Modeling epiphytic community production

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ABSTRACT: Mathematical models were used to quantify annual production of the epiphytic community on the saltmarsh cordgrass *Spartina alterniflora.* Hourly measurements of solar radiation and light attenuation (a function of plant canopy and tidal height) were used as forcing functions in the model. Steeper initial slopes (α) of photosynthesis vs. irradiance curves (*P-I* curves) were estimated in the summer (when the canopy was densest), indicating highest shade adaptation. Model validation showed a good agreement between actual hourly production measurements and hourly predicted net production ($r^2 = 0.90$). Predicted areal epiphytic community production was negative during all seasons and higher in the high marsh (short *S. alterniflora* zone) than in the low marsh (tall *S. alterniflora* zone), due to a more open canopy and less exposure to tidal waters. The results indicated that the epiphytic community on *S. alterniflora* in North Inlet is an energy sink (i.e. net heterotrophic community). When irradiance values were held constant at 615 µmol photons m^{-2} s^{-1} (mean daily irradiance value during daylight), production values were overestimated by 11.68 to 34.77 %. Therefore, building quantitative models that include hourly changes in light is key to the realistic estimation of epiphytic production in salt marshes.

KEY WORDS: Epiphytic community production · Mathematical modeling · *P-I* curves · Salt marsh · *Spartina alterniflora*

INTRODUCTION

A realistic and useful approach to estimate production is provided by mathematical models. Overall, production models describe photosynthesis with or without photoinhibition. The main parameters shown on photosynthesis vs. irradiance (*P-I*) curves have been used to develop these models: α (initial slope of the light saturation curve), P_{max} (maximum photosynthesis), and β (present when photoinhibition occurs, it represents the slope of the descending curve at high irradiances). Commonly, the hyperbolic tangent model of Jassby & Platt (1976) is applied when there is no photoinhibition. However, less complex and widely used models such as Smith's (1936) and Talling's (1957a,b)

can also describe *P-I* curves when photoinhibition is not observed (Lederman & Tett 1981). The models described by Steele (1962), Vollenweider (1965), Fee (1969), Parker (1974), and Platt et al. (1980) can be used when photoinhibition occurs. However, Coutinho & Zingmark (1987) suggested that only the parameters described in Platt et al. (1980) had a biological basis.

Traditional production models, such as the ones cited above, are used to extrapolate short-term photosynthetic rate measurements (e.g. hourly) to estimate daily, monthly, and annual production (Pinckney & Zingmark 1993). However, daily variability in production due to diurnal fluctuations of incident radiation cannot be accurately represented just by simple extrapolation (Peña et al. 1999), which generally re-

sults in overestimating production rates during periods of low irradiance (early morning or late afternoon). Also, extrapolating daily irradiance from a single hourly measurement does not yield accurate results, because fluctuations in irradiance during the day are not considered (Pinckney & Zingmark 1991). Therefore, accurate hourly estimates of daily photosynthetically active radiation (PAR) are necessary when modeling daily production, especially for understory intertidal algae. These algae are affected by different light regimes due to tidal cycles (Pinckney & Zingmark 1991, Peña et al. 1999), attenuation effects of the overlying canopy (Morris 1989), and solar angle (McPherson & Miller 1987, Pinckney & Zingmark 1993). According to Peña et al. (1999), the combined effect of plant canopy and overlying water drastically reduce the availability of PAR to algal assemblages during high tide. McPherson & Miller (1987) demonstrated that solar angle alone caused a 50% variation in the coefficient of attenuation (K) within a single day in Tampa Bay, Florida, USA. Pinckney & Zingmark (1993) showed that productivity measurements of benthic microalgae in the North Inlet estuary (South Carolina, USA) could vary largely if solar angles and tidal stages were not considered.

The main goal of the present study was to develop a realistic production simulation model based on the epiphytic community on the cordgrass *Spartina alterniflora* in the North Inlet estuary (NIE), a pristine salt marsh located near Georgetown, South Carolina, USA. This community, comprised of flagellates, cyanobacteria, diatoms, chlorophytes, amphipods, grass shrimp, and periwinkle snails (Grant 1981, Jackson 2004, Quiñones-Rivera & Fleeger 2005, Parker et al. 2008), is a potential carbon source to the commercial fishery stocks in many southern states in the USA (Dame et al. 2000).

MATERIALS AND METHODS

Study area. The NIE (33° 20' N, 79° 10' W) is an enclosed small marsh system (ca. 3200 ha) with a well-defined basin and a single inlet (Pinckney 1994). Tides in this estuary are semidiurnal with a mean range of 1.4 m (Kjerfve et al. 1991).

