Florida where the observed changes in *S. filiforme* in the SIRL from 2002 to 2007 provided the motivation for this study.

Water quality can serve as an indicator of seagrass abundance or vice versa (Morris et al. 2004; Nienhuis 2006; Duarte

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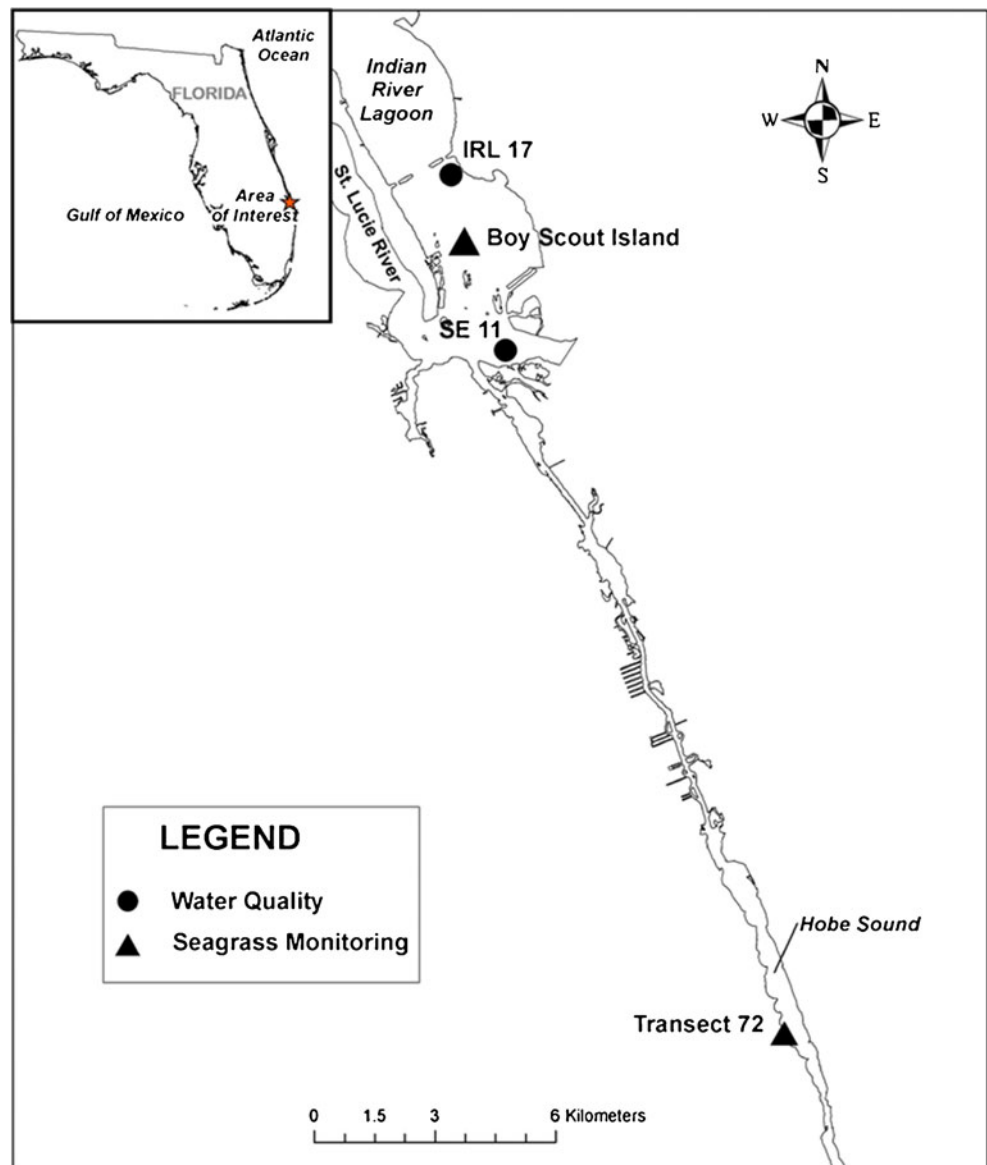
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et al. 2007). The maximum depth of seagrass habitat edge is an often invoked indicator that is highly correlated to light penetration (Gallegos and Kenworthy 1996; Steward et al. 2005; Crean et al. 2006). However, light penetration is governed by both total water depth and the concentrations of dissolved and particulate materials (McPherson and Miller 1994; Christian and Sheng 2003). In this regard, both the quantity (total amount of light at depth) and quality (differential absorbance of multiple visible wavelengths) are relevant (Livingston et al. 1997; Gallegos 2001; Ralph et al. 2007). Light quality is particularly important for Florida estuaries including the IRL where total light attenuation is partitioned among suspended inorganic sediments (60 %), colored dissolved organic matter (CDOM; 15 %), and chlorophyll *a* (15 %; Gallegos and Kenworthy 1996; Christian and Sheng 2003; P.H. Doering unpublished data). Estuarine CDOM concentrations generally behave

conservatively inverse to salinity (McPherson and Miller 1994; Bowers and Brett 2008).

Historically, salinity has not been widely investigated as a modulator of seagrass growth and survival (Montague and Ley 1993; Fong and Harwell 1994; Lee et al. 2007). However, modern changes in the delivery of freshwater to estuaries due to increased consumption in coastal watersheds emphasizes the need to understand responses of estuarine biota to altered salinity (Alber 2002; Montagna et al. 2002; Nienhuis 2006; Lirman et al. 2008). Many estuaries now require minimum freshwater inflows to combat conversion of freshwater to marine habitats and/or salt water intrusion in the coastal aquifer (Ridler et al. 2006; Flemer and Champ 2006). These same estuaries also can experience dramatically increased freshwater volume, decreased salinity, and rapid flushing during extreme discharge events (Hagy et al. 2006; Steward et al. 2006).

**Fig. 1** Location map for study components in South Florida (*inset*) including the St Lucie River Estuary, the BSI and Transect 72 seagrass habitats, and the IRL 17 and SE 11 water quality monitoring stations



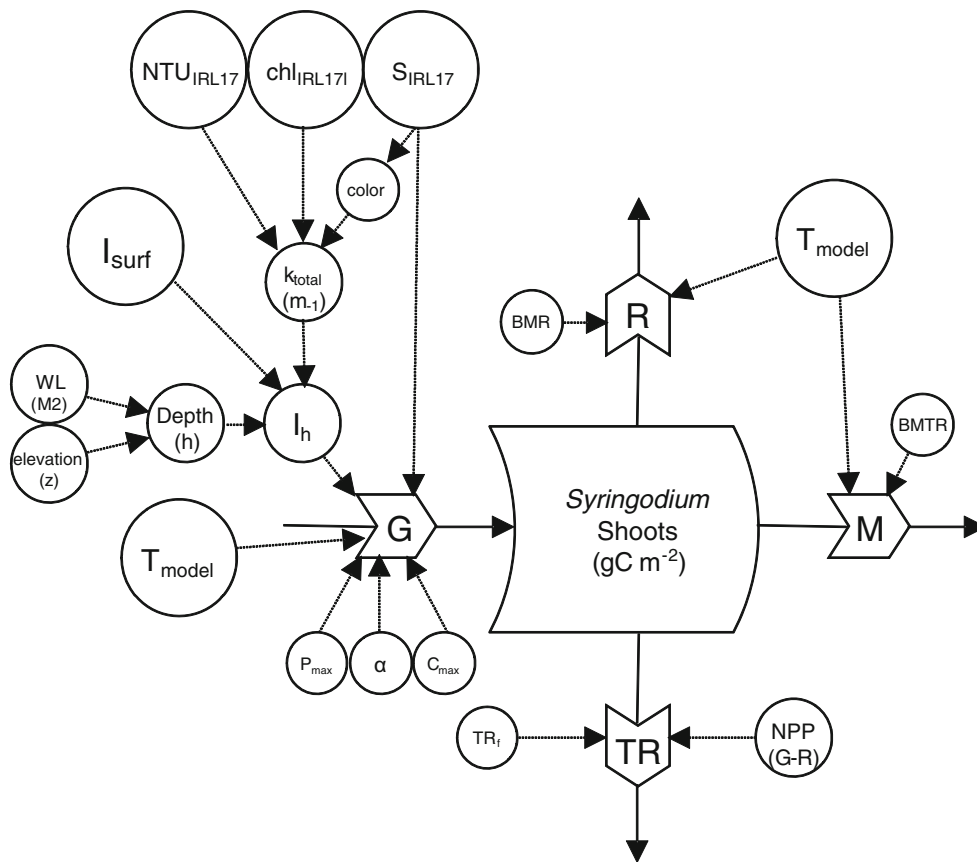
*S. filiforme* is a common tropical to sub-tropical seagrass that has been the focus of many studies (Short et al. 1993; Kenworthy and Fonseca 1996; Major and Dunton 2000; Kaldy et al. 2002; Schwarszchild 2004). While models have been formulated and published for a variety of SAV species (Buzzelli et al. 1999; Burd and Dunton 2001; Eldridge et al. 2004), there has been less effort devoted to *S. filiforme*. Several earlier efforts simulated *S. filiforme* communities under varying environmental conditions in Florida (Fong and Harwell 1994; Fong et al. 1997; Lirman and Cropper 2003). The present study builds upon this foundation by explicitly linking salinity-response experiments, field observations, and water quality records to assess *S. filiforme* dynamics at a particular place affected by intra- and inter-seasonal extremes in environmental drivers over a 6-year period. The model assumptions, equations, calibration data, and parameters will facilitate future usage and adaptation of the simulation framework to other locations.

