



# A Model for the Growth of Opportunistic Macroalgae (*Enteromorpha* sp.) in Tidal Estuaries

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Received 30th March 2001 and accepted in revised form 25 September 2001

The aim of this work was to develop a model capable of simulating the gross and the net growth of *Enteromorpha* sp. in tidal estuaries. The model was developed for the Mondego Estuary (Western Portugal) taking into account the key factors that control green macroalgae in the area. *Enteromorpha* gross growth was defined as a function of light, temperature, salinity and internal nutrients (N and P). Net growth was defined as gross growth minus respiration. The model was calibrated using a set of experimental data obtained in the laboratory under semi-controlled conditions. Sub-models of tidal height and light extinction coefficient variation were included for predicting macroalgal growth in the field, which constituted the model validation. According to the results, model predictions are well within the observed results, both in the laboratory and in the field. The largest discrepancies between predicted and observed values in the field refer to winter months and July. Possibly at these periods of the year, the prevailing external conditions (very low salinity in winter and high temperature and PFD in July) induced some physiological responses by *Enteromorpha*, which were not described by the model (e.g. sporulation, desiccation).

The model was also used to demonstrate the need to consider dynamic descriptions of the light extinction coefficient in the water column ( $k$ ) when assessing primary productivity in tidal environments. If macroalgal-specific (e.g. nutrient internal status) and site-specific parameters (e.g. minimal and maximal depth, photoperiod) are considered, the present model may be used in a broader scale.

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**Keywords:** *Enteromorpha* growth, model, validation, tidal, light extinction coefficient

## Introduction

In the last decade, the occurrence of an excessive growth of green macroalgae has been reported in a significant number of coastal areas (Kolbe *et al.*, 1995; Sfriso, 1995; Morand & Briand, 1996; Flindt *et al.*, 2000). Most of the works regarding this subject assess the quantification of macroalgal biomass (Lavery *et al.*, 1991; Hernández *et al.*, 1997; Schories *et al.*, 1997), the relationships of macroalgal growth with nutrients (Pedersen & Borum, 1996; Viaroli *et al.*, 1996) and with other external factors (temperature and photon flux density—Rivers & Peckol, 1995; precipitation and river management—Martins *et al.*, 2001) or the impacts of their excessive growth (Valiela *et al.*, 1997; Lopes *et al.*, 2000; Pardal *et al.*, 2000) and subsequent decomposition on the surrounding environment (Viaroli *et al.*, 1992; Neira & Rackemann, 1996). Although some works presented mathematical formulations of macroalgal population dynamics, growth and productivity (Ferreira & Ramos, 1989; Duarte & Ferreira, 1993; Bendoricchio *et al.*, 1993, 1994; Duarte, 1995; Solidoro *et al.*, 1997a, b; Duarte & Ferreira, 1997), there is still a lack

in scientific tools capable of integrating knowledge about macroalgal processes as a way of predicting their growth and productivity in coastal areas.

The aim of this work was to build a mathematical model able to predict *Enteromorpha* growth rates in the Mondego Estuary, taking into consideration previous studies about the factors and processes which control opportunistic macroalgal growth in the system.

## Methods

### *Study site and previous studies*

The Mondego Estuary (Western Portugal) consists of two different arms, north and south, separated by an alluvium-formed island (Murraceira Island) (Figure 1). Large accumulations of *Enteromorpha* spp. (mostly *E. intestinalis* and *E. compressa*) are more frequent in the inner area of the south arm (Pardal *et al.*, 2000). During high tide, the depth in the south arm ranges between 2 and 4 m and tidal range varies between 1 and 3 m. Due to siltation in its upstream section, the water circulation in this arm is mostly dependent on the tides and on the freshwater input from the Pranto River (Marques *et al.*, 1993;

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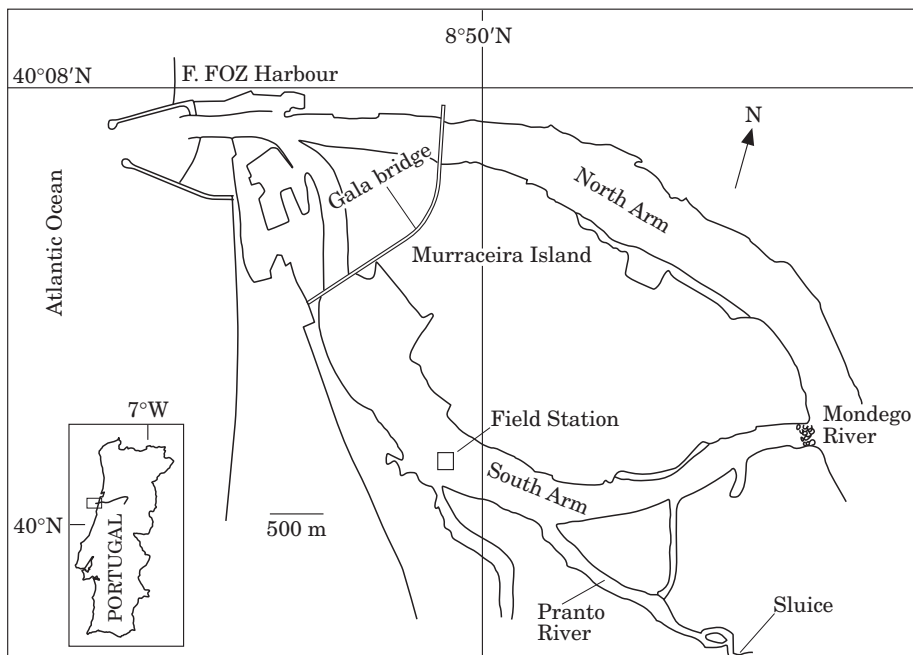


