Significant variations in the productivity of green macroalgae in a mesotidal estuary: Implications to the nutrient loading of the system and the adjacent coastal area

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Abstract

A spatially dynamic model for the productivity of spores and adults of green macroalgae (Enteromorpha sp.) was developed for a mesotidal estuary (Mondego estuary, Portugal). Many of the algal processes and parameters included in the model were experimentally obtained. Model predictions were compared to a real time series (1993–1997) of macroalgal biomass variation and the two sets show a good agreement (ANOVA, \( P < 0.001 \)). Results suggest that algal growth is highly sensitive to small changes in depth and exhibits different patterns of variation in different seasons. On a yearly basis, global calculations for the south channel of the estuary (137 ha) suggest that during bloom years, macroalgal biomass may reach about 21.205 ton DW compared to 240 ton DW in regular years. On a seasonal basis, the difference may be even more significant. The consequences of such variations on the nitrogen and phosphorus loading of the system and the adjacent coastal area are discussed.

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1. Introduction

In the last decades several ecological models of macroalgal productivity were developed (e.g. Ferreira and Ramos, 1989; Bendoricchio et al., 1993, 1994; Solidoro et al., 1997; Martins and Marques, 2002; Baird et al., 2003) aiming to increase the knowledge about the consequences of eutrophication processes ongoing in many coastal areas around the world (e.g. Ferreira et al., 2007). All these works describe the key processes of algal growth and the relationships with environmental parameters to make valuable predictions about algal growth and biomass per unit area. Nowadays, we have realized that in order to fully understand the impacts of eutrophication, we need to estimate global values of algal production and their impacts both on the local and adjacent coastal systems (e.g. Flindt et al., 1997). Such large-scale assessments, which are able to integrate the causes and effects of eutrophication in coastal areas, both temporally and spatially, can only be achieved with modelling (e.g. Korpinnen et al., 2004). Despite the recent use of this holistic approach to evaluate, control and manage coastal eutrophication (e.g. Simas et al., 2001; Alvera-Azcarate et al., 2003; Korpinnen et al., 2004; Nobre et al., 2005), there is still a lack in global calculations concerning many estuarine systems. On the other hand, although most of the works make an exhaustive description of the processes that determine the growth and biomass of adult macroalgal, no references are made, in general, to the processes that control macroalgal spore
germination and their relation to adult macroalgal biomass. However, experimental work suggests that the recruitment processes and the factors affecting early life stages determine the development and the dominance patterns of macroalgal blooms (Lotze and Worm, 2000). Additionally, it seems that the development of green algal mats is initiated either by overwintering and regrowth of adult plants or by the formation of small propagules (vegetative fragments, zospores or zygotes) (Schories et al., 2000). Thus, it becomes clear that the full understanding of macroalgal dynamics and, consequently of the consequences of eutrophication processes, can only be achieved if both macroalgal adult individuals and microscopic life stages are taken into consideration (Sousa et al., 2007).

Therefore, the aim of the present work was to develop a working tool (modelling coupled to GIS) able to estimate algal productivity (spores and adults) at the system-scale for the south channel of the Mondego estuary, in order to assess the impacts on nitrogen- and phosphorus-loading on the system and on the adjacent coastal area.

2. Material and methods

2.1. Study site

The Mondego estuary is a warm-temperate system located on the west coast of Portugal, and consists of two different channels, north and south, separated by an alluvial island (Fig. 1). The north channel is deeper (5–10 m during high tide), whilst the south channel is shallower (2–4 m during high tide). For a detailed characterisation of the system see e.g. Ferreira et al. (2003) and Lillebø et al. (2005).

During the 1980s and early 1990s, several studies assessed the ecological importance of the south channel (e.g. Marques et al., 1993) and during the 1990s, other works concluded about the ongoing eutrophication process and the impacts on established primary producers (Car-doso et al., 2004) and consumers (Lopes et al., 2000; Dol-beth et al., 2003; Verdelhos et al., 2005). Modelling and theoretical approaches aiming to describe and understand the local effects of eutrophication from a holistic perspective were also carried out (Martins and Marques, 2002; Pardal et al., 2004; Patrı ´cio et al., 2006).

The inter-annual variation of the biomass of opportunistic macroalgae (mainly represented by Enteromorpha) in the Mondego estuary is controlled by hydrodynamics, which in turn depends on precipitation and river management, according to the water requirements of paddy fields in the catchment (Martins et al., 2001). In dry years, characterized by decreased rainfall in late winter and spring, the biomass of Enteromorpha tends to increase significantly, frequently giving rise to a spring bloom (Pardal et al., 2000). In the present work, the definitions given in the ASSETS method for eutrophication assessment (Bricker et al., 2003) for Overall Eutrophic Condition (OEC) are used as follows: high OEC indicates significant expression of macroalgal symptoms of eutrophication (i.e. spring-early summer bloom), low OEC indicates low growth and biomass of Enteromorpha.