The primary goal of this study was to better understand how interactive environmental factors affect the survival and growth of seagrass. While this particular study focused on *S. filiforme*, it is part of a larger effort to monitor and model several interacting seagrass species in a variable environment. The specific objectives of this study were to assess observed spatial and temporal patterns of *S. filiforme*, to develop a process-based model to simulate *S. filiforme* growth from days to decades, and to use simulation modeling to investigate potential responses to variable salinity and submarine light.

**Methods**

Modeling Overview

The framework consisted of results from salinity-response experiments, empirically derived SAV distribution and abundance data, monthly time series of water column



**Fig. 2** Conceptual model for *Syringodium filiforme* shoot production. Water level (WL) from M<sub>2</sub> harmonic constituents for St Lucie Inlet is combined with base elevation (z) to predict depth (h) every 3 h from 2002 to 2007. Water temperature (T<sub>model</sub>) and surface irradiance (I<sub>surf</sub>) were modeled using trigonometric functions for 27°N latitude. Average turbidity (NTU), chlorophyll a (chl), and salinity (S) color relationships at station IRL17 were combined to calculate the total submarine light extinction coefficient (k<sub>total</sub>) and estimate irradiance at depth (I<sub>h</sub>). Gross

primary production (G) was a function of I<sub>h</sub>, T<sub>model</sub>, the maximum photosynthetic rate (P<sub>max</sub>), the initial slope of the P vs. I curve (alpha), the maximum attainable biomass (B<sub>max</sub>), and S. Respiration (R) and mortality (M) increase exponentially with T relative to basal rates (BMR and BMTR, respectively). Translocation (TR) fluctuates with net primary production (NPP=G-R) according to the fraction translocated to the root-rhizomes (TR<sub>f</sub>)

constituents, the simulation model, and a suite of potential model applications. The model had an integration interval (dt) of 0.125 days (3 h) with simulations spanning 2,190 days (6 years). The spatial domain of the model base case is the seagrass meadow located near Boy Scout Island approximately 3 km north of St. Lucie Inlet (BSI; Fig. 1).

Each time step the biomass of *S. filiforme* shoots ( $\text{gC m}^{-2}$ ) was calculated as the difference between source (gross primary production or  $G$ ) and the sum of the biological loss terms (respiration, mortality, and translocation; Fig. 2). The model included root-rhizomes as a sink for downward translocation although root-rhizome biomass was not formally calibrated for this study. Estimates of aboveground  $G$  resulted from functions for light at depth “ $h$ ” ( $I_h$ ), temperature ( $T$ ), and salinity ( $S$ ; Eq. 1, Table 1). Each of these functions contained key parameters that determined the specific relationships (Eq. 2; Tables 1 and 2).

The photosynthesis–irradiance relationship was a modified hyperbolic tangent function including the initial slope ( $\alpha$ ; Table 2; Major and Dunton 2000; Eldridge et al. 2004).  $G$  was scaled by the ratio between standing biomass ( $C_{\text{shoot}}$ ) and maximum attainable biomass ( $C_{\text{max}}$ ) as well as the sigmoidal salinity response function (Eq. 2). Increasing temperature ( $T$ ) had the effect to increase  $G$ , respiration

( $R$ ), and mortality ( $M$ ) exponentially relative to an optimal value ( $T_{\text{opt}}$ ). Calibration was used to determine that 35 % of net primary production ( $\text{NPP} = G - R$ ) was moved from the shoots to root-rhizomes each time step ( $\text{TR}_f$ ; Table 2).

Temperature changed daily following a trigonometric function (27 °N latitude; Eq. 3; Table 1). Daily maximum irradiance and photoperiod were modeled using similar trigonometric functions (Eqs. 4 and 5). Water level ( $\eta$ ; m) was modeled using the  $M_2$  tidal harmonics determined for St. Lucie Inlet (Eq. 6) with depth ( $h$ ; m) calculated as the difference between  $\eta$  and the base elevation ( $z_{\text{ref}}$ ; Eq. 7; Table 2). Monthly average values for salinity ( $S$ ), turbidity (NTU), and chlorophyll  $a$  concentration (CHL;  $\text{mg m}^{-3}$ ) were derived from grab samples taken at station IRL17 1.5 km north of BSI (Crean et al. 2006). Because estuarine color is a conservative property, the effect of color on light attenuation ( $k_{\text{color}}$ ) was calculated directly from  $S$  using a negative exponential relationship from data provided in McPherson and Miller (1987; Eq. 9). NTU and CHL values were multiplied by their corresponding coefficients to add to  $k_{\text{color}}$  and attenuation due to pure water ( $k_{\text{water}}$ ; Eq. 8; Tables 1 and 2). The coefficient values were derived from previous studies of S. Florida estuaries, combined with local constituent concentrations, and summed to calculate the

**Table 1** Primary equations used to simulate changes the biomass of *S. filiforme*

Object	Equation
(1) Syringodium shoot ( $C_{\text{shoot}}$ ; $\text{gC m}^{-2}$ )	$\frac{dC_{\text{shoot}}}{dt} = [f(I_h) * f(T) * f(S)] - R - M - \text{TR}$
(2) Syringodium shoot ( $C_{\text{shoot}}$ ; $\text{gC m}^{-2}$ )	$\frac{dC_{\text{shoot}}}{dt} = \left[ P_{\text{max}} * \left( \frac{a * I_h}{\sqrt{P_{\text{max}}^2 + (a * I_h)^2}} \right) * \left( 1 - \left( \frac{C_{\text{shoot}}}{C_{\text{max}}} \right) \right) * \left( \frac{K_{s1}}{1 + e^{-\frac{(S - K_{s2})}{K_{s3}}}} \right) * e^{K_T(T - T_{\text{opt}})} \right] * C_{\text{shoot}} \\ - \left[ \left( \text{BMR}_{\text{shoot}} * e^{K_T(T - T_{\text{opt}})} \right) + \left( \text{BMTR}_{\text{shoot}} * e^{K_T(T - T_{\text{opt}})} \right) \right] * C_{\text{shoot}} - [(G - R) * (\text{TR}_f)]$
(3) Temperature ( $T$ ; °C)	$T = 25 - 5 * \cos\left(\frac{2 * \pi * JD - 32}{365}\right)$
(4) Photoperiod ( $P_{\text{photo}}$ ; h)	$P_{\text{photo}} = 12 - 2 * \cos\left(\frac{2 * \pi * JD}{365}\right)$
(5) Max irradiance ( $I_0$ ; $\mu\text{mole m}^{-2} \text{s}^{-1}$ )	$I_0 = \text{MAX} \left[ \left( I_{\text{amp}} * \cos\left(\frac{2 * \pi * (\text{hour} - 12)}{2 * P_{\text{photo}}}\right) \right), 0.0 \right]$
(6) M2 Water level ( $\eta$ ; m)	$\eta_{\text{Slinlet}} = \text{MSL} + (0.376 * \cos(2 * \pi * \left(\frac{\text{hour} - 0.191}{12.42}\right)))$
(7) Water depth ( $h$ ; m)	$h_t = \eta_t - z_{\text{ref}}$
(8) Light extinction coefficient ( $k_{\text{total}}$ ; $\text{m}^{-1}$ )	$k_{\text{total}} = k_{\text{water}} + [k_{\text{color}}] + [a_{\text{NTU}} * \text{NTU}] + [a_{\text{CHL}} * \text{CHL}]$
(9) Light extinction color ( $k_{\text{color}}$ ; $\text{m}^{-1}$ )	$k_{\text{color}} = a_{\text{color}} * e^{(-b_{\text{color}} * S)}$
(10) Light at depth $h$ ( $I_h$ ; $\mu\text{mole m}^{-2} \text{s}^{-1}$ )	$I_h = I_0 * e^{(-k_{\text{total}} * h_t)}$