FIGURE 1. The Mondego Estuary with location of the field station in the inner area of the south arm of the estuary.

Flindt *et al.*, 1997). Freshwater discharge is regulated according to the water needs in the rice crop of the Pranto Valley (Martins *et al.*, 2001). For a more detailed characterization of the system see also Flindt *et al.* (1997), Pardal *et al.* (2000), Martins *et al.* (2001).

During the last decade the south arm of the Mondego Estuary has been almost continuously monitored with respect to environmental factors (Marques *et al.*, 1997; Lillebø *et al.*, 1999a; Pardal *et al.*, 2000; Martins *et al.*, 2001), primary producers (Lillebø *et al.*, 1999b; Martins *et al.*, 1999, 2001; Pardal *et al.*, 2000) and consumers (Múrias *et al.*, 1996; Martins *et al.*, 1997; Lillebø *et al.*, 1999a; Lopes *et al.*, 2000; Pardal *et al.*, 2000).

Previous studies with local *Enteromorpha intestinalis* (Martins *et al.*, 1999) showed that its growth varies along a bell-shaped curve with salinity and that the optimum salinity range for growth is 18–22. Nevertheless, *E. intestinalis* is more affected by lower than by higher salinity (Martins *et al.*, 1999). In the Mondego Estuary, *Enteromorpha* spp. biomass is usually significantly reduced in winter but in early spring, macroalgal growth starts to enhance (Pardal *et al.*, 2000). However, there are significant year-to-year differences in the yearly standing crop of *Enteromorpha* spp. (Martins *et al.*, 2001). At the system level, it was concluded that *Enteromorpha* biomass depends on hydrodynamics, which in turn controls salinity, N:P ratios, current velocities and light-extinction

coefficients within the system (Martins *et al.*, 2001).

#### Data for model calibration and validation

Data used to calibrate the model were obtained from the previously mentioned experiments, where the net growth of *Enteromorpha intestinalis* (N=5) was quantified along different salinity gradients in the laboratory (Martins *et al.*, 1999). *E. intestinalis* growth was estimated from wet weight variations assuming exponential growth. Daily measurements of temperature, salinity and photon flux density were taken and, at the beginning of each experiment, nutrients (NH<sub>4</sub>-N and PO<sub>4</sub>-P) were added to water in such a concentration that macroalgal growth was never limited. Experimental time was on average 6 days. For more details see Martins *et al.* (1999).

The model validation was achieved by comparing the predicted *Enteromorpha* growth rates with *Enteromorpha* net growth rates estimated in the inner area of the south arm of the Mondego Estuary (Figure 1). From January 1996 to January 1997, one growth experiment was carried out every month with an approximate duration of 20 days (Martins *et al.*, 2001). In each experiment the weight variation (initial and final weight) of 20 replicates (N=20) was used to estimate *Enteromorpha* net growth assuming exponential growth. In the field, macroalgal replicates were kept inside experimental devices, which were designed

to allow light penetration, water circulation inside and to prevent macroinvertebrates from entering. This experimental procedure was previously described in Martins *et al.* (2001).

#### Model formulation

*Main processes and state variables.* *Enteromorpha* gross growth ( $G_{growth}$ ) is described as a function of maximum growth rate at the optimum temperature ( $\mu_{max}$ ), light ( $f(I)$ ), temperature ( $f(T)$ ), salinity ( $f(S)$ ) and internal concentration of nutrients ( $f(NP)$ ):

$$G_{growth} = \mu_{max} \times f(I) \times f(T) \times f(S) \times f(NP) \quad (1)$$

Macroalgal net growth ( $N_{growth}$ ) is defined by the difference between gross growth ( $G_{growth}$ ) and respiration ( $Resp$ ):

$$N_{growth} = G_{growth} - Resp \quad (2)$$

Respiration is considered temperature ( $T$ ) dependent by an Arrhenius function

$$Resp = R_{max_{20}} \times \theta^{(T-20)} \quad (3)$$

$R_{max_{20}}$  - maximum respiration rate at 20 °C,  $\theta$  - empirical coefficient.