2.2. Model formulation

The model has four state variables: spore biomass, adult biomass N-internal concentration and P-internal concentration of adult macroalgae (Fig. 2). The state variables are defined as:

$$\frac{dS}{dt} = Sp - G - Z_S$$  \hspace{1cm} (1)

$$\frac{dA}{dt} = P + G - Adv - D - Z_A - U$$  \hspace{1cm} (2)

$$\frac{dN_{int}}{dt} = N_{upt} - N_{cons}$$  \hspace{1cm} (3)

$$\frac{dP_{int}}{dt} = P_{upt} - P_{cons}$$  \hspace{1cm} (4)

Fig. 1. Study area with bathymetry.
where $S$ is spore biomass (mg C m$^{-2}$), $A$, adult biomass (g DW m$^{-2}$); $N_{int}$, internal nitrogen concentration ($\mu$mol N (g DW)$^{-1}$); $P_{int}$, internal phosphorus concentration ($\mu$mol P (g DW)$^{-1}$), $Sp$, sporulation (mg C m$^{-2}$ d$^{-1}$); $G$, germination (d$^{-1}$); $Z_s$, grazing on spores (d$^{-1}$); $P$, net productivity (d$^{-1}$); $Adv$, advection (d$^{-1}$); $D$, decomposition (d$^{-1}$); $Z_A$, grazing on adults (d$^{-1}$); $U$, reproduction (d$^{-1}$); $X_{opt}$, uptake of nutrient ($\mu$mol X (g DW)$^{-1}$ d$^{-1}$); $X_{cons}$, consumed nutrient ($\mu$mol X (g DW)$^{-1}$ d$^{-1}$); $N$, nitrogen ($\mu$mol l$^{-1}$), and $P$ is phosphorus ($\mu$mol l$^{-1}$).

2.2.1. Spore biomass

It is assumed that spore biomass depends on three basic processes: sporulation ($Sp$), grazing by macroinvertebrates ($Z_s$) and germination ($G$). In general, sporulation is defined as the release of spores by adult macroalgae, which is a process followed by significant mortality rates (Santelices, 1990). In the present work, sporulation is defined as the concentration of spores present in the water column, which are able to attach to a hard substrate (mg C m$^{-2}$ were converted to g DW m$^{-2}$ assuming a conversion factor of 0.4) and to survive. This value was obtained experimentally in situ from January 2004 to January 2005 (Sousa et al., unpublished). Results showed that although Enteromorpha spores were present all year round in the water column of the Mondego, spore biomass was higher in spring and early summer. However, no significant regressions were found between the variation of spore biomass and environmental factors. For this reason, in the model, sporulation is defined as a data series in accordance with the values quantified by Sousa et al. (unpublished). Additionally, it is also assumed that the variation of spores in the water column does not differ significantly between years.

Experimental evidence suggests that herbivores may reduce Enteromorpha propagules by 0.06–0.14 d$^{-1}$ (Lotze and Worm, 2000). The maximum grazing rate on spores ($Z_{max}$) was set to 0.14 d$^{-1}$ and grazer activity was considered temperature-dependent, which was described by an $f(T)$ function similar to Eq. (8) but with the parameters corresponding to grazer activity (Table 1). This is in accordance with field data showing that amphipod grazers (e.g. Melita sp., Amphitoe sp.) exhibit higher biomass values during spring and summer (Pardal et al., 2000). Thus, the effect of grazers on spores was defined by:

$$Z_S = Z_{max} \cdot f(T_{is})$$

(5)

Spore germination was defined by:

$$G = G_{max} f(T) \cdot f(I) \cdot f(S_S) \cdot f(NP_S)$$

(6)

where $G_{max}$ is maximum spore germination rate (d$^{-1}$); $f(T)$, temperature limiting factor; $f(I)$, light limiting factor; $f(S_S)$, salinity limiting factor; $f(NP_S)$, nitrogen and phosphorus limiting factor. Limiting factors; $f(X)$, vary between 0 and 1 corresponding to null and optimum conditions for germination, respectively. The germination rate of opportunistic green macroalgae (Ulva rigida and Enteromorpha intestinalis) was found to vary between 40% and 100% (Hoffmann and Camus, 1989). In accordance with this, maximum spore germination rate was set at 0.8 d$^{-1}$. Spore germination depends on light and temperature, which may be described by a photoinhibition-type expression and by a temperature-optimum curve, respectively, as in the case of adult macroalgal growth (e.g. Martins and Marques, 2002). These variations are shown in Eqs. (7) and (8), respectively:

$$f(I) = \frac{I}{I_S} \cdot e^{(1-k)}$$

(7)

$$f(T) = \exp \left[-2.3 \cdot \left(\frac{T - T_{opt}}{T_{is} - T_{opt}}\right)^2\right]$$

(8)

where $f$ is photon flux density (µE m$^{-2}$ s$^{-1}$), and $I_S$ is optimum photon flux density for Enteromorpha (µE m$^{-2}$ s$^{-1}$).

$$f(T) = \exp \left[-2.3 \cdot \left(\frac{T - T_{opt}}{T_{is} - T_{opt}}\right)^2\right]$$

(8)

where $T_{is}$ = $T_{min}$ for $T \leq T_{opt}$ and $T_{is} = T_{max}$ for $T > T_{opt}$; $T_{opt}$, optimum temperature for growth ($^\circ$C); $T_{min}$, lower temperature limit below which growth ceases ($^\circ$C), and $T_{max}$ is upper temperature limit above which growth ceases ($^\circ$C).
The influence of salinity variation on Enteromorpha spore germination was experimentally assessed (Sousa et al., 2007). The results indicate that spore germination is enhanced at 35 psu and decreases with decreasing salinities. This effect was described by:

\[ f(S_x) = 1 - \left( \frac{S_x - S_{\text{opt}}} {S_{\text{max}} - S_{\text{opt}}} \right)^m \]  

(9)

where \( S_{\text{max}} = S_{\text{min}} \) and \( m = 2.5 \) for \( S_x < S_{\text{opt}} \), \( S_{\text{max}} = S_{\text{opt}} \) and \( m = 2 \) for \( S_x \geq S_{\text{opt}} \), \( S_{\text{opt}} \), optimum salinity for growth (psu); \( S_{\text{min}} \), lower salinity limit below which growth ceases (psu); \( S_{\text{max}} \) is upper salinity limit above which growth ceases (psu).