Spartina alterniflora is the dominant intertidal vegetation and presents well-defined tall and short forms. The tall *S. alterniflora* (≥1.5 m height) zone or low marsh extends along the creeks, while short plants (≤1 m height) are located in the high marsh, i.e. between the high tide line and the low marsh (Pinckney 1994). Due to seasonal variation in aboveground *S. alterniflora* biomass (Dame & Kenny 1986, Morris & Haskin 1990), cordgrass epiphytes are exposed to dif-

ferent irradiance levels under the canopy (Morris 1989). Submersion of these plants at high tides also influences the light regime that epiphytes are exposed to due to variations in water depth and the diffuse attenuation coefficient of the overlying water (Vant 1991).

Epiphytic production. Production experiments were conducted monthly from June 2002 to May 2003. Standing tall, dead *Spartina alterniflora* were randomly sampled at low tide, and their 10 cm bottom-most section, where the highest epiphytic biomass is generally found (Jackson et al. 2006), was cut and incubated at different light intensities. Epiphytes of *S. alterniflora* were incubated intact on their own stem in order to minimize disturbance and keep the original integrity and geometry of the community. The definition of *S. alterniflora* stem in the present study consists of imbricate leaves forming the bottom and middle sections of the plant (culm). In the top section, these leaves are found both imbricate and separate from one another.

Glass shell vials (total volume = 47 ml) were used for incubation, each containing one 5 cm stem segment from the bottom-most part of dead, tall, standing *Spartina alterniflora*. Five cm was the height of the stem that fit into the vials and allowed space to insert an oxygen probe. Stems were placed into 1 cm stem holders (silicon vacutainer caps taken from 13 × 75 mm hematology tubes and glued upside-down to the bottom of each vial with silicon aquarium cement). The 1 cm section of the stem located inside of the stem holder did not receive light and therefore epiphytes on this section were scraped off in order to preclude their contribution to respiration measurements. Vials containing stems were filled by submerging them in a 4 l beaker containing creek water previously filtered through GF/F filters and then capping them while still submerged to avoid contamination by air bubbles. They were then placed upright in a small aquarium (15 × 20 × 30 cm) containing circulating water at constant ambient (creek water) temperature. Incubations were then performed outdoors under full natural light for 30 min. Initial measurements showed that this length of time provided maximum photosynthesis values (P_{max}) compared to incubations carried out for 15, 45, and 60 min. All vials were gently rocked every 5 min.

After the first set of samples was incubated under 100% full sunlight, vials were incubated with progressive layers of neutral density nylon screening to simulate 75, 50, 25, and 12.5% of full sunlight. Six replicates were used for each light intensity. The last set of samples was wrapped in aluminum foil to measure respiration. Multiple measurements were not taken from the same sample because the stirrer of the oxygen meter probe caused epiphytes and sediments to detach from the stems, increasing water turbidity and compromis-

ing the results of incubations. The absolute photon fluence rate (µmol photons m^{-2} s^{-1} of PAR, 400 to 700 nm) was calculated as the average of values taken at 5 min intervals during each incubation using a quantum meter (LI-COR model 185B) connected to a spherical quantum sensor (LI-193S).

Dissolved oxygen (DO, mg l^{-1}) and water temperature (°C) in the vials were measured using an oxygen probe (YSI, model 5905), attached to an oxygen meter (YSI, model 59). Oxygen measurements were taken by opening the vials inside a small plastic tent (30 × 20 × 20 cm), where a continuous flow of nitrogen was used to displace gaseous oxygen inside the tent. This procedure was applied because initial measurements showed that the oxygen inside the tent diffused into the water (due to the oxygen probe stirrer), increasing the final concentrations of DO in the vials. The oxygen meter was selected to estimate net production because it analyzes sequential samples faster and is non-destructive (Pinckney & Zingmark 1991). Frequent comparisons with Winkler titration differed by ≤1%. A major drawback of the oxygen method is a possible overestimation of primary production when NO_3^- is the nitrogen source, because additional oxygen is released during the reduction of NO_3^- to NH_4^+ in the algal cells (Raine 1983). The major nitrogen source in NIE for phytoplankton growth is NH_4^+ (Lewitus et al. 1998); therefore, the oxygen method might have not presented a problem for production estimates associated with the epiphytic community.

Final DO measurements were recorded as the difference between the total DO measured at the end of each incubation and initial DO in the creek water at the beginning of incubation. Following all incubations, water in the vials was filtered through a GF/F filter in order to include, in the final biomass analysis, loose epiphytes detached from the stems due to stirring.

Individual stem diameter was measured, and each stem was gently scraped with a rubber policeman 3 times to remove attached epiphytes (Jackson et al. 2006). Epiphytic biomass was measured as chlorophyll *a* (chl *a*). All chl *a* analyses were performed using a Turner Model 450 fluorometer. Details on this pigment extraction were reported in Jackson et al. (2006).

Modeling *P-I* curves. Several mathematical models (Table 1) were tested to estimate *P-I* curves, and the selection of the best model to fit the experimental data was based on analyses of the fitting curves and their residuals. If photoinhibition occurred, the models of

Steele (1962), Fee (1969), and Platt et al. (1980) were tested. Other photosynthetic models, such as Vollenweider (1965) and Parker (1974), were not considered as they were designed to calculate photosynthesis–depth curves. If no photoinhibition occurred, Jassby & Platt (1976) and Smith's (1936) models were tested.