The model state variables are *Enteromorpha* internal nitrogen ( $N_{int}$ ) and internal phosphorus ( $P_{int}$ ) concentrations:

$$\frac{\partial N_{int}}{\partial t} = \psi_{NO3, NH4} - \gamma_N \quad (4)$$

$$\frac{\partial P_{int}}{\partial t} = \psi_{PO4} - \gamma_P \quad (5)$$

$\psi$  - uptake of nutrients (described by equation 12),  $\gamma$  - consumed nutrients (described by equation 13).

*Forcing functions.* The light harvesting efficiency of algae is influenced by light intensity, temperature and nutrients (Duarte, 1995). Therefore, all these factors were considered as model forcing functions ( $f(I)$ ,  $f(T)$ ,  $f(N,P)$ ). Moreover, due to the dependency of *Enteromorpha* growth on salinity evidenced from the work of several authors (e.g. Martins *et al.*, 1999; Kamer & Fong, 2000, 2001), salinity ( $f(S)$ ) was also considered as a forcing function of the model.

*Light.* *Enteromorpha* is photoinhibited by high photon flux densities (Häder *et al.*, 1999), thus Steele's photoinhibition relationship (in EPA, 1985) was

used to describe the effect of light on *Enteromorpha* growth:

$$f(I) = \frac{I}{I_s} \times e^{\left(1 - \frac{I}{I_s}\right)} \quad (6)$$

$I$  - photon flux density that reaches *Enteromorpha* surface,  $I_s$  - optimal photon flux density for photosynthesis.

*Temperature.* According to experimental evidence (e.g. Poole & Raven, 1997), the effect of temperature on *Enteromorpha* growth follows an optimum curve, which may be described by the following expression (Lehman *et al.*, in EPA, 1985):

$$f(T) = \exp \left[ -2.3 \times \left( \frac{T - T_{opt}}{T_x - T_{opt}} \right)^2 \right] \quad (7)$$

$T_x = T_{min}$  for  $T \leq T_{opt}$  and  $T_x = T_{max}$  for  $T > T_{opt}$ ,  $T_{opt}$  - optimum temperature at which growth rate is maximum,  $T_{min}$  - lower temperature limit below which growth ceases,  $T_{max}$  - upper temperature limit above which growth ceases.

*Salinity.* The best fit with the real variation of *Enteromorpha intestinalis* growth rates vs salinity according to the results of Martins *et al.* (1999) was obtained with modified Najarian & Harlem (1975) and Harlem *et al.* (1977) (in EPA, 1985) expressions.

For salinity  $\geq 5$ :

$$f(S) = 1 - \left( \frac{S - S_{opt}}{S_x - S_{opt}} \right)^m \quad (8.1)$$

$S_x = S_{min}$  and  $m = 2.5$  for  $S < S_{opt}$ ,  $S_x = S_{max}$  and  $m = 2$  for  $S \geq S_{opt}$

For salinity  $< 5$ :

$$f(S) = \frac{S - S_{min}}{S_{opt} - S_{min}} \quad (8.2)$$

$S_{opt}$  - optimum salinity at which growth rate is maximum,  $S_{min}$  - lower salinity limit at which growth rate ceases,  $S_{max}$  - upper salinity limit at which growth ceases.

*Nutrients.* The dependency of *Enteromorpha* growth on nutrients was described according to 'Liebig's law of the minimum' (in EPA, 1985), which assumes that only the nutrient in shortest supply limits macroalgal growth. Considering that the optimum interval for the internal N:P ratio of *Enteromorpha* is 12–16

(Björnsäter & Wheeler, 19890), the dependency of *Enteromorpha* growth on the internal ratio of nutrients was described by:

$$\text{If } N:P \geq 12 \text{ and } N:P \leq 16: f(NP) = 1 \quad (9.1)$$

$$\text{If } N:P < 12: f(NP) = f(N) \quad (9.2)$$

$$\text{If } N:P < 16: f(NP) = f(P) \quad (9.3)$$

**Nitrogen.** Experimental evidence (e.g. Björnsäter & Wheeler, 1990; Lavery & McComb in Solidoro *et al.*, 1997a) supports the idea that the dependency of green macroalgae (e.g. *Enteromorpha* spp., *Ulva* spp.) growth on internal nitrogen concentration ( $N_{int}$ ) can be defined by an hyperbolic function of the type:

$$f(N) = \frac{N_{int} - N_{i \min}}{kq + N_{int} - N_{i \min}} \quad (10)$$

$N_{i \min}$  - minimum cell quota or subsistence quota for nitrogen,  $kq$  - nitrogen half-saturation constant for growth limitation.

**Phosphorus.** Chlorophyte macroalgae, like *Ulva* and *Enteromorpha*, have a considerably lower (less than 20%) internal phosphorus concentration than that of nitrogen (Björnsäter & Wheeler, 1990). Additionally, their phosphorus internal variability seems to occur within a narrow range (1–5 mg P g<sup>-1</sup> dw) (Solidoro *et al.*, 1997a). For such reasons, some authors prefer to model the dependency of chlorophyte growth only on external phosphorus and through Monod kinetics (e.g. Solidoro *et al.*, 1997a,b).