The effect of the nutrients \( (N \) and \( P) \) on spore germination was described according to Eqs. (10) and (11), which reflect the dependency of spor growth on external nutrient concentration, assuming an optimum N:P range of 12–16, and “Liebig’s law of the minimum”:

If \( N : P \geq 12 \) and \( N : P \leq 16 : f(NP_x) = 1 \)

If \( N : P < 12 : f(NP_x) = f(N) \)

If \( N : P > 16 : f(NP_x) = f(P) \)

The uptake of nutrients by spores follows a simple Michaelis–Menten kinetics:

\[ f(X_x) = V_{X_{\text{Max}}} \cdot \frac{[X]}{[X] + K_X S} \]  

(11)

where \( V_{X_{\text{Max}}} \) is maximum uptake rate of nutrient \( X \) by spores (\( \mu \text{mol} (\text{g DW})^{-1} \) \( \text{d}^{-1} \)), \( K_X S \), half-saturation constant for the uptake of the nutrient \( X \) by spores (\( \mu \text{mol} (\text{g DW})^{-1} \)), and \( X \) is nutrient concentration (\( \mu \text{mol} l^{-1} \)).

Spore half-saturation constants and maximum uptake rates for \( P \) and \( N \) (Table 1) follow Jorgensen et al. (1991) and Lindenschmidt (2006).

2.2.2. Adult macroalgal biomass

The biomass of adults depends on spore germination, net productivity of adults, grazing on adults by herbivores, reproduction/sporulation, decomposition and advection out of the system.

2.2.3. Net productivity

The net productivity of adult macroalgae \( (P, \text{d}^{-1}) \) is defined by:

\[ P = GP - R \]  

(12)

where \( GP \) is gross productivity (\( \text{d}^{-1} \)) and \( R \) is respiration (\( \text{d}^{-1} \)), which were defined by Eqs. (13) and (14), respectively:

\[ GP = \mu_{\text{max}} \cdot f(I) \cdot f(T) \cdot f(S) \cdot f(NP) \]  

(13)

where \( f(I) \) and \( f(T) \) were previously described in Eqs. (7) and (8), respectively.

\[ R = R_{\text{max}20} \cdot \theta^{T-20} \]  

(14)

where \( R_{\text{max}20} \) is maximum respiration rate at 20 °C, and \( \theta \) is an empirical coefficient.

2.2.4. Salinity

The influence of salinity on the growth of adult Enteromorpha \( (f(S)) \) is based on the experimental work by Martins et al. (1999) and described by:

For salinity \( \geq 5 \) \( f(S_A) = 1 - \left( \frac{S_A - S_{\text{opt}}} {S_{\text{max}} - S_{\text{opt}}} \right)^m \) \n
(15)

where \( S_x = S_{\text{min}} \) and \( m = 2.5 \) for \( S_A < S_{\text{opt}} \), \( S_x = S_{\text{max}} \) and \( m = 2 \) for \( S_A \geq S_{\text{opt}} \).

For salinity \( < 5 \) \( f(S_A) = \frac{S_A - S_{\text{min}}} {S_{\text{opt}} - S_{\text{min}}} \).

\( S_{\text{opt}} \) is optimum salinity at which growth rate is maximum (psu); \( S_{\text{min}} \), lower salinity limit at which growth rate ceases (psu); \( S_{\text{max}} \) is upper salinity limit at which growth ceases (psu).

2.2.5. Nutrients

It is assumed that the growth of adult macroalgae depends on their internal nitrogen (\( N \)) (Björnsäter and Wheeler, 1990) and internal phosphorus (\( P \)) concentrations. These dependencies were defined by:

If \( N_{\text{int}} : P_{\text{int}} \geq 12 \) and \( N_{\text{int}} : P_{\text{int}} \leq 16 : f(NP_A) = 1 \)

If \( N_{\text{int}} : P_{\text{int}} < 12 : f(NP_A) = f(N) \)

If \( N_{\text{int}} : P_{\text{int}} > 16 : f(NP_A) = f(P) \)

\[ f(X) = \frac{X_{\text{int}} - X_{\text{min}}}{K_{q_X} + X_{\text{int}} - X_{\text{min}}} \]  

(17)

where \( X_{\text{int}} \) is the subsistence quota for nutrient \( X \) (\( \mu \text{mol} (\text{g DW})^{-1} \)); \( K_{q_X} \), nutrient half-saturation constant for growth limitation (\( \mu \text{mol} (\text{g DW})^{-1} \)), \( X - N \) or \( P \).