SAS software (version 6.2 for MacIntosh, SAS Institute) was used to perform all *P-I* curve fitting (through nonlinear least-squares regression) and determine its residuals. Nonlinear regression used the derivative-free Dudley algorithm of Ralston & Jenrich (1978) to fit *P-I* curves. Graph Pad Prism (version 4 for MacIntosh, Graph Pad Software) was used to display the graphs. Initial estimates of the main parameters of the equations (P_{max}, α, and β) were based on visual inspection of *P-I* curves built with raw data points (Gallegos & Platt 1981), where P_{max} is the maximum primary production at light saturation, α is the initial linear slope of the curve and represents photosynthetic efficiency, and β is the negative slope of the curve generated by photoinhibition. The parameters *a* and *n* used in Fee's (1969) equation were the shape parameters of the curve.

Validation of *P-I* curves. *P-I* curves used in the present study were validated by randomly splitting the monthly incubation data in half. Each half was treated as an independent set of data and was run separately. The suitability of the equations were evaluated based on: (1) r^2 values, (2) how closely the data sets followed the raw data plots, (3) how closely the data sets matched each other, and (4) random distribution of the residuals along the *x*-axis.

Production model. The production model developed in the present study was based on the models developed by Pinckney & Zingmark (1993) for the benthic microalgal community in NIE and by Peña (1998) for mangrove-associated epiphytic macroalgae in Colom-

Table 1. Models used to build seasonal *P-I* curves of the epiphytic community on *Spartina alterniflora* in the North Inlet estuary, South Carolina, USA. The equations were recast in terms of *P* (final primary production), α (initial slope of the light-saturated curve), P_{max} (maximum photosynthetic rate at I_k, i.e. minimum light intensity necessary to produce saturated photosynthesis). *I* is the irradiance at which measurements were made; P_s is similar to P_{max} and numerically equal when β = 0. The shape parameters of the curves are indicated by *a* and *n* in Fee's (1969) equation. *R* (respiration) was inserted into the original equations

Equation	Source
Photoinhibition	
$P = \alpha I \times \exp(-\alpha I / P_{max} e) + R$	Steele (1962)
$P = P_{max} \times (I/I_k)/\{[1 + (I/I_k)^2] \times (1 + (aI/I_k)^2)]^n\}^{1/2} + R$	Fee (1969)
$P = P_s \times [1 - \exp(-\alpha I/P_s)] [\exp(-\beta I/P_s)] + R$	Platt et al. (1980)
No photoinhibition	
$P = P_{max} \times \{(\alpha I)/[(P_{max})^2 + (\alpha I)^2]^{1/2}\} + R$	Smith (1936)
$P = P_{max} \times [\tanh(\alpha I/P_{max})] + R$	Jassby & Platt (1976)

bia, South America. The model incorporated 3 parameters considered important in estuarine production of epiphytes on *Spartina alterniflora* in a tidally driven estuary: irradiance beneath the canopy, *in situ* irradiance (i.e. irradiance on *S. alterniflora* stems relative to tidal height), and biomass-specific production (based on *P-I* curves) (Fig. 1).

It was assumed that the light quality was not significantly modified as it passed through the canopy and overlying waters. Various factors that may play an important role in controlling epiphytic production, such as grazing, sloughing/scouring of epiphytes, and self-shading, are difficult to quantify and were not included in the model.

Irradiance beneath the canopy (L_0). The canopy light attenuation (L_0) model developed by Morris (1989) (Table 2) was used to determine hourly average irradiance beneath the canopy of *Spartina alterniflora* from June 2002 to May 2003. Morris' (1989) model includes the following parameters: hourly average incident irradiance above the canopy (L_i) (http://links. baruch.sc.edu/Data/) (Fig. 2), solar declination for the hour interval (β), (HMNAO 2002, 2003) and monthly aboveground *S. alterniflora* weight estimates (w). The canopy weight data for 2002 to 2003 (J. Morris pers. comm.) was restricted to living tall and short *S. alterniflora* plants. Dead *S. alterniflora* weight for these growth forms was calculated based on the ratio between the weight of dead and living *S. alterniflora* (Dame & Kenny 1986). These authors did not measure the biomass of the medium form of *S. alterniflora*; therefore, the production of epiphytes on this plant form was not included in the current final model.