Respiration ( $R$ ), mortality ( $M$ ), and translocation ( $\text{TR}$ ) provide the loss terms for shoot biomass (Eq. 1). See Table 3 for all parameter definitions and values

**Table 2** Parameter abbreviations, definitions, units, and values

Abbreviation	Definition	Unit	Value	Source
JD	Julian day	unitless	0–2,190	
$P_{\max}$	Maximum photosynthetic rate	$\text{d}^{-1}$	0.05	M&D
$A$	Initial slope of $P$ vs $I$ curve	$\text{d}^{-1} (\mu\text{mole m}^{-2} \text{h}^{-1})^{-1}$	0.00012	Kaldy et al.
$I_{\text{amp}}$	Amplitude of daily irradiance	$\mu\text{moles m}^{-2} \text{s}^{-1}$	1,000	Data
$C_{\max}$	Maximum shoot biomass	$\text{g Cm}^{-2}$	50	BSI
$K_{S1}$	Salinity constant 1	unitless	1.02	calib/D&C
$K_{S2}$	Salinity constant 2	Ppt	16.8	calib/D&C
$K_{S3}$	Salinity constant 3	Ppt	4.72	calib/D&C
$\text{BMR}_S$	Shoot basal respiration rate	$\text{d}^{-1}$	0.008	M&D
$\text{BMRT}_S$	Shoot basal mortality rate	$\text{d}^{-1}$	0.003	calib
$K_T$	Shoot temperature constant	$^{\circ}\text{C}^{-1}$	0.069	Buzz et al.
$T_{\text{opt}}$	Shoot optimal temperature	$^{\circ}\text{C}$	27	calib
$\text{TR}_f$	Fraction of shoot C to RR	unitless	0.35	calib
MSL	Mean sea level	m	0.000	
$A_{\text{SLinlet}}$	Amplitude of M2 tide at Inlet	m	0.376	NOAA
$\varphi_{\text{SLinlet}}$	Phase angle of M2 tide at Inlet	Radians	0.191	NOAA
$t_{\text{SD}}$	Period of semi-diurnal M2 tide	h	12.42	NOAA
$z_{\text{ref}}$	Base elevation of SAV habitat	m	–1.0	BSI
$a_{\text{color}}$	Coefficient for salinity vs. $k_{\text{color}}$	$\text{m}^{-1}$	2.89	M&M87
$b_{\text{color}}$	Coefficient for salinity vs. $k_{\text{color}}$	$\text{ppt}^{-1}$	0.096	M&M87
$a_{\text{NTU}}$	Coefficient for $k_{\text{NTU}}$	$\text{NTU}^{-1}$	0.062	M&M94
$a_{\text{CHL}}$	Coefficient for $k_{\text{CHL}}$	$\text{m}^{-3} \text{mg}^{-1}$	0.058	M&M94
$k_{\text{water}}$	Light attenuation due to water	$\text{m}^{-1}$	0.049	M&M94

All values for *S. filiforme*

M&D Major and Dunton 2000, data amplitude from observed daily irradiance from local data (Kaldy et al. 2002), BSI Boy Scout Island field observation, calib model calibration including curve-fitting of *S. filiforme* salinity responses derived in suite of SAV experiments (Doering and Chamberlain 2000; Doering et al. 2002; see Fig. 3), Buzz Buzzelli et al. 1999, NOAA <http://tidesandcurrents.noaa.gov>, M&M87 and M&M94 McPherson and Miller 1987, 1994

total light extinction coefficient ( $k_{\text{total}}$ ) for prediction of irradiance at depth (McPherson and Miller 1994; Christian and Sheng 2003).

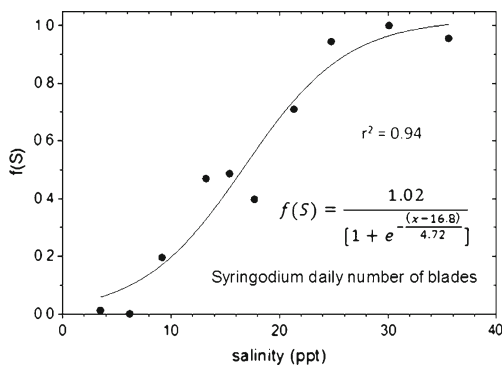
### Salinity Response Experiments

The effects of salinity on the growth and mortality of several SAV species were investigated in mesocosm experiments conducted from 1996 to 2001 (for details see Doering and Chamberlain 2000; Doering et al. 2002). This study incorporated results from *S. filiforme* incubations in model development. Briefly, 4–8 whole *S. filiforme* individuals were planted in rectangular tubs with sediment from a collection site in Biscayne Bay, Florida. There were ten cylindrical mesocosms each with five tubs and a constant water depth of 0.6 m. A 1,000 Watt metal halide lamp with a 12-h photoperiod supplied light to each tank. Target salinities were maintained by mixing appropriate volumes of fresh and salt water from header tanks located above each of the ten

mesocosms. The header tanks emptied into the mesocosms using timer-induced solenoid valves that pulsed water three times daily.

Each mesocosm represented one of ten salinity treatments ranging from 3.5 to 35 over the 34-day incubations. Counts of the numbers and lengths of blades and shoots of *S. filiforme* within each of the five tubs per mesocosm were conducted weekly. Blade lengths from all five tubs exposed to a particular salinity treatment were regressed vs. the exposure time to derive a rate of change in blades per day. The net daily blade production rates were transformed to scalar values and fit to a sigmoid relationship over the range of experimental salinities (Fig. 3). Parameters from this relationship provided the salinity function in the *S. filiforme* shoot gross production equation (Tables 1 and 2). While this parameterization accounted for a decreased gross growth rate, net negative growth required a separate M function increasing linearly from 0.002 to 0.015  $\text{day}^{-1}$  as  $S$  decreased from 15.0 to 0.0.





**Fig. 3** Scalar function to predict effects of salinity on growth of *Syringodium filiforme*. The sigmoidal curve was fit using the total daily blade production (# day<sup>-1</sup>) determined in salinity-response experiments

### Field Monitoring

Boy Scout Island (27° 11' N; 80° 11' W) is located north of St. Lucie Inlet and south of the A1A Bridge in the SIRL (Figs. 2 and 4). This site had an historically dense seagrass meadow which was intensively monitored from 2002 to 2007. Three seagrass monitoring transects were established from the BSI shoreline to the deep edge of the meadow approximately 275–320 m in distance. Different vegetative measurements were taken at various temporal and spatial resolutions. From 2002 to 2007, total percent cover was estimated at regular increments (0.5–10 m) along each of the three transects. At monthly intervals, *S. filiforme* shoot densities. Technically speaking, did not determine for other seagrass species. The biomass and blade attributes of the seagrasses were intensively monitored by coring at 3 locations along each transect every 2 months from 2004 to 2005. Shoots and root-rhizomes for each species were separated, dried, and weighed to derive biomass units (shoots plant<sup>-1</sup>, blades shoot<sup>-1</sup>, cm shoot<sup>-1</sup>, gdw m<sup>-2</sup>).

The initial size of the meadow in 2002–2003 was a maximum of 13.8 ha with *S. filiforme* as the dominant species (Fig. 4a, b). Some *H. wrightii* was observed near the shoreline with more bare sediments occurring northward or upstream from the BSI. This pattern persisted until the sampling and subsequent mapping from 2006 revealed that the meadow extent shrunk to 5.2 ha with an almost a complete loss of *S. filiforme* (Fig. 4e). There was a mixture of seagrass species (including *Halophila* sp.) and bare sediments observed in 2007 (Fig. 4f).