The uptake of nitrogen (nitrate and ammonia) \( (N_{\text{opt}} \) in Eq. (3)) and phosphorus \( (P_{\text{opt}} \) in Eq. (4)) by Enteromorpha adults was described by:

\[ X_{\text{opt}} = \frac{X_{\text{max}} - X_{\text{int}}}{X_{\text{max}} - X_{\text{min}}} \cdot \frac{V_{\text{max}} \cdot X_{\text{ext}}}{K_X + X_{\text{ext}}} \]  

(18)

where \( X_{\text{int}} \) is internal nutrient concentration (\( \mu \text{mol} (\text{g DW})^{-1} \)); \( X_{\text{max}} \), maximum internal concentration of nutrient (\( \mu \text{mol} X (\text{g DW})^{-1} \)); \( X_{\text{min}} \), minimum internal concentration of nutrient (\( \mu \text{mol} X (\text{g DW})^{-1} \)); \( V_{\text{max}} \), maximum uptake rate of nutrient (\( \mu \text{mol} X (\text{g DW})^{-1} \) \( \text{d}^{-1} \)); \( K_X \), half-saturation constant for the uptake of nutrient (\( \mu \text{mol} X (\text{g DW})^{-1} \)); \( X_{\text{ext}} \), external concentration of nutrient (\( \mu \text{mol} X (\text{g DW})^{-1} \)); \( X \), \( N \) (NO\(_3\) and NH\(_4\)) and \( P \) (\( \mu \text{mol} l^{-1} \)).

The consumption of internal nutrients \( (N_{\text{cons}} \) in Eq. (3) and \( P_{\text{cons}} \) in Eq. (4)) was defined by

\[ N_{\text{cons}} = X_{\text{int}} \cdot X_{\text{requirement}} \]  

(19)

where \( X_{\text{int}} \) is internal nutrient concentration (\( \mu \text{mol} X (\text{g DW})^{-1} \)); \( X_{\text{requirement}} \), amount of nutrient required for growth (\( \text{d}^{-1} \)). Daily nitrogen requirement rate for Enteromorpha was set at 45% of internal N \( \text{d}^{-1} \), while the
phosphorus requirement was set at 25% of internal-P d\(^{-1}\). Nitrogen requirement rate was based on the range 37.3 and 7.4 mg N (g DW\(^{-1}\)) d\(^{-1}\) obtained for phytoplankton and Ulva lactuca, respectively (Pedersen and Borum, 1996), and assuming that nitrogen represents 3.25% of macroalgal dry weight (Neto, 2004). Phosphorus requirement rate was established by calibration and taking into consideration that P represents a lower % of macroalgal dry weight com-