However, the work of Björnsäter and Wheeler (1990) suggests that chlorophyte growth depends on internal phosphorus by a linear relationship. This approach was followed in the present model and defined by equations 11. The existence of a maximum internal phosphorus concentration ( $P_{i \max}$ ) is considered, even if experimental evidence suggests that such a concentration is seldom reached (Björnsäter & Wheeler, 1990).

$$\text{If } P_{int} < P_{i \max}: f(P) = \frac{P_{int}}{P_{i \max}} \quad (11.1)$$

$$\text{If } P_{int} \geq P_{i \max}: f(P) = 1 \quad (11.2)$$

#### *Uptake and consumption of nutrients*

As previously described in equations 4 and 5, the variation of internal nutrient concentrations (N and P) is defined by the uptake of nutrients ( $\psi$ ) minus consumed nutrients ( $\gamma$ ).

The uptake of nutrients by *Enteromorpha* is generically defined by:

$$\psi_x = \frac{X_{i \max} - X_{int}}{X_{i \max} - X_{i \min}} * \frac{V_{\max} * X_{ext}}{K_x + X_{ext}} \quad (12)$$

$X_{int}$  - internal nutrient concentration,  $X_{i \max}$  - maximum internal concentration of nutrient,  $X_{i \min}$  - minimum internal concentration of nutrient,  $V_{\max}$  - maximum uptake rate of nutrient,  $K_x$  - half-saturation constant for the uptake of nutrient,  $X_{ext}$  - external concentration of nutrient. In turn, the amount of consumed nutrients depends on macroalgal growth rate, which is generically described by:

$$\gamma_x = X_{int} * G_{growth} \quad (13)$$

$X_{int}$  - internal nutrient concentration,  $G_{growth}$  - gross growth rate.

#### *Sub-models for tidal height and light variation with depth*

Tidal movements in estuaries regulate the depth of immersion of ephemeral macroalgae (Henley & Ramus, 1989). Depth variation caused by tide follows a sinusoidal pattern, which may be described by a generic sinusoidal expression:

$$\text{depth} = a + b * \sin \frac{2\pi t + c}{T_i} \quad (14)$$

where  $a = \frac{d_{ht} + d_{lt}}{2}$ ,  $b = \frac{d_{ht} - d_{lt}}{2}$  and

$$c = \frac{T_i}{2\pi} * \arcsin \left( \frac{d_{(t_0)} - a}{b} \right)$$

$d_{ht}$  - maximum depth,  $d_{lt}$  - minimum depth,  $d_{t_0}$  - depth at time=0,  $T_i$  - time interval between high and low water.

The variation of light (as photon flux density-PFD)( $I$ ) with depth ( $z$ ) was described through Beer's law (e.g. Parsons *et al.*, 1990):

$$I_z = I_0 * e^{-kz} \quad (15)$$

$I_0$  - PFD at the water surface,  $k$  - light extinction coefficient.

The Geophysics Institute of the University of Coimbra provided data on total daily irradiation and daily photoperiod. Daily values of photon flux density at the surface ( $I_0$ ) were calculated from total daily irradiation during the study period following the methodology described in Ferreira and Ramos (1989), which assumes that the visible fraction (400–750 nm) of total irradiation energy corresponds to a