***In situ* irradiance (I_s).** Irradiance beneath the canopy (L_0), diffuse attenuation coefficient (K_d), and depth of the overlying tidal water (z) were used to calculate *in situ* irradiance (I_s) based on the Beer-Lambert Law. The average hourly K_d for NIE waters from June 2002 to May 2003 was computed based on linear regressions between turbidity (nephelometer turbidity units, NTU)
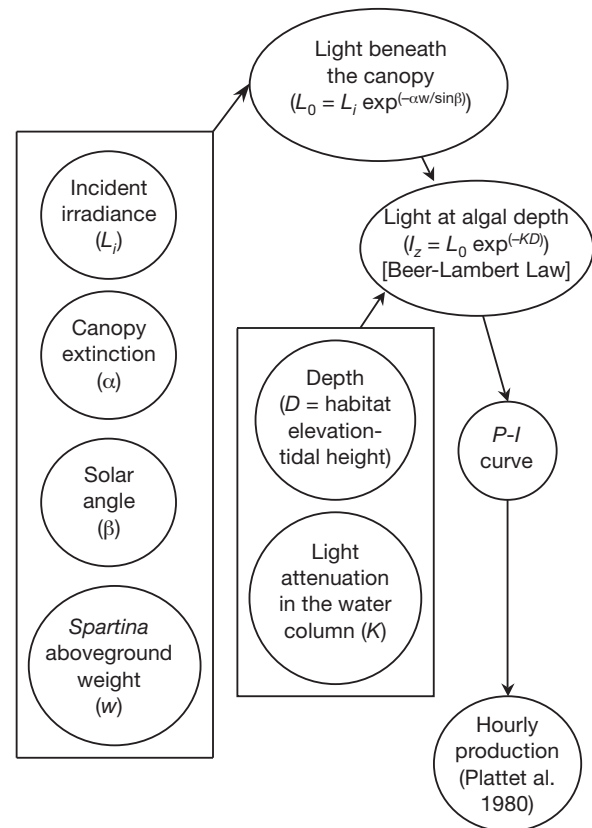

Fig. 1. Conceptual model (adapted and modified from Peña 1998) of the primary factors that affect incident irradiance and production of epiphytes on *Spartina alterniflora*. *I*: irradiance; I_z: irradiance at depth *z*; *P*: photosynthesis; L_0: irradiance beneath canopy

Table 2. Parameters used to build the mathematical production model of epiphytes on *Spartina alterniflora* in the North Inlet estuary. D_s: Secchi disk depth (m); L_i: photosynthetically active radiation (PAR) at the top of the *S. alterniflora* canopy (µmol photons m^{-2} s^{-1}); β: light extinction coefficient in *S. alterniflora* canopy (0.002 m^{-1}) (Morris 1989); *w*: *S. alterniflora* canopy dry weight (g m^{-2}); α: solar angle above the horizon; K_d: PAR diffusion attenuation coefficient (m^{-1}); *z*: depth of the overlying tidal water (m); *I*: irradiance; P_s: maximum photosynthetic rate at I_{ki}; *R*: respiration; P_b: biomass-specific production (calculated using Platt et al.'s 1980 equation); *B*: average monthly epiphytic biomass (mg chl *a* m^{-2} stem)

| Parameter	Units	Description	Equation	Source
K_d	–	Coefficient of attenuation	$1.92/D_s$	Coutinho & Zingmark (1987)
L_0	µmol photons m^{-2} s^{-1}	Irradiance beneath *S. alterniflora* canopy	$L_i \times \exp^{(-\alpha w/\sin\beta)}$	Recast from Morris (1989)
I_s	µmol photons m^{-2} s^{-1}	*In situ* irradiance	$L_0 \times \exp^{(-K_d z)}$	Beer-Lambert law
P_b	mg C mg chl a^{-1} h^{-1}	Biomass-specific production	$P_s \times [1 - \exp(-\alpha I/P_s)] \times [\exp(-\beta I/P_s)] + R$	Platt et al. (1980)
P_{as}	mg C m^{-2} stem	Areal epiphytic production per stem	$P_b \times B$	–
P_{am}	mg C m^{-2} marsh	Areal epiphytic production in the marsh	$P_{as} \times$ no. stems m$^{-2} \times$ surface area stem^{-1}	–
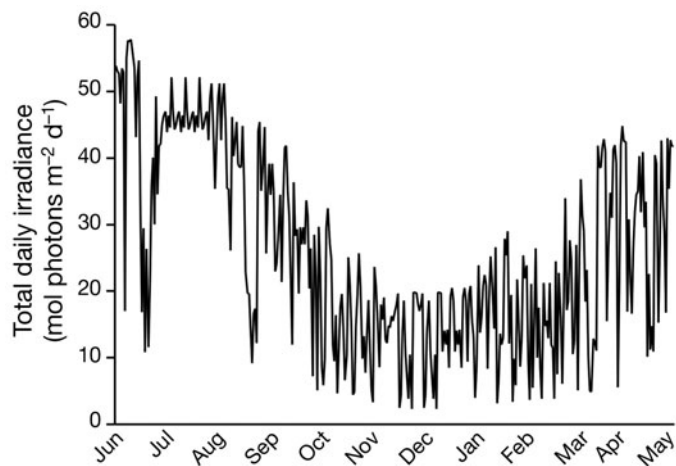
Fig. 2. Daily irradiance from June 2002 through May 2003 at Oyster Landing, North Inlet estuary, South Carolina, USA (http://links.baruch.sc.edu/Data/)

and Secchi disk (cm) measurements taken during 15 consecutive days per month at 2 h intervals during daytime from June 2002 to May 2003. The coefficient of determination (r^2) between those parameters was 0.97, and the equation describing the relationship between them was: Secchi disk = (–0.0845 × turbidity) + 1.7872.