Table 1
Definitions, values and source of the parameters used in the model

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Units</th>
<th>Value used</th>
<th>Literature range</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\mu_{\text{max}})</td>
<td>Maximum growth rate at (T_{\text{opt}})</td>
<td>d(^{-1})</td>
<td>0.8</td>
<td>0.2–1.5</td>
<td>EPA (1985)</td>
</tr>
<tr>
<td>(R_{\text{maxNO}})</td>
<td>Maximum respiration rate at 20 °C</td>
<td>d(^{-1})</td>
<td>0.1</td>
<td>0.02–0.1</td>
<td>EPA (1985)</td>
</tr>
<tr>
<td>(\theta)</td>
<td>Empirical coefficient</td>
<td></td>
<td>1.047</td>
<td>1.01–1.2</td>
<td>EPA (1985)</td>
</tr>
<tr>
<td>(I_s)</td>
<td>Optimum light intensity for photosynthesis</td>
<td>μmolE m(^{-2}) s(^{-1})</td>
<td>600</td>
<td>500–1000</td>
<td>Shlelem and Josselyn (1982), Beer and Shragge (1987), Shlelem and Josselyn (1982), Fitzgerald (1978)</td>
</tr>
<tr>
<td>(T_{\text{opt}})</td>
<td>Optimum temperature for growth</td>
<td>°C</td>
<td>22</td>
<td>15–30</td>
<td></td>
</tr>
<tr>
<td>(T_{\text{max}})</td>
<td>Upper temperature tolerance limit at which growth ceases</td>
<td>°C</td>
<td>35</td>
<td>–</td>
<td>Poole and Raven (1997)</td>
</tr>
<tr>
<td>(T_{\text{min}})</td>
<td>Lower temperature tolerance limit at which growth ceases</td>
<td>°C</td>
<td>10</td>
<td>–</td>
<td>Poole and Raven (1997)</td>
</tr>
<tr>
<td>(S_{\text{opt}})</td>
<td>Optimum salinity for growth</td>
<td>psu</td>
<td>18</td>
<td>18–22</td>
<td>Martins et al. (1999)</td>
</tr>
<tr>
<td>(S_{\text{max}})</td>
<td>Upper salinity tolerance limit at which growth ceases</td>
<td>psu</td>
<td>45</td>
<td>–</td>
<td>Poole and Raven (1997)</td>
</tr>
<tr>
<td>(S_{\text{min}})</td>
<td>Lower salinity tolerance limit at which growth ceases</td>
<td>psu</td>
<td>0</td>
<td>0</td>
<td>Poole and Raven (1997) and Martins et al. (1999)</td>
</tr>
<tr>
<td>(N_{\text{min}})</td>
<td>Minimum internal quota (subsistence quota) for nitrogen</td>
<td>μmol N (g DW(^{-1}))</td>
<td>500</td>
<td>499–1717</td>
<td>Solidoro et al. (1997)</td>
</tr>
<tr>
<td>(N_{\text{max}})</td>
<td>Maximum internal quota for nitrogen</td>
<td>μmol N (g DW(^{-1}))</td>
<td>3000</td>
<td>1928–4285</td>
<td>Solidoro et al. (1997), Bendoricchio et al. (1994)</td>
</tr>
<tr>
<td>(k_q)</td>
<td>Nitrogen half-saturation constant for growth</td>
<td>μmol N (g DW(^{-1}))</td>
<td>1786</td>
<td>Maximum 1786</td>
<td>EPA (1985)</td>
</tr>
<tr>
<td>(V_{\text{maxNO}})</td>
<td>Maximum nitrate uptake rate</td>
<td>μmol NO(_3) (g DW(^{-1})) d(^{-1})</td>
<td>1200</td>
<td>1200–1406</td>
<td>Bendoricchio et al. (1994)</td>
</tr>
<tr>
<td>(V_{\text{maxNH}})</td>
<td>Maximum ammonium uptake rate</td>
<td>μmol NH(_4) (g DW(^{-1})) d(^{-1})</td>
<td>1500</td>
<td>3428–8913</td>
<td>Bendoricchio et al. (1994)</td>
</tr>
<tr>
<td>(K_{\text{NO}})</td>
<td>Half-saturation constant for nitrate</td>
<td>μmol NO(_3) l(^{-1})</td>
<td>18</td>
<td>18</td>
<td>Bendoricchio et al. (1994)</td>
</tr>
<tr>
<td>(K_{\text{NH}})</td>
<td>Half-saturation constant for ammonium</td>
<td>μmol NH(_4) l(^{-1})</td>
<td>20</td>
<td>14–43</td>
<td>Bendoricchio et al. (1994)</td>
</tr>
<tr>
<td>(P_{\text{max}})</td>
<td>Maximum internal quota for phosphorus</td>
<td>μmol P (g DW(^{-1}))</td>
<td>126</td>
<td>Maximum 126</td>
<td>Bendoricchio et al. (1994)</td>
</tr>
<tr>
<td>(P_{\text{min}})</td>
<td>Minimum internal quota (subsistence quota) for phosphorus</td>
<td>μmol P (g DW(^{-1}))</td>
<td>16</td>
<td>16–35</td>
<td>Bendoricchio et al. (1994)</td>
</tr>
<tr>
<td>(V_{\text{maxPO}})</td>
<td>Maximum phosphorus uptake rate</td>
<td>μmol PO(_4) (g DW(^{-1})) d(^{-1})</td>
<td>96</td>
<td>178–844</td>
<td>Bendoricchio et al. (1994)</td>
</tr>
<tr>
<td>(K_{\text{PO}})</td>
<td>Half-saturation constant for phosphorus</td>
<td>μmol PO(_4) l(^{-1})</td>
<td>1</td>
<td>0.81–3.64</td>
<td>Bendoricchio et al. (1994)</td>
</tr>
<tr>
<td>(\text{decMax})</td>
<td>Maximum decomposition rate</td>
<td>d(^{-1})</td>
<td>0.025</td>
<td>Maximum 0.65</td>
<td>Paaume et al. (2002)</td>
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<tr>
<td>(\text{ReprodRate})</td>
<td>Reproduction rate - amount of biomass lost by sporulation</td>
<td>d(^{-1})</td>
<td>0.01</td>
<td>Maximum 0.6</td>
<td>Niesenbaum (1988)</td>
</tr>
<tr>
<td>(\text{GermMax})</td>
<td>Maximum germination</td>
<td>d(^{-1})</td>
<td>0.8</td>
<td>0.4–1.0</td>
<td>Hoffmann and Camus (1989)</td>
</tr>
<tr>
<td>(\text{SporGrazrate})</td>
<td>Maximum macroinvertebrate grazing rate on spores</td>
<td>d(^{-1})</td>
<td>0.14</td>
<td>0.06–0.14</td>
<td>Lotze and Worm (2000)</td>
</tr>
<tr>
<td>(T_{\text{optGrazSp}})</td>
<td>Optimum temperature for grazers</td>
<td>°C</td>
<td>22</td>
<td>15–30</td>
<td>Pardal et al. (2000)</td>
</tr>
<tr>
<td>(T_{\text{maxGrazSp}})</td>
<td>Upper temperature for grazers</td>
<td>°C</td>
<td>35</td>
<td>–</td>
<td>Poole and Raven (1997)</td>
</tr>
<tr>
<td>(T_{\text{minGrazSp}})</td>
<td>Lower temperature for grazers</td>
<td>°C</td>
<td>10</td>
<td>–</td>
<td>Poole and Raven (1997)</td>
</tr>
<tr>
<td>(S_{\text{optSp}})</td>
<td>Optimum salinity for growth of spores</td>
<td>psu</td>
<td>35</td>
<td>–</td>
<td>Sousa et al. (2007)</td>
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<td>(S_{\text{maxSp}})</td>
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<td>psu</td>
<td>10</td>
<td>0</td>
<td>Sousa et al. (2007)</td>
</tr>
<tr>
<td>(V_{\text{maxNSp}})</td>
<td>Maximum nitrogen uptake rate by spores</td>
<td>μmol N (g DW(^{-1})) d(^{-1})</td>
<td>4568</td>
<td>–</td>
<td>Lindenschmidt (2006)</td>
</tr>
<tr>
<td>(K_{\text{NSp}})</td>
<td>Spore half-saturation constant for nitrogen</td>
<td>μmol N l(^{-1})</td>
<td>1.7857</td>
<td>–</td>
<td>Lindenschmidt (2006)</td>
</tr>
<tr>
<td>(V_{\text{maxPSp}})</td>
<td>Maximum phosphorus uptake rate by spores</td>
<td>μmol PO(_4) (g DW(^{-1})) d(^{-1})</td>
<td>116</td>
<td>–</td>
<td>Lindenschmidt (2006)</td>
</tr>
<tr>
<td>(K_{\text{PSp}})</td>
<td>Spore half-saturation constant for phosphorus</td>
<td>μmol PO(_4) l(^{-1})</td>
<td>0.03225</td>
<td>–</td>
<td>Lindenschmidt (2006)</td>
</tr>
</tbody>
</table>
pared to N and that the depletion of P appears to occur faster than N-depletion due to different types of internal pools (Björnsater and Wheeler, 1990).