Shoot density at three locations (shore, middle, edge) along the east transect at BSI provided three time series from 2002 to 2007 (Fig. 5a). The intensive data on shoot density and biomass collected in 2004 were used to establish calibration targets in model development. *S. filiforme* shoot biomass was regressed against the corresponding shoot

**Fig. 4 a–f** Location map (inset) and time series (2002–2007) of seagrass habitat near Boy Scout Island in southern Indian River Lagoon. Seagrass community composition, vegetative cover, and shoot density were recorded along three separate transects from the BSI shore to the edge of the seagrass habitat. *Syringodium filiforme* is shown in red with bare bottom highlighted by the light blue color. Aerial images obtained between May and August each year

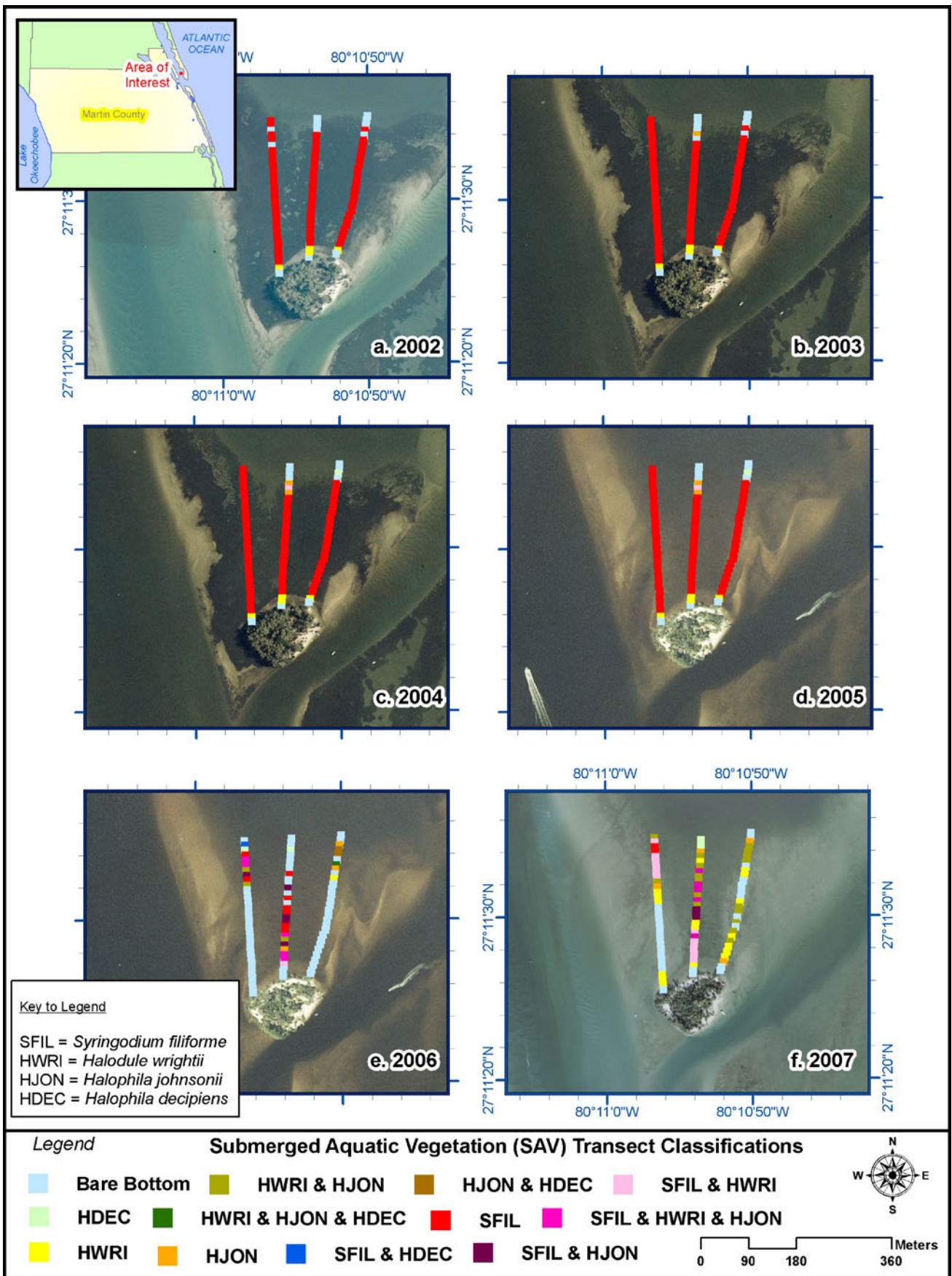
density ( $r^2=0.52$ ; Fig. 5b). The resulting regression equation was used to create an above-ground biomass (gdw m<sup>-2</sup>) time series from 2002 from average shoot densities along all transects. Literature values for shoot carbon (C) contents were used to convert from g C m<sup>-2</sup> (34 %C; Duarte 1990; Schwarzschild 2004). These data and unit conversions provided that target biomass ranges and patterns for the *S. filiforme* simulation model.

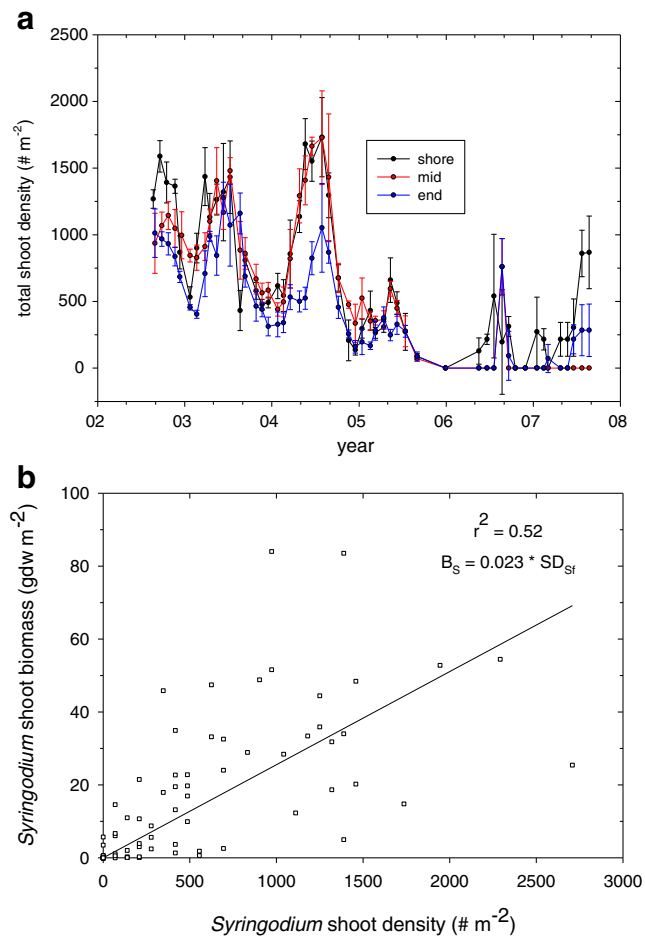
### Model Formulation and Simulation

Key model parameters were adjusted during calibration to improve representation of the base case model to the BSI seagrass habitat from 2002 to 2007. These parameters included the maximum shoot biomass ( $C_{max}$ ) and the basal respiration and mortality rates (BMR<sub>S</sub> and BMRT<sub>S</sub>). However, the greatest model sensitivity was attributable to  $C_{max}$  and the net production fractional translocation (TR<sub>f</sub>).

Base model prediction of shoot biomass was verified by creating a separate 6-year model for a different time and place. Visual censuses for seagrass shoot density and community cover occurred along seagrass transects in the SIRL since the 1990s. Shoot densities observed at Transect 72 in Hobe Sound from 1997 to 2002 were converted to biomass using the previously described regression equations. Biomass predicted using the observed shoot densities were compared to those from the simulation model. Model environmental drivers (S, NTU, CHL) were derived from water quality monitoring data observed at SE 11. SE 11 was the nearest station with the most comprehensive water quality monitoring during this earlier time period (Fig. 1). Finally, an optimal model case was developed to predict maximum biomass and production over 6 years of constant conditions for S (35), NTU (5.2), and CHL (3.5 mg m<sup>-3</sup>). While S was chosen to maximize G, values for NTU and CHL represent average values from IRL 17 from 2002 to 2007. Biomass and net primary production were compared among the three model cases.

High coastal population density and the potential for eutrophication of Floridian estuaries motivated an experimental application of the *S. filiforme* model (Cloern 2001; Kemp et al. 2005). While the present model does not include nutrients or phytoplankton as state variables, effects of increased algal biomass on submarine light penetration and seagrass growth were quantified. Model water column CHL concentrations were increased over the base case in a