The depth of the overlying water was calculated for each hourly interval during the daytime hours as the difference between tidal height measurements and the average habitat elevation (relative to mean low water) of 0.10 and 0.35 m for tall and short *Spartina alterniflora* zones, respectively. These values were based on the frequency distribution of *S. alterniflora* plants (Morris et al. 2005). It was assumed that the marsh elevation for tall plants in the NIE ranged from 0 to 0.20 m, and short forms were located at elevations between 0.2 and 0.8 m above mean low water (J. Morris pers. comm.). Based on data from Morris et al. (2005), the estimated area occupied by tall and short plant forms in the NIE was 1.75 and 16.25 km^2, respectively.

Tidal height measurements were not available from the National Estuarine Research Reserve System database for Oyster Landing (OL, a site in the NIE) for the months of August through December 2002 and January 2003. The missing data points were estimated from a regression analysis between tidal height measurements of OL vs. tidal height measurements from the NOAA National Water Level Observation Network in Charleston, South Carolina (r^2 = 0.87).

Biomass-specific production (P_b). Biomass-specific production (P_b, mg C mg chl a^{-1} h^{-1}) was obtained experimentally for the bottom section of tall *Spartina alterniflora* forms from June 2002 to May 2003 and was included in the model. It was assumed that it could also be applied to short forms, as the taxonomic composi-

tion of the community on tall and short *S. alterniflora* stems was similar (Jackson 2004).

Model simulation. P_b values were simulated based on hourly I_s (Table 2) incorporated into the equations that best fit the *P-I* curves generated monthly (Table 1). For each day from June 2002 to May 2003, a daily-integrated value of P_b was calculated by summing the values for all the hours from sunrise to sunset, except the hours just after sunrise and just before sunset (i.e. insufficient light for photosynthesis); monthly-integrated values were obtained by summing the values for all days in the month. Monthly values of biomass-specific productivity (mg C mg chl a^{-1} mo^{-1}) were converted to a stem-basis (mg C m^2 stem^{-1} mo^{-1}) by multiplying biomass-specific productivity by the mean chl a biomass m^2 stem^{-1}. Monthly values of epiphytic areal net productivity (mg C m^2 marsh^{-1} mo^{-1}) were calculated separately for the tall and short forms of *Spartina alterniflora*. For each form, monthly areal net productivity was calculated as: [stem-basis productivity × surface area (dead stem)$^{-1}$ × no. dead stems m^{-2} marsh] + [stem-basis productivity × surface area (living stem)$^{-1}$ × no. living stems m^{-2} marsh], where the values of surface area (stem)$^{-1}$ and no. stems m^{-2} marsh correspond to monthly values and were obtained from Morris (1989), Morris & Haskin (1990).

Finally, yearly values of epiphytic areal net productivity were obtained by summing over all months in the year.

Model validation. The simulation model was validated through the analyses of the regression coefficient (r^2) and residual plots from the regression analysis between model-hourly production rates (predicted production) and additional, separate incubations run independently from the ones used to build the model (observed production). A regression coefficient of 0.70 was considered as a minimum value for acceptable reliability of the regression analysis (Cohen et al. 2003). A plot of residuals against the predictor variable was analyzed for linearity of the regression function. If the residuals did not display positive or negative trends, then the appropriateness of the regression model for the data and therefore for the model validation would be supported (Neter et al. 1996).

Sensitivity analyses. Sensitivity analyses (Pinckney & Zingmark 1993) were used to evaluate the effects of model parameters on annual estimates of epiphytic community production. The effects of cloud cover and daily changes in the amount of sunlight on annual epiphytic production were determined by assuming a constant irradiance of 615 μmol photons m^{-2} s^{-1} during the daylight period. The effects of canopy shading and light attenuation during submersion were evaluated by removing each variable and recalculating separately annual production on tall and short *Spartina alterniflora* forms.

RESULTS

The light intensity at the onset of light saturation, I_k, for the epiphytic community on *Spartina alterniflora* ranged between 210 and 609 µmol photons m^{-2} s^{-1}. Analysis of the raw data obtained from the production experiments showed that photoinhibition was evident in all months. Therefore, the models of Steele (1962), Fee (1969), and Platt et al. (1980) were tested to build *P-I* curves. Visual inspection of the curves, coefficients of determination (ranging between 0.50 and 0.80), and residuals showed that the Platt et al. (1980) model was able to best fit the data sets in most of the months (Fig. 3).