2.2.6. Herbivory

Ephemeral algae have significant losses due to herbivory both at the microscopic and at the adult stages (Lotze and Worm, 2000; Giannotti and McGlathery, 2001). Based on experimental values, the maximum grazing rate on adults \( Z_{\text{maxA}} \) was set at 0.02 d\(^{-1}\) and, as in the case of spores, grazing is considered to be a temperature-dependent process (Eq. (8)):

\[
Z_A = Z_{\text{maxA}} \cdot f(T)
\]

(20)

2.2.7. Sporulation

Macroalgae may allocate a significant amount of their biomass to the formation of zoospores and gametes (Nielsenbaum, 1988), especially during warmer months, when the percentage of reproductive biomass may reach 60%. To account for this adult biomass loss process, a maximum reproduction rate of 0.01 d\(^{-1}\) at 20 \(^\circ\)C is considered and sporulation is defined by:

\[
Sp = Sp_{\text{max}} \cdot \theta^{(T-20)}
\]

(21)

where \( \theta \) is an empirical coefficient.

2.2.8. Decomposition

Decomposition is another important loss process, particularly when during intensive growing periods, macroalgae accumulate in layers where growth rate decreases exponentially through the canopy (Vergara et al., 1998). In this situation, the upper layers remain photosynthetically active, whereas the deeper layers undergo decomposition due to extreme self-shading (Hernández et al., 1997). Due to spring and summer high air and water temperatures, this process may be particularly significant in warm-temperate estuaries such as the Mondego estuary. Thus, decomposition was described by:

\[
D = D_{\text{max}} \theta^{(T-20)}
\]

(22)

Decomposition rate \( D_{\text{max}} \) at 20 \(^\circ\)C was calibrated to 0.025 d\(^{-1}\), which is in accordance to a decomposition rate of 65% during 28 days for Cladophora glomerata obtained by Paalme et al. (2002).

2.2.9. Advection

In estuaries and other coastal systems with significant hydrodynamics, the loss of macroalgae and other macrophytes to the ocean is a process with significant impacts on the mass balance of plant biomass and nutrients within these systems (Flindt et al., 1997; Salomonsen et al., 1997). The present model does not explicitly simulate hydrodynamics. However, based on predicted macroalgal production and on \textit{in situ} quantification of the amount of drifting macroalgae (Neto, 2004), it was possible to describe Enteromorpha advection as being dependent on sluice operation through a “binary” effect, ranging from 0.4 to 10% d\(^{-1}\) of macroalgal biomass drifted out of the system when the sluice is closed or opened, respectively.

2.2.10. Desiccation

In some coastal systems, where temperature and light intensities are seasonally very high, intertidal macroalgae frequently undergo desiccation stress, at least during some parts of the day (Bell, 1993, 1995; Matta and Chapman, 1995). This process has been related to the summer decline of some macroagal populations (Rivers and Peckol, 1995; Hernández et al., 1997). It was previously argued that productivity models of macroalgae inhabiting such areas should include the description of macroalgal desiccation (Martins and Marques, 2002). Therefore, the model accounts for the seasonal and daily effect of desiccation on algae. Desiccated thalli have no water for evaporative cooling and can greatly exceed air temperature (up to 20 \(^\circ\)C above air temperature) (Bell, 1995). In the model, it is assumed that from April to September and from 11 a.m. until 4 p.m., emerged algae will exceed the air temperature in 5 \(^\circ\)C. This value accounts for the fact that thallus within aggregations prolongs the hydrated state (Bell, 1995) and consequently, desiccation is not as severe as in isolated thallus.

2.2.11. Light climate and tidal height

To estimate the light intensity at surface, the Brock model (1981) was used assuming a mean cloud cover of 0.41 based on values measured for the Mondego estuary. Photon flux density at surface \( PFD_0, \mu E m^{-2} s^{-1} \) after conversion) was calculated from \( I_0 \) assuming that 42% of the overall energy is available for photosynthesis (Ferreira and Ramos, 1989). Photon flux density at depth \( z \) \( PFD_z \) was calculated according to the Lambert–Beer equation:

\[
PFD_z = PFD_0 \times e^{-kz}
\]

(23)

where \( k \) is the light extinction coefficient \( (m^{-1}) \).