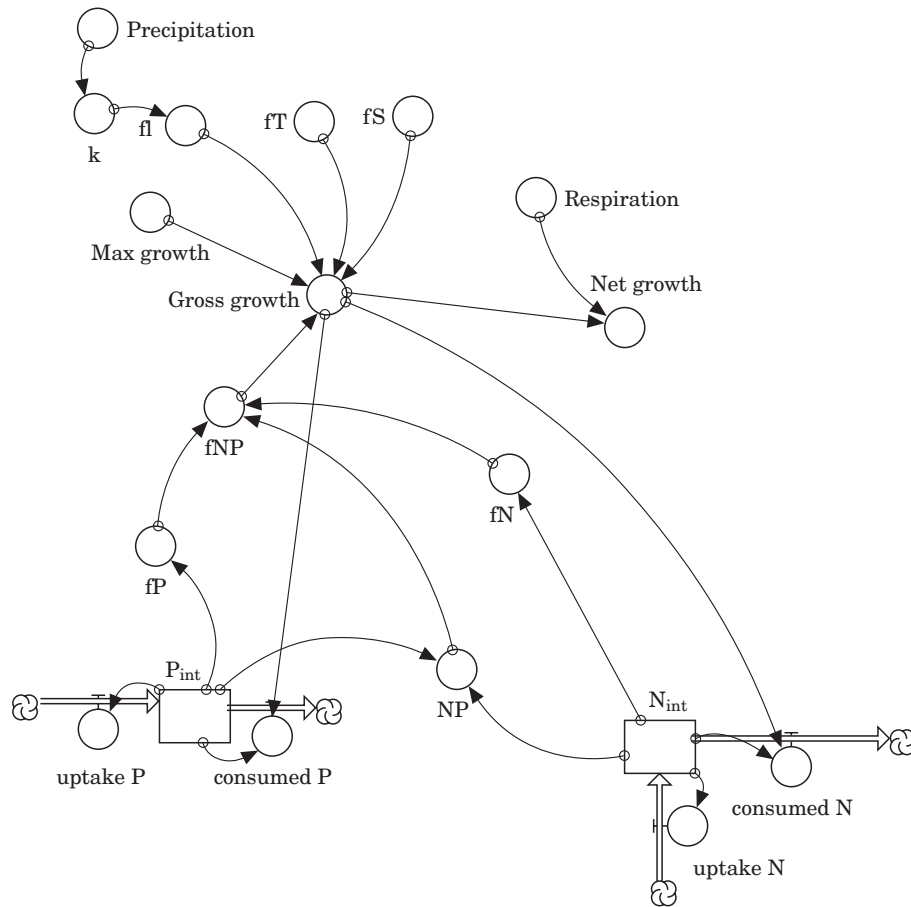


FIGURE 2. Simplified STELLA diagram of the model. State variables: internal nitrogen concentration ( $N_{int}$ ) and internal phosphorus concentration ( $P_{int}$ ). Forcing functions: light limitation factor ( $f(I)$ ), temperature limitation factor ( $f(T)$ ), salinity limitation factor ( $f(S)$ ) and nutrient limitation factor ( $f(NP)$ ).

reduction of 58% of the total and that, consequently, only 42% of the overall energy are available for photosynthesis. Additionally, due to losses related to the angle of incidence of sun and wind stress on the water surface, an average decrease of 15% in the total irradiation was also considered (Ferreira & Ramos, 1989; Parsons *et al.*, 1990). Furthermore, an additional reduction of 48% in total irradiation corresponding to losses related with sediment settling on the surface of experimental cages where *Enteromorpha* individuals were kept was also considered. This value was based on experimental measurements (Martins, unpublished). Photoperiod duration was also considered to estimate daily PFD.

In aquatic systems, primary production also depends on the light extinction coefficient of the water column ( $k$ ). In estuaries, this coefficient presents significant daily and seasonal variations (Ferreira & Ramos, 1989; Kirk in Vergara *et al.*, 1997). Daily variations of  $k$  are caused mainly by tides and are characterized by important increases of  $k$  during ebb

and flood due to re-suspension of bottom sediments (e.g. Vergara *et al.*, 1997). In the Mondego Estuary, the seasonal variations of  $k$  depends mainly on river flow variations, which in turn depends both on precipitation and river management practices (Martins *et al.*, 2001).

To account for seasonal variations,  $k$  was defined by two different expressions (equations 16.1 and 16.2) depending on precipitation. The model also accounts for daily variations of  $k$  through  $k$ -dependency on depth, which varies daily with tidal movements (equation 14). Equations 16.1 and 16.2 are based on real measurements obtained in the Mondego Estuary by the author.

If precipitation < 3 mm:  

$$k = 4.5984 \times e^{-1.0935 \times depth} \quad (16.1)$$

If precipitation  $\geq$  3 mm:  

$$k = 10.853 \times e^{-1.3753 \times depth} \quad (16.2)$$

precipitation is expressed as daily precipitation.

TABLE 1. Definitions and values of the parameters used in the model. All biological parameters refer to *Enteromorpha*. The final values were obtained by experimental procedure, field measurement, literature and/or calibration