The relationship between epiphytic algal biomass and P_{max} was analyzed to determine if production to be incorporated in the model could be predicted based on epiphytic biomass measurements. Least-squares linear regression showed that the coefficient of determination was ca. 0.60. Regression analysis of observed production vs. hourly-predicted production showed a positive relationship with $r^2 = 0.90$.

Net monthly areal production on tall *Spartina alterniflora* ranged from −0.07 g C m^{-2} (July) to −83.7 g C m^{-2} (February), while that on short forms varied between −0.08 (July) and −68 g C m^{-2} (December) (Fig. 4). Monthly values generated by the model showed that epiphytic production tended to follow the day length in
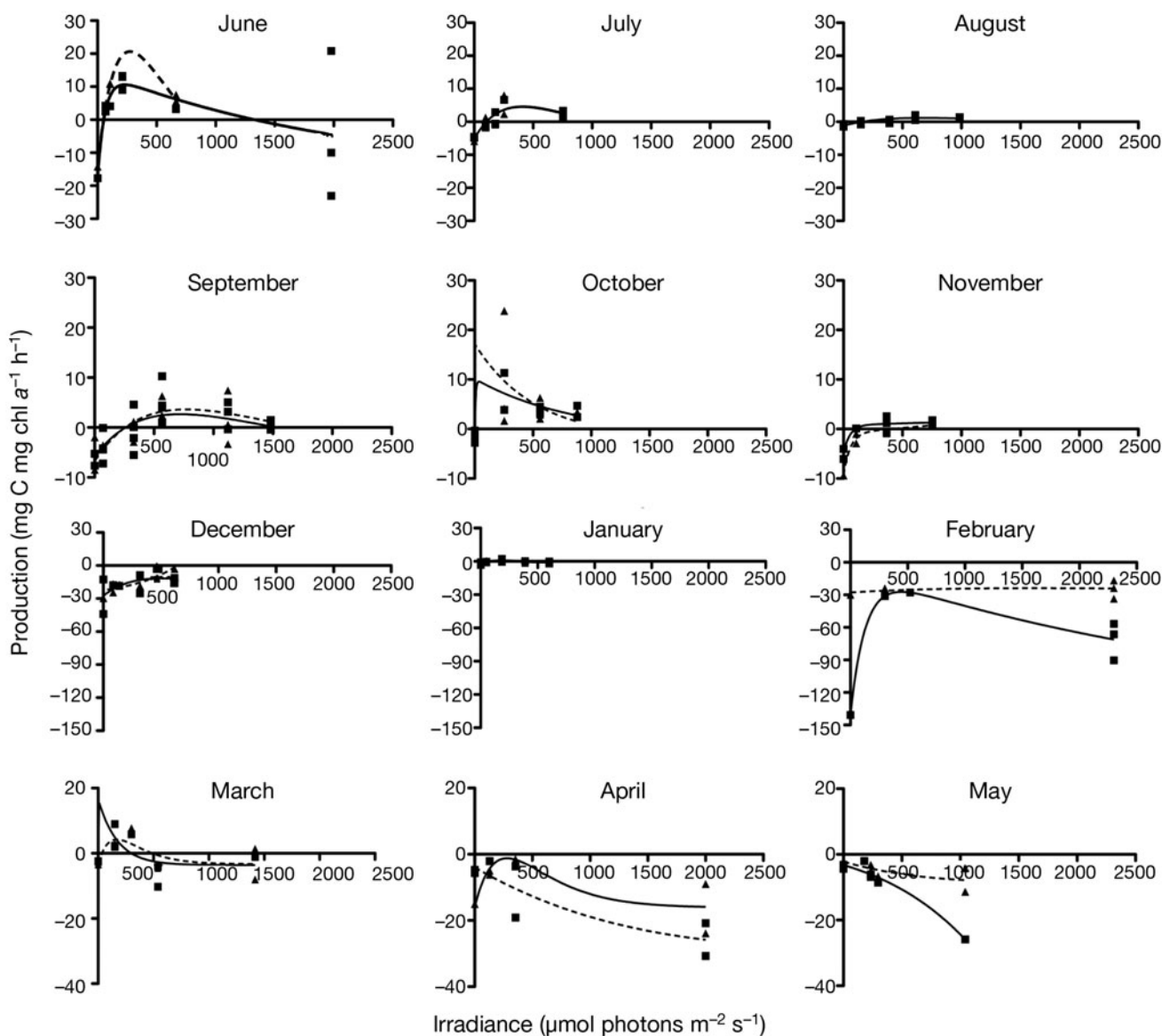