Based on values estimated \textit{in situ} by Martins et al. (2001), the model assumes that \( k \) depends on the amount of freshwater entering the system, which in turn is controlled by an upstream sluice status (opened or closed expressed in the model as 1 or 0, respectively). The sluice status depends on the amount of rainfall and on rice crop management (Martins et al., 2001). Additionally, whenever adult biomass exceeds a certain value (>50 g DW m\(^{-2}\)), the value of \( k \) is considered biomass-dependent to account for self-shading:

\[
k = \begin{cases} 
2 \cdot (\text{Sluice} = 0, \text{AdultBiomass} < 50) \\
5.59 \cdot (\text{Sluice} = 1, \text{AdultBiomass} < 50) \\
2 + (0.01 \times \text{AdultBiomass}) \cdot (\text{Sluice} = 0, \text{AdultBiomass} \geq 50) \\
5.59 + (0.01 \times \text{AdultBiomass}) \cdot (\text{Sluice} = 1, \text{AdultBiomass} \geq 50)
\end{cases}
\]

(24)

In estuaries, the immersion depth of ephemeral macroalgae and other attached macrophytes is regulated by tides. Tidal height was simulated using the basic harmonic
constituents, where HBM and HPM are low tide and high tide heights, respectively, and vary according to the spring neap oscillation. The depth of any individual is space and time-dependent, since it depends both on the bathymetry of the point where the individual is located and on tidal height:

\[
\text{TidalHeight} = \frac{\text{HBM} + \text{HPM}}{2} \cdot \cos \left( 2 \cdot \pi \cdot \frac{\text{TIME}}{\text{TidePeriod}} \right) \quad (25)
\]

HBM = If SpringNeapOscillation \( \geq 0 \)

THEN 0.2 + SpringNeapOscillation

ELSE 0.2 – SpringNeapOscillation

HPM = If SpringNeapOscillation \( \geq 0 \)

THEN 3.7 – SpringNeapOscillation

ELSE 3.7 + SpringNeapOscillation

where 0.2 and 3.7 m correspond to the maximum tidal range in the south channel of the Mondego estuary:

\[
\text{AlgaeDepth} = \text{TidalHeight} - \text{Bathymetry} \quad (28)
\]

2.3. From modelling to GIS

The model was run with STELLA software for 1490 days using a time step of 1.2 h and simulations were performed at 33 different bathymetries (from −0.9 m to 2.30 m with a discriminatory value of 0.1 m) using the Sensitivity specifications of STELLA software (High Performance Systems Inc., USA). The model uses a 1.2 h time step in order to resolve the tidal and diel cycles, and the non-linearity of their interactions. However, predicted macroalgal biomass is expressed at a larger scale (monthly) to allow for comparison with real values.

Model results where obtained at the scale of 1 m² and subsequently upscaled to the system using a bathymetric map and GIS (ArcGis 9.1, ESRI, USA). Global calculations were obtained for the whole area of the south channel of the Mondego estuary (136.5 ha). Furthermore, since Enteromorpha shows a patchy distribution within the system, the variation of the area covered with adult algae throughout time estimated in situ (Lopes et al., 2006) was considered and used to perform global calculations.

Estimations of Enteromorpha internal N and P are based on values obtained, in situ, from January 1999 to January 2001 and correspond to 3.25% and 0.11% of dry weight, respectively (Neto, 2004). The macroalgal internal C content was considered to be 29% of dry weight (Duarte, 1992).

2.4. Calibration, sensitivity and statistical analysis

Parameter calibration was achieved by optimisation algorithms. Sensitivity analysis was performed in accordance to Jorgensen (1994). To assess for model reliability, model predictions for adult biomass at depth +1.8 m were compared with real data of Enteromorpha biomass quantified in the south channel of the Mondego estuary between January 1993 and January 1997, in a field station located at +1.8 m. Model II-regression was used to compare predictions with observations. This regression model is recommended whenever both variables are subject to error (Sokal and Rohlf, 1995). The significance of the regression was tested by analysis of variance (ANOVA), since it is the only means of testing it in model II-regression (Fowler et al., 1998). ANOVA was also used to assess for differences between macroalgal biomass in different years.

3. Results

Predicted adult algal biomass variation followed the same pattern as observed biomass variation (Fig. 3). Nevertheless, there are some deviations between the two sets of values, particularly, during spring 1993, when the model tends to overestimate macroalgal biomass and from June onwards, when the predicted values are lower than observations. Such discrepancies are not unusual considering that observed values correspond to a medium-term time series of field data, which is affected by numerous stochastic effects. Nevertheless, the regression between observed and predicted values is highly significant (ANOVA, \( F_{1,41} = 85, P < 0.001, r^2 = 0.68 \) (Fig. 3).

The predicted variation of Enteromorpha spore biomass is very similar during the four studied years and, although spore biomass presents seasonal fluctuations, they are present all year round within the water column (minimum = 37.48 mg C m⁻²) (Fig. 4), which is in agreement with field measurements.

Fig. 3. Predicted (---) and observed (-----) biomass variation ± standard error of adult Enteromorpha (g DW m⁻²) at +1.8 m (a). Model II-regression between observed and predicted values (b).
Adult algal biomass was significantly different (ANOVA, \( P < 0.05 \)) between the four studied years. Maximum predicted adult biomass at +1.8 m for 1993, 1994, 1995 and 1996 was 256.23, 14.06, 50.95 and 8.41 g DW m\(^{-2}\), respectively (Fig. 5). This clearly indicates that 1993 was the most favourable year for macroalgal growth, whilst 1996 was the least favourable. In 1995, Enteromorpha presented the second highest biomass value but the maximum depth distribution was lower than in 1994, which suggests the occurrence of increased light limitation conditions for macroalgal growth between 1993 and 1996 (Fig. 5). The results also indicate that algal growth is very sensitive to depth variations and that, according to prevailing conditions, it varies differently in different seasons and in different years. In 1993, from autumn until spring, the biomass of Enteromorpha increased exponentially from the highest (−0.9 m) to the lowest depth (+2.3 m), while in 1996 the increase was only linear. In general during spring (April–May) and early autumn (October), macroalgal biomass increased exponentially towards the lowest depth, whilst in summer, this pattern of variation changed and either macroalgal biomass varied according to saturation-type kinetics with bathymetry or macroalgal biomass decreased at the lowest bathymetry (Fig. 6).