Symbol	Description	Units	Used value	Lit. range	Source
$V_{max}$	Maximum growth rate at $T_{opt}$	$d^{-1}$	0.45/experimental, calibration	0.2-1.5	EPA, 1985
$R_{max20}$	Maximum respiration rate at 20 °C	$d^{-1}$	0.05/literature, calibration	0.02-0.1	EPA, 1985
$\theta$	Empirical coefficient		1.047/literature	1.01-1.2	EPA, 1985
$I_s$	Optimum light intensity for photosynthesis	$\mu mol.P.m^{-2}.s^{-1}$	600/literature	500-100	Shellem & Josselyn, 1982; Beer & Shragge, 1987
$T_{opt}$	Optimum temperature for growth	°C	25/measurement	15-30	Shellem & Josselyn, 1982; FitzGerald, 1978;
$T_{max}$	Upper temperature tolerance limit at which growth ceases	°C	35/experimental	max. 42	in Poole & Raven, 1997
$T_{min}$	Lower temperature tolerance limit at which growth ceases	°C	5/calibration	min. -20	in Poole & Raven, 1997
$S_{opt}$	Optimum salinity for growth		18/experimental	18-22	Martins <i>et al.</i> , 1999
$S_{max}$	Upper salinity tolerance limit at which growth ceases		45/literature	max. 95	in Poole & Raven, 1997
$S_{min}$	Lower salinity tolerance limit at which growth ceases		0/experimental	0	in Poole & Raven, 1997; Martins <i>et al.</i> , 1999
$N_{imin}$	Minimum internal quota (subsistence quota) for nitrogen	$\mu mol.N.gdw^{-1}$	500/calibration	499-1717	Solidoro <i>et al.</i> , 1997a,b
$N_{imax}$	Maximum internal quota for nitrogen	$\mu mol.N.gdw^{-1}$	2400/calibration	1928-4285	Solidoro <i>et al.</i> , 1997a,b; Bendoricchio <i>et al.</i> , 1994
$kq$	Nitrogen half-saturation constant for growth	$\mu mol.N.gdw^{-1}$	400/calibration	max. 1786	EPA, 1985
$V_{maxNO3}$	Maximum nitrate uptake rate	$\mu mol.NO_3.gdw^{-1}.d^{-1}$	1732.8/calibration	1200-1406	Bendoricchio <i>et al.</i> , 1994
$V_{maxNH4}$	Maximum ammonium uptake rate	$\mu mol.NH_4.gdw^{-1}.d^{-1}$	4440/calibration	3428-8913	Bendoricchio <i>et al.</i> , 1994
$K_{NO3}$	Half-saturation constant for nitrate	$\mu mol.NO_3.l^{-1}$	12.72/calibration	17.85	in Bendoricchio <i>et al.</i> , 1994
$K_{NH4}$	Half-saturation constant for ammonium	$\mu mol.NH_4.l^{-1}$	20.8/calibration	14-43	in Bendoricchio <i>et al.</i> , 1994
$P_{max}$	Maximum internal quota for phosphorus	$\mu mol.gdw^{-1}$	80/calibration	max. 126	in Bendoricchio <i>et al.</i> , 1994
$P_{imin}$	Minimum internal quota (subsistence quota) for phosphorus	$\mu mol.P.gdw^{-1}$	20/calibration	16-35	in Bendoricchio <i>et al.</i> , 1994
$V_{maxPO4}$	Maximum phosphorus uptake rate	$\mu mol.PO_4.gdw^{-1}.d^{-1}$	96/calibration	178-844	in Bendoricchio <i>et al.</i> , 1994
$K_{PO4}$	Half-saturation constant for phosphorus	$\mu mol.PO_4.l^{-1}$	5/calibration	0.81-3.64	in Bendoricchio <i>et al.</i> , 1994
$d_{lt}$	Minimum depth during low tide	m	0 (intertidal area)		
$d_{ht}$	Maximum depth during high tide	m	2/measurement		
$T_I$	Time interval between high and low water	h	12.5		

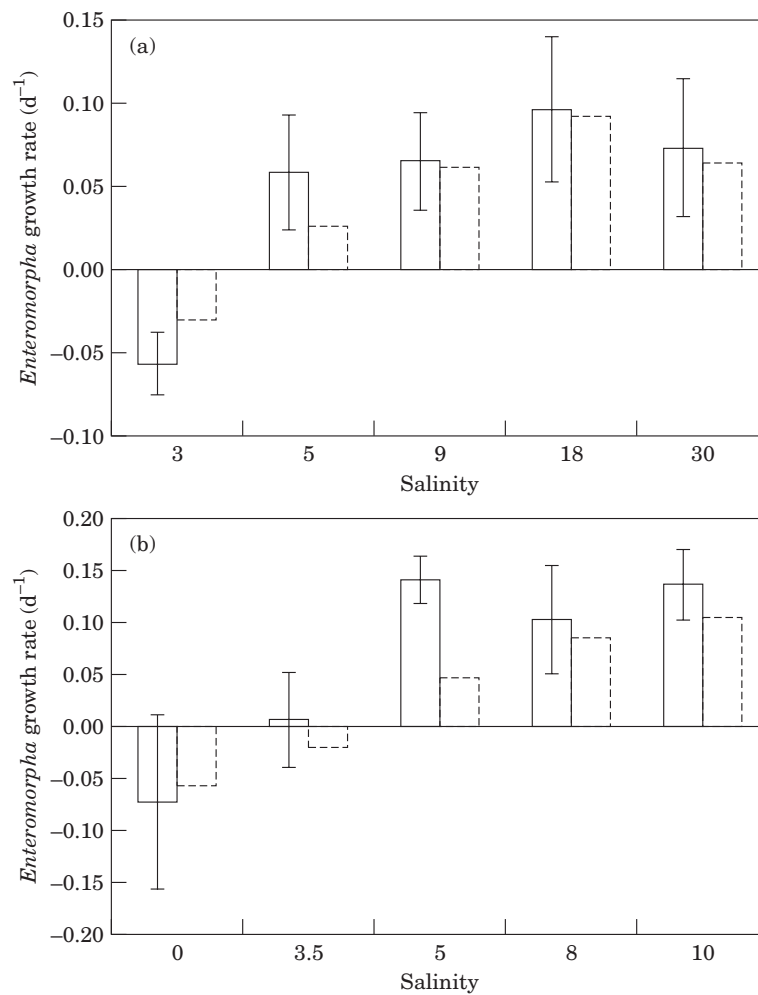


FIGURE 3. Observed net growth rates  $\pm$  standard error ( $N=5$ ) versus predicted net growth rates of *Enteromorpha intestinalis* ( $d^{-1}$ ) estimated in the laboratory at 2 different experiments: (a) within a salinity range of 0–30; (b) within a salinity range of 0–10. Experiment (a) and (b) were run at different times of the year under different natural light conditions.  $\square$  Observed,  $\square$  Predicted.