Fig. 3. Photosynthesis vs. irradiance curves built using the model developed by Platt et al. (1980). The raw data were split in half and run separately. (■): raw data for set 1; (▲): raw data for set 2; (—): curve generated by data set 1; (- - -): curve generated by data set 2
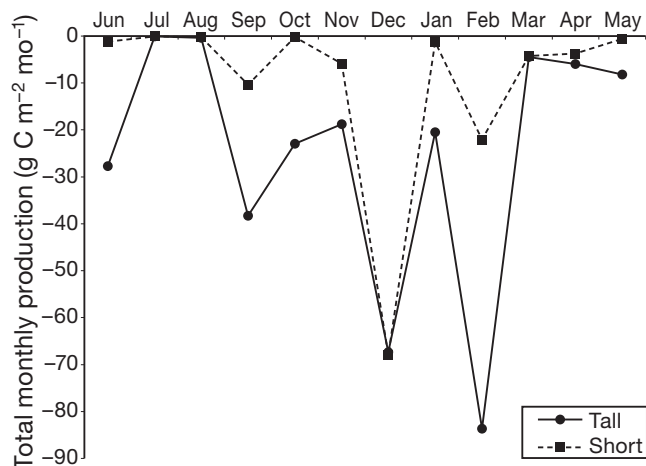
Fig. 4. Model-estimated total monthly production for 2002 and 2003 on tall and short *Spartina alterniflora* (low and high marsh zones, respectively)

each season, with longer days (summer) (Fig. 2) promoting higher production (Fig. 4). Net production on short *S. alterniflora* tended to be greater than on tall plants (Fig. 4).

Total net annual epiphytic production in the NIE was -2.94×10^3 g C. Although annual production was higher on short *Spartina alterniflora* (ca. -143 g C m^{-2} yr^{-1}) than on tall forms (-352 g C m^{-2} yr^{-1}; *t*-test, p = 0.016), total system production on tall plants (-0.6×10^3 g C m^{-2}) was higher than on short plants (-2.3×10^3 g C m^{-2}) (Table 3).

Table 4 shows estimates of annual epiphytic community production when the irradiance was kept constant, and when the effects of canopy and light attenuation by the water column were removed. As a result, the estimated annual production increased but still remained negative. If the irradiance was kept constant, epiphytes on tall *Spartina alterniflora* increased production by 6.5%, whereas epiphytes on short plants increased production by 15.1%. Removing the effects of the canopy caused the annual production to increase by 25.1 and 21.4% on tall and short plants, respectively. When light attenuation was not considered in the model, annual epiphytic community production increases of 41.1 and 12.1% were estimated on tall and short *S. alterniflora*, respectively.

Table 3. Estimates of total annual production of the *Spartina alterniflora* epiphytic community in the North Inlet estuary obtained by multiplication of annual net production by the total area occupied by tall and short *S. alterniflora*, respectively. Estimates of area were based on Morris et al. (2005)

Spartina growth forms	Area (km^2)	Annual net production (g C m^{-2} yr^{-1})	Total system production ($\times 10^6$ g C yr^{-1})
Tall	1.75	-351.7	-615.48
Short	16.25	-142.81	-2320.66

Table 4. Sensitivity analysis of the model of epiphytic production on tall and short *Spartina alterniflora* growth forms. Annual values are reported in g C m^{-2}

Function	Growth form	
	Tall	Short
All parameters included	-351.70	-142.81
Effects of cloud cover and daily changes in light removed	-328.74	-121.32
Effects of light attenuation by *Spartina* canopy removed	-263.43	-112.19
Effects of light attenuation by water column removed	-207.3	-125.63

DISCUSSION

P-I curves

Plots of the raw data in the *P-I* curves showed that production (mg C mg chl a^{-1} h^{-1}) of the epiphytic community on *Spartina alterniflora* stems was variable at each light intensity in almost all months. Natural variability of the epiphytic community production from stem to stem (Jackson 2004) might have contributed to this variability. The lowest epiphytic production was registered in the winter. Even though the canopy was more open to light (Morris & Haskin 1990), lower creek water temperatures during this season likely limited epiphytic production rates.

Photoinhibition occurred in all seasons, suggesting that the epiphytic community was adapted to low irradiance due to *Spartina alterniflora* canopy. The lowest irradiance values occurred mostly during the summer, when the canopy was densest (Dame & Kenny 1986, Morris & Haskin 1990). Steeper initial slopes (higher α values) of *P-I* curves, characteristic of a more photosynthetically efficient, shade-acclimated community, were computed during this season. Alpha (α) is limited by photochemical processes of photosynthesis, and its seasonal pattern is influenced by abiotic factors, such as temperature and light (Platt & Jassby 1976, Côté & Platt 1983). Biotic parameters, such as community structure (Côté & Platt 1983, Binzer & Middelbore 2005), also influence this parameter, but they did not seem to play an important role in the NIE, as the epiphytic community structure remained similar throughout the seasons (Jackson 2004).