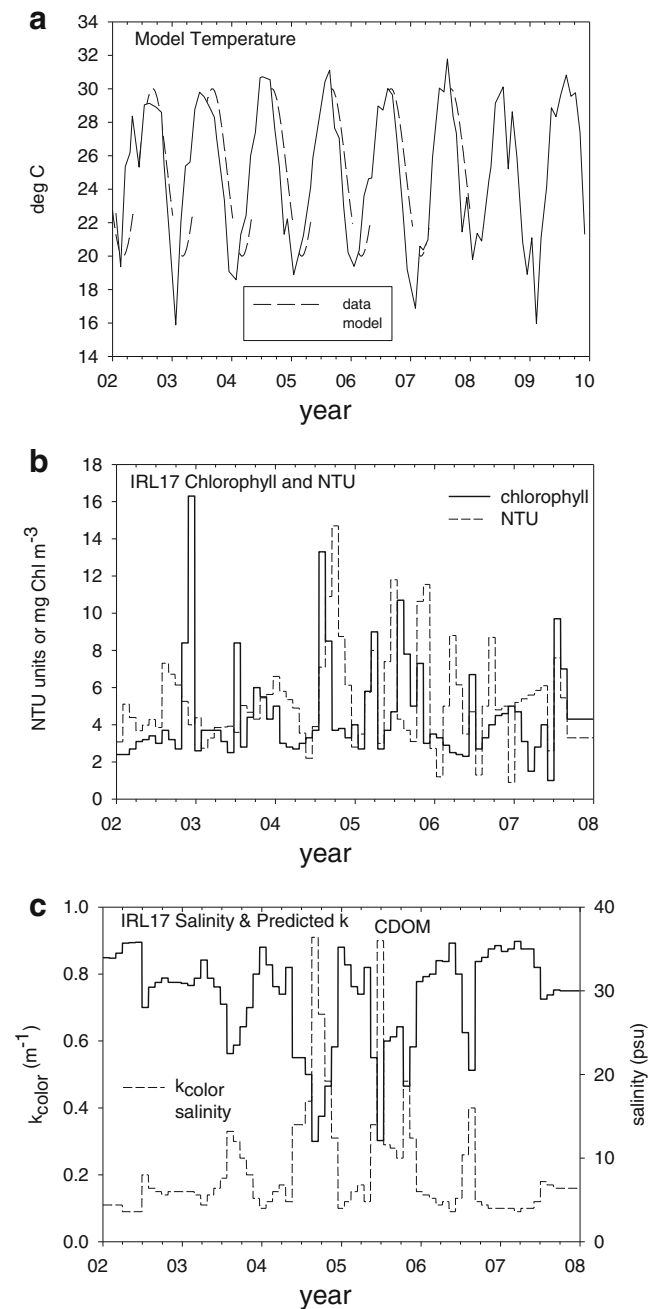
**Fig. 5** **a** Time series of *Syringodium filiforme* shoot density (# m<sup>-2</sup>) at three locations of the east transect at Boy Scout Island from 2002 to 2007. **b** Linear regression and statistics to predict the relationship between *Syringodium filiforme* shoot biomass from shoot density determined at Boy Scout Island from 2004 to 2005

systematic series. The monthly average CHL concentrations from 2002 to 2007 were altered by 0.5×, 1.0×, 1.5×, 2.0×, and 3.0× relative to 6-year base case to assess changes in *S. filiforme* shoot biomass.

Model performance was examined using experiments to isolate and quantify effects of reductions in salinity vs. submarine light. Salinity and attenuation due to color were de-coupled to derive separate modeling experiments each for salinity and light. The 6-year BSI model was split into two 3-year models with the first 3 years (2002–2004) representing favorable salinity and submarine light and the second 3 years (2005–2007) representing decreased salinity and light (i.e. increased  $k_{total}$ ). The 2005–2007 model was then run with either increased salinity (2002–2004 or *S* test) or increased light availability (2002–2004 or  $k_{total}$  test) with all other drivers unaltered from base conditions. Effects of decreased *S* or increased  $k_{total}$  were quantified using the percent difference between base and test conditions (%DIFF=[(Test–Base)/Base]×100).

## Results

Model temperature ranged from 20 °C to 30 °C (Eq. 3; Fig. 6a). The trigonometric model represented in situ temperature data well except for depressed values in the winters of 2003 and 2007. Monthly values for CHL (mg m<sup>-3</sup>) and NTU from IRL17 were on a similar scale ranging from <2.0 to >15 (Fig. 6b). CHL concentrations peaked in December 2002,



**Fig. 6** Forcing functions to drive the Boy Scout Island *Syringodium filiforme* model from 2002 to 2007. **a** Average daily temperature model. **b** Average monthly water column turbidity (NTU) and chlorophyll *a* observed at station IRL 17. **c** Average monthly salinity observed at IRL 17 and light attenuation due to color calculated using Eq. 9



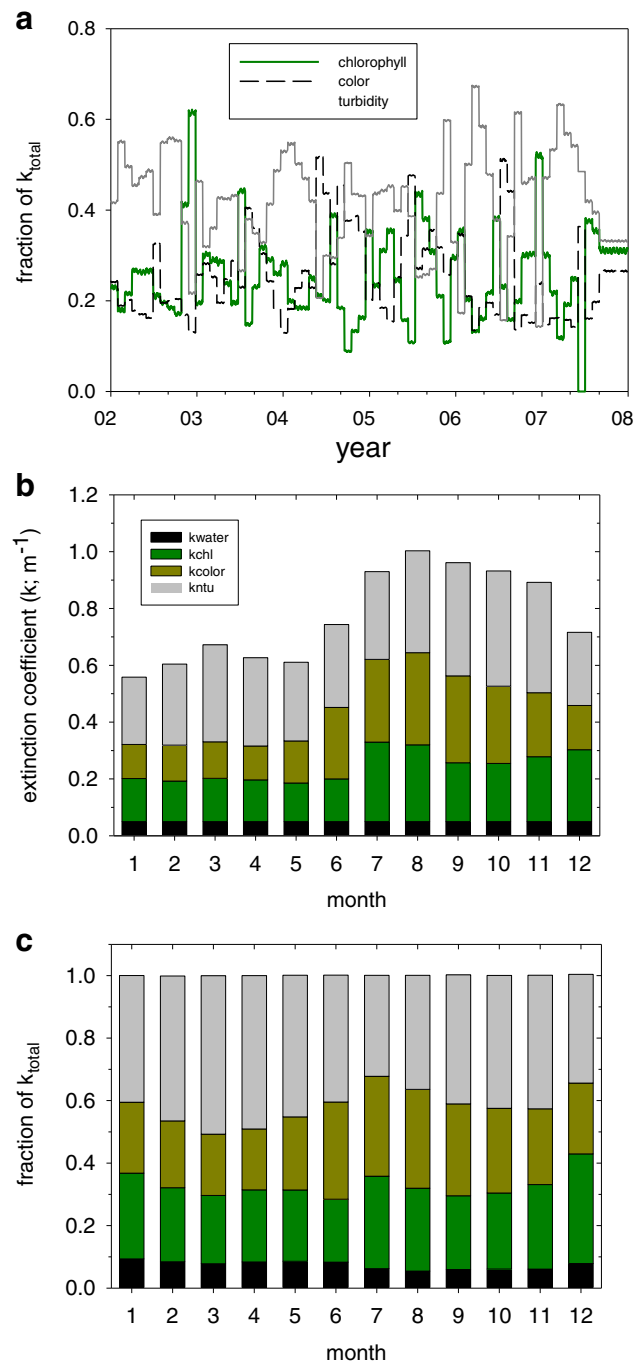
September 2004, and October 2005. Turbidity was greatest in October 2004 and October 2005.  $S$  and  $k_{\text{color}}$  were inversely proportional with minimum  $S$  and maximum  $k_{\text{color}}$  occurring in September/October 2004 and 2005 (Fig. 6c).

The present model uses partitioning coefficients and in situ data derived from the IRL to account for total light attenuation in the seagrass meadow (Fig. 7a; Table 2). The effects of turbidity were apparent throughout the time series while attenuation due to color increased greatly with the freshwater input of 2004 and 2005. Total light extinction was greatest from July to August peaking at  $1.0 \text{ m}^{-1}$  (Fig. 7b). The partitioning of light extinction among components showed that the effects of CHL were greatest in January, July, and December (Fig. 7c). While turbidity always occupied a significant percentage, NTU increased to >50 % of total light extinction in March and April.

The model tracked favorably with field shoot densities converted to  $\text{gC m}^{-2}$  (Fig. 8a). Model shoot biomass was within the range of observed levels in winter and summer 2004, respectively. The model captured the dramatic decrease in *S. filiforme* biomass in 2005 and 2006 while predicting a modest recovery in 2007. Average model biomass was similar to average *S. filiforme* shoot biomass observed at BSI from 2002 to 2007 ( $r^2=0.70$ ; Fig. 8b). The modeling framework was successfully applied to the simulation of shoot density at site Transect 72 using water quality data from SE11 from 1997 to 2002.