The model was run with STELLA 5.0 software using a time step of approximately 1 h (1.2 h) for approximately 13 months (397 days). The conceptual diagram of the model is shown in Figure 2 and parameter values are shown in Table 1.

## Results

Model predictions for the variations of *Enteromorpha intestinalis* net growth with salinity were well within the observed results obtained in the laboratory under semi-controlled conditions [Figures 3(a) and (b)]. Except for macroalgal growth at a salinity of five in the second experiment [Figure 3(b)], all the predicted values are within the standard error bars of the observed growth rates. Additionally, the Model II-regression between observed and simulated values

(Sokal & Rolf, 1995; Duarte, 1995; Macedo *et al.*, 1998) is significant (ANOVA,  $P=0.001$ ). The intercept of the regression is not significantly different from 0 and the slope is not significantly different from 1, which highlights the good fitting level between observed and predicted values (Figure 4).

Results from validation suggest that the model is able to predict the yearly variations in the net growth of *Enteromorpha* in the Mondego Estuary (Figure 5). However, in winter and July there are larger discrepancies between observed and simulated results. Although in winter, both the observed and the simulated macroalgal growth rates were negative, which is in accordance with the prevailing external conditions, the observed growth rates were much lower than the simulated ones (Figure 5, values in the legend). Additionally, the model did not predict the negative

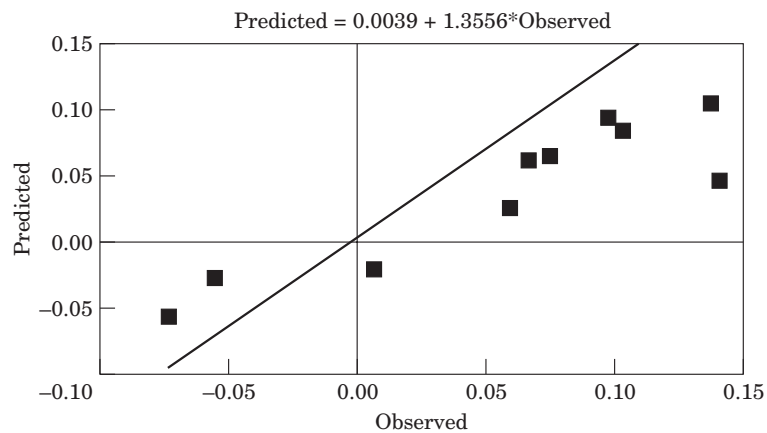


FIGURE 4. Model II regression between observed and predicted net growth rates of *Enteromorpha intestinalis* ( $\text{d}^{-1}$ ) for calibration results (observed values obtained under laboratory conditions). The regression is significant (ANOVA,  $P < 0.001$ ).

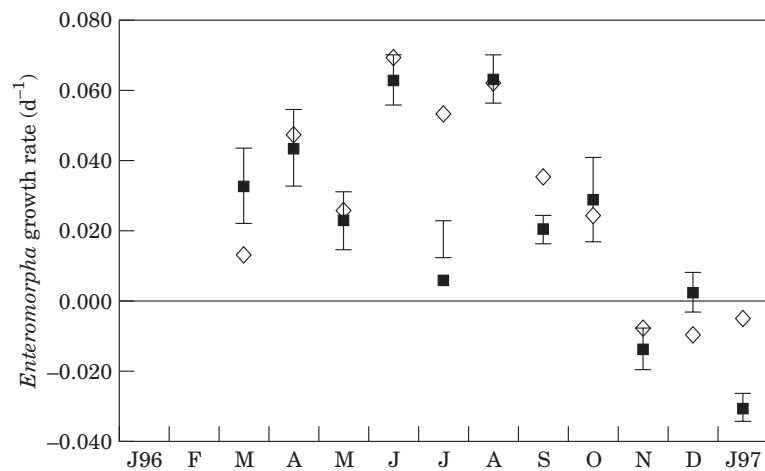


FIGURE 5. Observed net growth rates  $\pm$  standard error ( $N=20$ ) versus predicted net growth rates of *Enteromorpha* ( $\text{d}^{-1}$ ) estimated in the south arm of the Mondego estuary. Real/simulated values of January 1996 ( $-0.33/-0.023 \text{ d}^{-1}$ ) and February 1996 ( $-0.18/0.008 \text{ d}^{-1}$ ) are not shown. ■ Observed; ◇ Predicted.

growth of *Enteromorpha* observed in July. Nevertheless, considering the rest of the months, almost 70% of the predicted values are within the observed macroalgal growth rates (average  $\pm$  standard error) (Figure 5).