Model validation, simulation, and sensitivity analyses

The regression analysis of observed hourly production vs. the hourly production obtained by the model exhibited co-

efficients of determination of 0.90, which showed that the model could adequately predict changes in epiphytic production on *Spartina alterniflora* in the NIE. Daily and seasonal light variability are important factors in deriving production models. For example, sensitivity analyses revealed that if changes in irradiance (due to daily variability and light attenuation by the *S. alterniflora* canopy and water column) are not considered, annual production of the epiphytic community might be overestimated by 6.5 to 41.1 %, depending on the habitat considered (tall or short *Spartina* zones). Changes in irradiance (i.e. PAR) and photophysiological responses to shade habitats (i.e. *P-I* characteristics) played an important role in determining more realistic values of production.

Production estimates and implications for the ecosystem functioning

All production estimates were negative, indicating net heterotrophic metabolism in the epiphytic community on *Spartina alterniflora* stems. It is possible that dead stems were loaded with bacteria and, during the incubation, substantial oxygen consumption masked the epiphytic production. However, despite the presence of a heterotrophic community, a relatively high coefficient of determination (r^2 = 0.60) between biomass of epiphytes and their production suggested that the use of an oxygen meter is a reliable method to measure production of epiphytes on *S. alterniflora* stems. The oxygen method has been commonly used to determine primary production of undisturbed (intact) epiphytic communities (Meulemans 1988), despite the preference of some authors (e.g. Jones 1980, Wear et al. 1999) for the ^{14}C method, which has been considered to provide a more sensitive estimate of the contribution of different taxa to the primary production of the community (Gieskes & Kraay 1986). The ^{14}C method is relatively expensive and slow when handling multiple samples, and it is not free from experimental artifacts and assumptions that may significantly alter production estimates (Hunding & Hargrave 1973, Gonzalez et al. 2008). Comparatively, the oxygen method is non-destructive and allows multiple measurements on the same sample over time (Pinckney & Zingmark 1991).

Monthly and annual epiphytic production differed within *Spartina alterniflora* zones. Generally, higher marsh elevation and consequently shorter periods of tidal submersion contributed to higher production rates in the high marsh (short *S. alterniflora* zone) compared to the low marsh (tall *S. alterniflora* zone). Lower epiphytic respiration levels in the high marsh may also be the result of a limited the number of heterotrophs due to

a lower canopy coverage (lower canopy weight), desiccation stress (high temperature, salinity, and sulfide levels), and a more difficult access from the low marsh to more elevated areas due to dense, tall *S. alterniflora* along the creeks. Higher production in the high marsh also occurs in the microphytobenthos (Pinckney & Zingmark 1993), and indicates a paradox as the most productive habitat — the short *Spartina* zone — is the least utilized by herbivores (Pinckney & Zingmark 1993). However, the presence of just a few predators and abundant food may represent an ideal nursery habitat for herbivores (e.g. meroplanktonic larvae and juveniles) that live in habitats subjected to extreme environmental conditions (Pinckney & Zingmark 1993).

Epiphytic production also differed between seasons. Seasonal trends in P_{max} showed a peak in primary production in the summer and fall (October) followed by a second, smaller peak in the spring (May). This trend also was shown for phytoplankton production in the NIE (Sellner et al. 1976), suggesting that seasonal trends in phytoplankton and epiphytic production are similar and therefore these 2 components of the marsh production may be utilized as food resources during the same period of the year.

Water column nutrient limitation may have caused the lowest production observed in the winter, especially in February. During this season, nitrogen and phosphorus concentrations in the NIE are at their lowest (http://links.baruch.sc.edu/data/). It is known that the low concentration of nutrients during the winter is the most important limiting factor to phytoplankton population growth (Lewitus et al. 1998, 2000). Stowe (1982) suggested that nutrients released by the decaying plant host *Spartina alterniflora* in the winter might be an alternative supply for the epiphytic community. Although *S. alterniflora* senescence is highest during this season in the NIE, nutrients are more available from these plants during the summer, when higher decomposition rates of aboveground *S. alterniflora* occur (Dame & Kenny 1986).

Salt marshes are among the most productive of the earth's ecosystems (Gallagher et al. 1980, Dame & Kenny 1986). Measurements of productivity are necessary to quantify specific potential contributions to food webs, as most species of fish and shellfish landed for commercial and sport in the coastal southern states depend on food and energy supplied by specific producers (Hettler 1989). For instance, epiphytes are preyed upon by *Littorina irrorata* (Currin et al. 1995, R. Zingmark unpubl. data) and *Palaemonetes pugio* (Quiñones-Rivera & Fleeger 2005), which in turn are prey for pennaeid shrimps (Kneib & Knowlton 1995), blue crabs *Callinectes sapidus* (Silliman & Bertness 2002), and bay anchovies *Anchoa mitchilli* (Fulling & Peterson 1999, Dame et al. 2000). The development of

the mathematical model presented in the present study, which was based on hourly variability of irradiance due to different parameters, provides more accurate estimates of production and therefore better estimates of food availability (epiphytes) for the ecosystem.

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