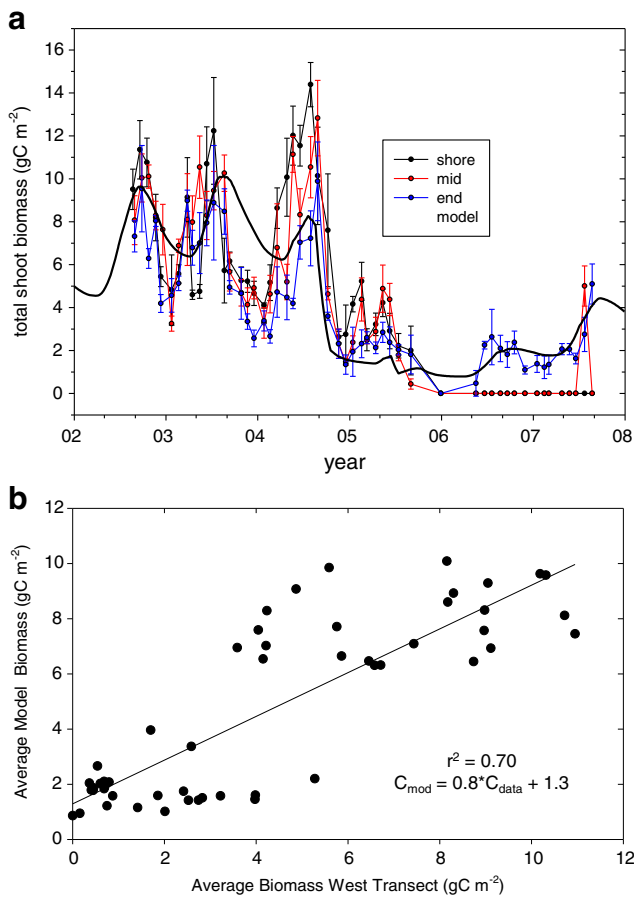
Seasonal surveys of Transect 72 indicated lower *S. filiforme* shoot densities and biomass from 1997 to 2002 ( $1\text{--}7 \text{ gC m}^{-2}$ ) than observed at BSI from 2002 to 2007. While overall depressed, predicted biomass was responsive to the forcing variables ( $T$ ,  $I$ ,  $S$ ) adequately reflecting observed patterns (Fig. 9). Salinity observed at station SE11 from 1997 to 2002 was similar to IRL17 from 2002 to 2007 except for lower extremes at 15 and 35 months of the simulation (Fig. 10a). Despite a significant spike in month 15 of the SE11 time series, turbidity levels were similar between the two time series (Fig. 10b). Water column chlorophyll a concentrations were greater and more variable at SE11 (1997–02) than IRL17 (2002–2007; Fig. 10c). While model runs compared favorably given the subtle differences in environmental drivers, the combined effect of these drivers was to limit the biomass attained by *S. filiforme* when run with the environmental data from SE11 from 1997 to 2002 (Fig. 10d).

*S. filiforme* exhibits a wide range in growth forms, cover attributes, biomass, and net primary production (NPP) values (Kenworthy and Fonseca 1996; Fourqurean et al. 2001; Schwarzschild 2004; Ridler et al. 2006). Shoot densities can range from less than a few hundred to  $>3,500 \text{ m}^{-2}$  at different locations and times (Table 3; Short et al. 1993). Field estimates of biomass are generally  $<100 \text{ gdw m}^{-2}$  although some areas of Florida Bay have extreme values  $>600 \text{ gdw m}^{-2}$



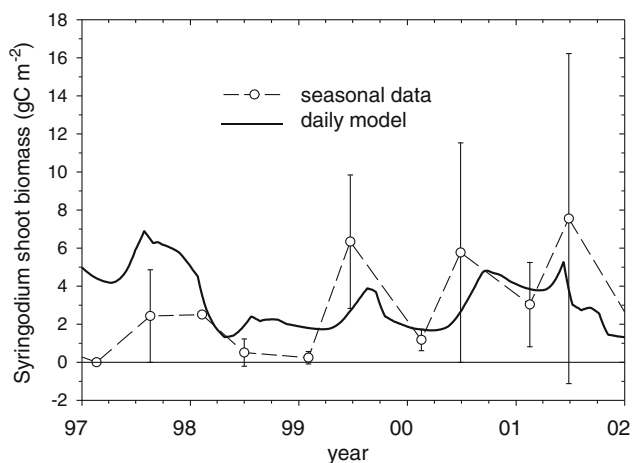
**Fig. 7** Partitioning of submarine light extinction coefficients among chlorophyll a (green), color (brown), and turbidity (gray) from the 2002 to 2007 IRL 17 observations. **a** Time series for each of the three constituents for the extinction coefficients ( $k=\text{m}^{-1}$ ) including contribution of pure water. **b** Fraction of total light extinction ( $k_{\text{total}}$ ) contributed by each of the four constituents

(Schwarzschild 2004). The LRE and SIRL provided values of 10 to  $150 \text{ gdw m}^{-2}$  (Table 3). Average biomasses predicted among the 3 model cases (BSI, Transect 72, optimal) were 11.3, 7.6, and  $34.8 \text{ gdw m}^{-2}$ , respectively (Table 3).

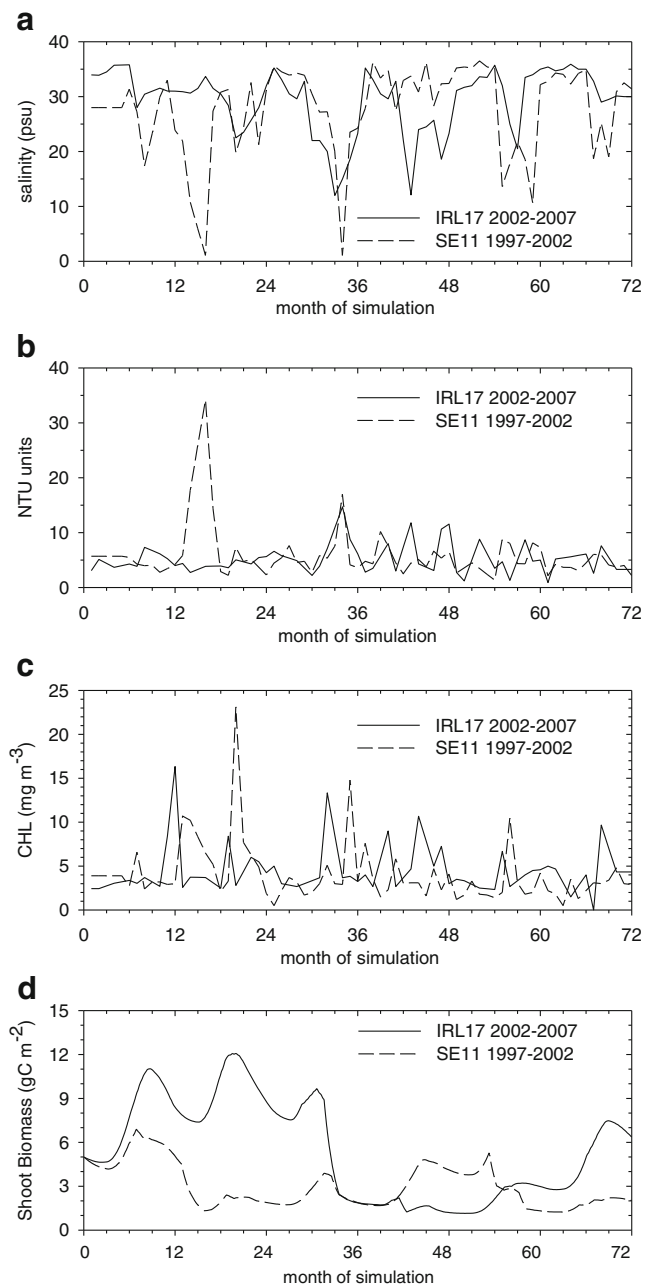


**Fig. 8** **a** Time series comparison of monthly average *Syringodium filiforme* biomass ( $\text{gC m}^{-2}$ ) converted from field shoot densities and that predicted by the model from 2002 to 2007. **b** Linear regression between average monthly values presented in *top panel*

The NPP values provided in Schwarzschild (2004) were among the highest recorded for any seagrass and can be considered as maximum rates. BSI model NPP ranged from



**Fig. 9** Time series comparison of seasonal seagrass monitoring data from Transect 72 and the verification model from 1997 to 2002



**Fig. 10** Time series comparisons between two different versions of the *Syringodium filiforme* model. The baseline Boy Scout Island model was driven with water quality data from IRL 17 observed from 2002 to 2007. The verification model intended to represent long term seagrass Transect 72 south of St. Lucie Inlet was driven with water quality data from station SE11 near the inlet. Both models were run for 2,190 days (72 months or 6 years). **a** Salinity. **b** Turbidity. **c** Chlorophyll *a*. **d** *Syringodium filiforme* shoot biomass

0.3 to 0.9  $\text{gdw m}^{-2} \text{day}^{-1}$ . Macrophyte shoot biomass approached optimal levels during the first 2 years of the BSI base scenario but dropped dramatically with increased freshwater discharge in years 3–5 (2004–2006; Table 4). This decline was not observed in the optimal case with constant environmental conditions. Predicted average

**Table 3** Summary of shoot density (SD; # m<sup>-2</sup>), shoot (S) biomass (BIO; gdw m<sup>-2</sup>), and net primary productivity (NPP; gdw m<sup>-2</sup> day<sup>-1</sup>) for *Syringodium filiforme*