To assess for the effects of using a dynamic description of the light extinction coefficient ( $k$ ) or considering a constant  $k$ , the model standard simulation (where  $k$  is precipitation- and depth-dependent) was compared with a simulation using a constant value of  $k$  ( $k=2.76 \text{ m}^{-1}$ ) based on real values (Martins, unpublished). According to the results (Figure 6), *Enteromorpha* growth is considerably lower when  $k$  is described as a constant value, especially during spring, summer and autumn. In winter the results from both simulations show similar values.

## Discussion

The model seems capable of predicting *Enteromorpha* sp. net growth rates close to real values. Nevertheless, predicted growth rates were closer to real ones for data obtained in the laboratory than for field values. This is explained by the higher number of random effects and processes which occur in the field compared to laboratory experiments. Some of these processes (e.g. decay/leaching, sporulation, desiccation) may be related with the occurrence of the largest differences between predicted and observed results during winter and July. Future model approaches on this matter should thus try to describe these processes and the factors that regulate them. The level of importance of such processes may however vary from system to



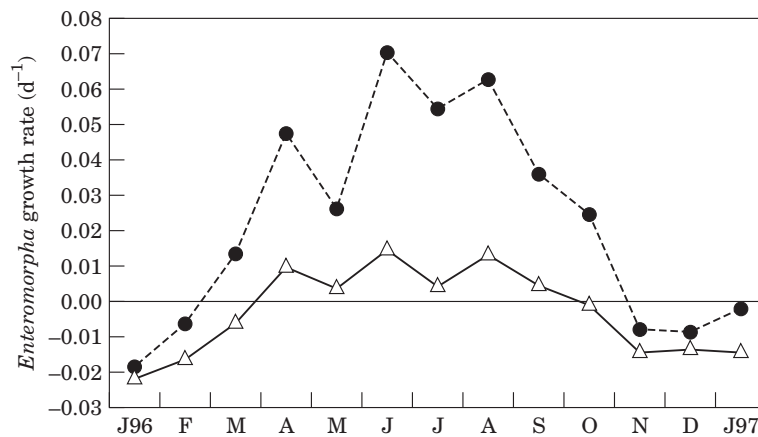


FIGURE 6. Predicted variation of the net growth rate of *Enteromorpha* using a dynamic description of  $k$  and using a constant value of  $k$  (see text for explanation). ● Dynamic description of  $k$ ; △ Constant  $k$ .

system according to natural and geographic characteristics of each system. In the case of systems where summer temperatures and PFD can be high, such as the Mondego Estuary, desiccation stress may be an important process related to the summer decline of macroalgal populations (e.g. Rivers & Peckol, 1995; Hernández *et al.*, 1997).

The present model was deliberately built to predict only *Enteromorpha* net growth, defined as gross growth minus respiration. Although many other processes (e.g. herbivory, advective transport) are important to the final balance of *Enteromorpha* productivity in the Mondego Estuary, the model was only developed to predict macroalgal net growth, in part because reliable quantification of these rates in the field are not easily done. On the other hand, net growth rates of *Enteromorpha* obtained in the field do not correspond exclusively to macroalgal gross growth minus respiration. In fact, although experimental cages were built to prevent grazers from entering (Martins *et al.*, in press), it was not possible to exclude completely the presence of small grazers. This aspect may have contributed to the larger differences between predicted and observed growth rates of *Enteromorpha* in the field compared with results obtained in the laboratory.

Contrary to previous models of primary productivity in tidal systems (e.g. Solidoro *et al.*, 1997a,b), the present model uses a dynamic-description of the light extinction coefficient in the water column ( $k$ ) and demonstrates that such approach generates more accurate results than the previous one. According to the present model, the use of a constant  $k$  (which was based on a real measurement in the Mondego Estuary) underestimates the growth rate of *Enteromorpha* sp. This is explained by the fact that, although

during ebb and flood  $k$  increases assumes low values even during high tide, which is related with shallowness of the south arm of the Mondego Estuary. The importance of using an accurate description of the light extinction, both due to its great variations in tidal systems and its importance to primary production levels (Ferreira & Ramos, 1989), is thus highlighted by these results. In the case of the Mondego Estuary, the seasonal variations of  $k$  are not only dependent on precipitation but also on river management (Martins *et al.*, 2001). Although it is not easy to establish a mathematical formulation between  $k$  and river management practices, the description of  $k$ -variation in the south arm of the estuary may still be improved.

Ultimately, the present model may be understood as the sub-model for the net growth of *Enteromorpha*, which will be integrated in a wider model for the Mondego Estuary. Apart from describing *Enteromorpha* net growth, the new model will also account for other processes (e.g. herbivory, macroalgal transport mechanisms) which are important to the final balance of green macroalgal productivity in the Mondego Estuary.

#### Acknowledgements

The Portuguese Foundation for Science and Technology (FCT) supported this work through a PhD grant attributed to I. Martins (PRAXIS XXI/BD/3744/94).

The authors wish to thank Dr Alves from the Geophysics Institute for providing irradiance data, to Pedro Duarte for critical reading of the manuscript and suggestions, to João Gomes Ferreira and Maria Fiolmena Macedo for discussion and suggestions.

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