Study	Site	Years	Method	SD	BIO	NPP
Short et al. (1993)	IRL	1982–1983	Cores; marking	300–2,826	87.0±151	2.2
Fourqurean et al. (2001)	FB	1995–1998	Counts; BB	0–1,200 <sup>a</sup>	10–100 <sup>a</sup>	0.15 <sup>a,*</sup>
Schwarzschild (2004)	FB	2000–2001	Cores; marking	3,268, 4,229 <sup>b</sup>	658, 842 <sup>b</sup>	8.8–15.0
Ridler et al. (2006)	LRE	2003–2005	Cores + visual	<400 to <100 <sup>c</sup> <700 to <200 <sup>c</sup>	>150 to <25 <sup>c</sup>	
BSI (this study)	SIRL	2002–2007	Cores + visual; model	521±598 <sup>d</sup>	15.9±19.7 <sup>d</sup> 11.3±6.8 <sup>d</sup>	0.6±0.3 <sup>d</sup>
Transect 72 (this study)	SIRL	1997–2002	Visual; model	412±206 <sup>e</sup>	7.6±1.9 <sup>d</sup>	0.5±0.2 <sup>d</sup>
Optimal 1 (this study)	SIRL	2002–2007	model		34.8±1.0 <sup>d</sup>	2.0±0.01 <sup>d</sup>

Data and results are from Florida Bay (FB), the Loxahatchee Estuary (LRE), and southern Indian River Lagoon (SIRL). Fourqurean et al. (2001) utilized the Braun–Blanquet (BB) method coupled with biomass estimates. *S. filiforme* model values for Boy Scout Island (BSI), Transect 72, and Optimal 1 are averages from years 3–6 of simulation in each case. Data and model conversions assumed 0.35 gC gdw<sup>-1</sup> (Duarte 1990). Either the data ranges or the average±standard deviations were reported

<sup>a</sup> See Figs. 4 and 5 in Fourqurean et al. (2001). \*converted 2.4×10<sup>11</sup> gdw shoots, 4,400×10<sup>6</sup> m<sup>2</sup>=54.5 gdw m<sup>-2</sup> year<sup>-1</sup> to daily rate

<sup>b</sup> See Table 2.1 in Schwarzschild (2004). Study was conducted at two depths (0.5 vs. 1.5) representing different *Syringodium* habitats

<sup>c</sup> See Fig. 3 in Ridler et al. (2006). Surveyed two sites that both experienced decline in *Syringodium* during study period, data range shown

<sup>d</sup> Values at top of cells from field observations; values at bottom of cells from model predictions (this study)

<sup>e</sup> Only visual census and shoot counts, no coring for biomass

biomass and NPP for the BSI base case was approximately 50 % of optimal values in the last simulation year (Table 4). Differences in these spatially normalized rates (gdw m<sup>-2</sup> d<sup>-1</sup>) become much more significant when multiplied by fluctuations in seagrass habitat size (m<sup>2</sup>) to examine changes in total system carbon production with variations in discharge and salinity (Kaldy et al. 2002).

Average water column CHL ranged from 2.2 to 13.4 mg m<sup>-3</sup> in the 0.5–3.0× series to simulate potential bloom effects on seagrass growth (Table 5). Total light attenuation ( $k_{\text{total}}$ ) and percent light transmission to the bottom (% $I_h$ ) decreased and increased by -12.6 % and +6.8 %, respectively, when CHL concentrations were halved. Average annual shoot biomass was -13.6 %, -5.8 %, and -44.7 % lower when CHL was increased by 1.5–3.0× (Table 5).

Model experiments to isolate and quantify the individual effects of salinity vs. submarine light emphasized the

importance of salinity effects on *S. filiforme* shoot biomass (Fig. 11). The 12 % increase in salinity between base and S test versions of the 2005–2007 model led to 86.6 % more shoot biomass from Julian Day 151–941. By contrast in separate submarine light experiments, a 5.7 % decrease in  $k_{\text{total}}$  increased *S. filiforme* biomass only by 17.7 % over the same time period (Table 6).

## Discussion

Freshwater discharge to the estuaries of S. Florida is modulated by climatic, seasonal, and anthropogenic factors over a range of scales (Childers et al. 2006). This is true for all the coastal water bodies including the SIRL and its upstream water body, the St. Lucie Estuary, as the combination of precipitation, managed surface flow, and intense coastal

**Table 4** Comparisons of annual values for *Syringodium filiforme* shoot biomass (gC m<sup>-2</sup>), daily net primary production (NPP<sub>d</sub>; gC m<sup>-2</sup> day<sup>-1</sup>), and annual net primary production (NPP<sub>y</sub>; gC m<sup>-2</sup> year<sup>-1</sup>) resulting from

Year	Biomass (gC m <sup>-2</sup> )			NPP <sub>d</sub> (gC m <sup>-2</sup> day <sup>-1</sup> )			NPP <sub>y</sub> (gC m <sup>-2</sup> year <sup>-1</sup> )		
	Optimal	T72	BSI	Optimal	T72	BSI	Optimal	T72	BSI
3	11.3±2.1	2.4±0.7	6.6±2.7	0.7±0.5	0.2±0.2	0.2±0.3	245.5	55.4	80.4
4	11.9±2.1	3.0±1.3	1.6±0.3	0.7±0.6	0.3±0.2	0.1±0.1	248.9	91.9	26.9
5	12.0±2.0	3.2±1.1	2.2±0.9	0.7±0.6	0.2±0.2	0.2±0.1	249.6	56.7	59.4
6	12.1±2.0	1.7±0.4	5.0±1.9	0.7±0.6	0.1±0.1	0.4±0.3	250.4	43.9	128.8

The average and standard deviations for biomass and NPP<sub>d</sub> and summed annual NPP were calculated for model years 3–6

6-year runs of three different model versions (optimal, Transect 72 or T72, Boy Scout Island or BSI)

**Table 5** Effects of altered water column chlorophyll a (CHL) concentrations on the total light attenuation coefficient ( $k_{\text{total}}$ ) and shoot and biomass ( $C_S$ )

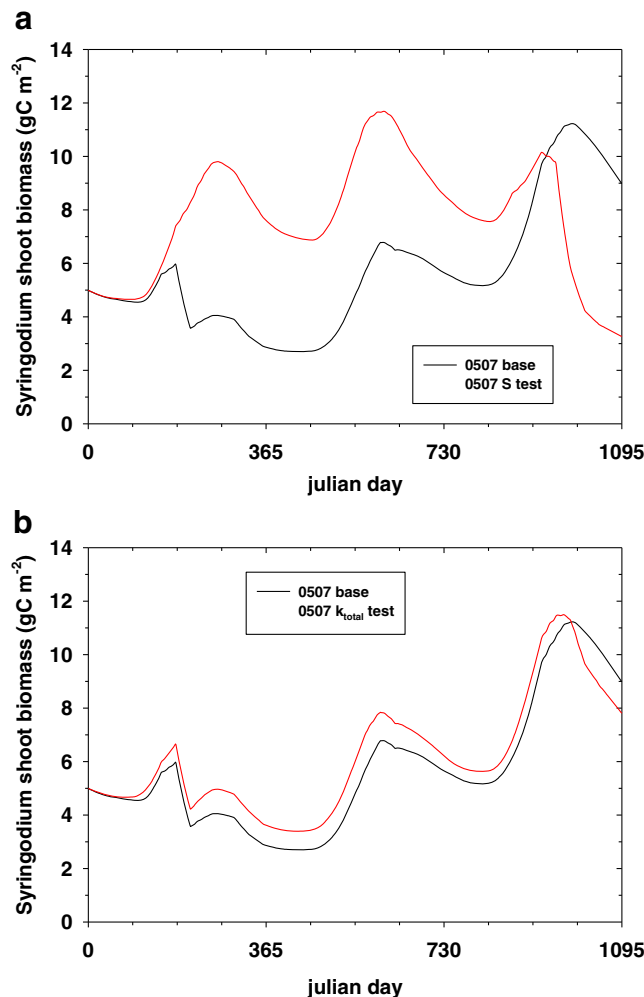
Trial	CHL <sub>avg</sub>	$k_{\text{total}}$	% $I_h$	$C_S$
0.5×	2.2	0.67 (−12.6 %)	31.0 (6.8 %)	6.0 (14.4 %)
1.0×	4.5	0.77	29.0	5.3
1.5×	6.7	0.87 (12.6 %)	27.3 (−6.0 %)	4.6 (−13.6 %)
2.0×	8.9	0.97 (25.1 %)	25.7 (−11.4 %)	3.9 (−25.8 %)
3.0×	13.4	1.2 (50.3 %)	23.0 (−20.6 %)	2.9 (−44.7 %)

Time series of monthly average CHL concentrations from 2002 to 2007 used in the Boy Scout Island base case (1.0×) shown in Figure 8b. CHL magnitudes were reduced (0.5×) or increased (1.5×, 2.0×, 3.0×) in a sequence of different simulations. The average values for CHL,  $k_{\text{total}}$ , percentage of surface light at the bottom (% $I_h$ ), and  $C_S$  over each 6-year simulation are shown along with the (percent difference) from the base case in parentheses

development establish watershed conditions (Sime 2005; Crean et al. 2006). Biological production and biogeochemical cycling naturally increase with temperature, precipitation, and material loading characteristic of the May–November wet season that includes all hurricane activity (Schwarzchild 2004; Childers et al. 2006; Steward et al. 2006; Hagy et al. 2006). However, anthropogenic impacts superimpose extra complexity onto the abiotic inputs and biotic signatures of managed estuaries (Cloern 2001; Alber 2002). These impacts can be synoptic, as in the case of short-term freshwater releases for flood management, or long-term as estuarine salinity increases with heightened consumption of fresh water resources in the watershed (Livingston et al. 1997; Wolanski et al. 2004; Sime 2005; Flemer and Champ 2006).

The distribution of Florida seagrasses is largely modulated by a combination of depth, submarine light, and salinity fluctuations (Montague and Lee 1993; Fong et al. 1997; Livingston et al. 1998; Fourqurean et al. 2003; Steward et al. 2005; Crean et al. 2006; Kahn and Durako 2008). Model results presented here emphasize salinity as a key driver for the distribution and density of seagrass habitats in Florida estuaries. Although salinity fluctuations influence all estuarine biota, it is important to remember that reductions in both salinity and submarine light coincide with increased freshwater discharge to sub-tropical estuaries during the wet season. Therefore, the partitioning of  $k_{\text{total}}$  into its constituents should offer additional insight into relationships between estuarine freshwater inflow, water quality, submarine light, and seagrass survival.

Inorganic suspended solids and CDOM account for approximately 80 % of submarine light attenuation in Charlotte Harbor, Florida Bay, and Indian River Lagoon (McPherson and Miller 1994; Gallegos and Kenworthy 1996; Christian and Sheng 2003; Kelble et al. 2005). The contribution due to CDOM is directly related to proximity and composition of the



**Fig. 11** Results of 3-year model calibration experiments to isolate and quantify individual effects of salinity and submarine light. Three-year (1,095 days) models were created for the 2005–2007 period representing base model, the salinity test case (*S* test), and the light attenuation test case ( $k_{\text{total}}$  test). Average daily *Syringodium filiforme* shoot biomass is shown for base vs. **a** *S* test and **b**  $k_{\text{total}}$  test. See the “Methods” section for details

adjacent watershed (Maie et al. 2006; Bowers and Britt 2008). While overall turbidity is often greatest near the turbidity maximum in a given estuary, large amounts of inorganic suspended material can be released with freshwater discharge (Park et al. 2008; C. Buzzelli, unpublished data). The final component accounting for  $\leq 20$  % of submarine light attenuation in the IRL and other locations is water column CHL (Christian and Sheng 2003; Kelble et al. 2005). This is an important point because short- and long-term increases in phytoplankton biomass related to allochthonous nutrient loading are often invoked manifestations of estuarine eutrophication (Cloern 2001; Kemp et al. 2005; Kelly 2008). *S. filiforme* simulations indicated that biomass could almost disappear with the introduction of low salinity water but decreased by only 40 % with a 300 % increase in water column CHL.



**Table 6** Summary of 3 years (1,095 Julian days) model calibration experiments to isolate and quantify independent effects of salinity (top half) and submarine light (bottom half)

	%DIFF S	%DIFF $k_{\text{total}}$	%DIFF Syring
MIN	-23.3		0.0
MAX	131.5		166.3
AVG±SD	12.0±32.1		86.8±59.2
MIN		-59.4	7.0
MAX		88.7	28.7
AVG±SD		-5.7±17.7	17.7±7.3

The minimum (MIN) and maximum (MAX) values for model salinity (S), the total light attenuation coefficient ( $k_{\text{total}}$ ), and *Syringodium filiforme* shoot biomass (Syring) were from the entire 1,095 days simulation. The average±standard deviation (AVG±SD) and % difference (%DIFF) were calculated using from Julian Day 151 to 941 ( $N=790$  days). %DIFF=[(Test-Base)/Base]×100 where “Test” is the 2005–2007 model run with 2002–2004 (A) salinity and (B)  $k_{\text{total}}$ . See the “Methods” and “Results” sections for details

The distribution and abundance of *S. filiforme* fluctuates with seasonal variations in temperature as well as in response to episodic changes in salinity and light due to weather fronts and associated discharge (Montague and Ley 1993; Fourqurean et al. 2001; Steward et al. 2006). While salinity and light can decline rapidly, levels returned to pre-hurricane levels within 2 months in 2004 but lingered longer with extended discharges late in 2005 (Steward et al. 2006; this study). These periods of freshwater input not only decreased NPP but caused thinning and shrinking of the seagrass habitat (Steward et al. 2006). While the composition and size of the BSI seagrass meadow changed greatly as a result of the wind wave and discharge events of September of 2004 and 2005, long-term seagrass community composition often reflects the hydrologic conditions of the area (Ridler et al. 2006; Lee et al. 2007; Lirman et al. 2008). In fact, recent field surveys (2009–2010) revealed re-establishment of *S. filiforme* across the existing habitat footprint (R. Robbins, unpublished data).

Provided with the optimal environmental conditions representative of a shallow site in Florida Bay *S. filiforme* can achieve very high levels of shoot density, biomass, and NPP (Schwarzschild 2004). However, plant morphology can be extremely variable within and between different locations. For example, differences between *S. filiforme* shoot density and aboveground biomass at the BSI seagrass meadow from 2002 to 2007 account for the variance in the regression relationship presented in Fig. 7b. *S. filiforme* appears to be among the most sensitive seagrasses to fluctuating salinity with an S-shaped response function up to 35 (Fong and Harwell 1994; Lirman and Cropper 2003; Lirman et al. 2008). While the plants used in the mesocosm experiments were from Biscayne Bay and the resulting function was utilized in a study of SIRL, it was assumed that *S. filiforme*

from all environments would exhibit the same salinity response relationship. If this assumption is valid, then plant morphology should reflect environmental conditions and the sigmoidal curve supports the assumed plant preference for near oceanic salinities. More local and regional variable-response-rate studies are needed to quantify effects of multiple inter-related environmental variables on seagrass survival.

Both the rate of change and the duration of decreased salinity have obvious effects on the growth of manatee grass. The sigmoidal curve produces a growth factor that decreases rapidly from 0.75 to 0.2 as salinity declines from 20 to 10 (Fig. 5). Salinities less than 15 triggered net negative growth in experimental mesocosms. Therefore, a moderate depression in salinity during the early wet season (> 24) when water might be released from Lake Okeechobee to the SLE could reduce macrophyte biomass production in SIRL by 20 %. In many of the regional estuaries, it is possible for salinity to return to baseline levels on weekly time scales if meteorological conditions and watershed reserves permit. This is the key consideration for monitoring, modeling, and management of estuarine habitats in S. Florida (Childers et al 2006).

Freshwater inputs via rainfall or watershed management may not be substantial enough to drive changes in seagrass community composition except when low salinity persists in areas historically occupied by *S. filiforme* (Steward et al. 2006). Simulation frameworks provide the capability to quantify the effects independent or multiple environmental drivers on biological survival and production (Buzzelli et al. 1999; Hunt and Doering 2005). Because discharge and salinity fluctuate on daily–weekly time scales, future model versions must be driven by environmental observations at much finer resolutions rather than monthly estimates. Coupling seagrass habitat models to calibrated hydrodynamic models of estuarine circulation enhance the ability to simulate responses of estuarine biota to watershed inputs over a range of temporal (days–decades) and spatial (10–1,000 m) scales.

The variable shoot sizes and allocation of above- to below-ground resources of *S. filiforme* render estimates of net plant growth very difficult and results in few published studies. Like other seagrasses, *S. filiforme* alters above- and belowground morphology and internal storage depending upon local conditions (Schwarzschild and Zieman 2008). These characteristics may have profound implications for the interpretation and application of the *S. filiforme* modeling framework. For example, the present model holds key parameters such as  $C_{\text{max}}$  and  $\text{TR}_f$  (35 %) constant when they are likely to be quite variable in time and space. Minor differences in the capacity of *S. filiforme* populations to accommodate local changes in salinity, light, and nutrients may preclude direct usage of the model approach across all geographic locations. Application of the present model to different geographic locations should be done with specific

consideration for variations in local growth form, field observational methods, and empirical data conversions for comparison to model responses.

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