Sensitivity analysis highlighted the dependency of algal growth on environmental factors, namely, temperature, salinity and light. Additionally, sensitivity analysis suggested that spore dynamics has significant impacts on adult macroalgae in some years, particularly, low OEC years (Martins et al., unpublished).

Global estimations for the south channel of the Mondego estuary indicate that the inter-annual variations of macroalgal production are very significant, ranging from 21,205 ton DW in high OEC years (1993) to 239 ton DW in low OEC years (1996). Total macroalgal production in 1993 was 15-, 9- and 89-times higher than algal biomass in 1994, 1995 and 1996, respectively. However, monthly values between different years may be even more significant. For instance, in February 1993 there were 5000-, 940- and 117,000-times more algae than in February 1994, 1995 and 1996, respectively (Fig. 7). Consequently, the amounts of C, N and P uptake by macroalgae and retained within the system, as well as the amounts of nutrients exported to the adjacent coastal areas are also highly variable between different years. In 1993, the fixation of C, N and P by macroalgae was about 6150, 689 and 23 ton, respectively, while in 1996 the values decreased to 69, 8 and 0.26 ton, respectively. Assuming that 40% of the macroalgal biomass is decomposed within the system (Duarte and Cebrián, 1996), in 1993 about 276 ton of N and 9.3 ton of P were retained within the south channel of the Mondego estuary, whilst in 1996 the values decreased to 3.1 ton of N and 0.11 ton of P. Consequently, for a PEQ (population equivalents) of 4.4 kg N yr\(^{-1}\) (Alvera-Azcárate et al., 2003), the amount of N retained in the system during high OEC years (1993) corresponds to 156,631 inhabitants, whilst in low OEC years (1996) the value decreases to 1763 inhabitants (Table 2).

![Fig. 5. Variation of Enteromorpha adult biomass (g DW m\(^{-2}\)) with depth during the study period.](image-url)
4. Discussion

The present model describes quite accurately the annual variation of opportunistic macroalgal biomass in a temperate mesotidal estuary for a significant period of time (January 1993–January 1997). This suggests that the processes included in the model (e.g. dependency between hydrodynamics and algal growth, desiccation, decomposition, advection, etc.) and the equations used to describe them, represent fairly well the variation of macroalgal biomass in nature. Additionally the present work is, to our knowledge, the first model that describes macroalgal spore...
dynamics and its relationships with adult macroalgae, which is undoubtedly a more complete approach to describe algal dynamics, since frequently factors affecting early life stages determine the development and the dominance patterns of macroalgal blooms (Lotze and Worm, 2000). According to simulations, although the contribution of spore biomass is relatively low compared to adult biomass, spore dynamics has a significant impact on adult biomass, particularly during low OEC years. Specific and detailed analysis of the effects of spore dynamics on adult growth and biomass are reported elsewhere (Martins et al., unpublished).

The present results indicate that there are significant spatial variations within the same system regarding macroalgal growth. In the present model, spatial variability is due to different temperature and light conditions at different times of the year.
depths which determines that, during winter and autumn, macroalgae will be preferably located at low depths (between +2.1 and +2.3 m) and, thus benefit from higher light availability. Conversely, in summer macroalgae will be located mostly at higher depths (between +1.8 and +2.2 m) with longer immersion periods, which confers a higher protection against desiccation. However, in intertidal areas, bathymetry is only one of the factors contributing to the patchy distribution of macroalgae and, consequently, to the patchiness of other benthic organisms (Raffaelli et al., 2003; Kraufvelin et al., 2006). Also the type of substrate (which affects the attachment rate of spores, Martins, unpublished data), the organic matter content of the underlying sediment (Lillebø et al., 2002), the presence or absence of rooted macrophytes (Martins et al., 2002) and grazing pressure (Albrecht, 1998) contribute to the differential growth of macroalgae in different areas within the intertidal zone.

Calculations at the system level suggest that, in estuaries where hydrodynamics plays a major role, macroalgal biomass and consequently the amounts of carbon, nitrogen and phosphorus bounded to macroalgae show enormous differences between different years. The non-monotonic character of macroalgal variations and its effects have been previously reported (e.g. Raffaelli et al., 1998). According to our results, this type of variation will have significant impacts both in estuarine systems and on the adjacent coastal areas. Considering that the population in the watershed of the Mondego estuary is about 65,700 inhabitants with an annual domestic load into the south channel of 51 ton of nitrogen and 23 ton of phosphorus (Ferreira et al., 2003), in high OEC years, macroalgal internal N- and P- requirements exceed 14-times and 1-time more the domestic load of N and P, respectively. On the contrary, in low OEC years, macroalgal uptake accounts only for 15% and 0.1% the annual domestic load of N and P, respectively. This suggests that, during years with low macroalgal growth (low OEC years), there may be a potential nutrient surplus (dissolved N and P) to the adjacent coastal area which, in turn may be used by coastal phytoplankton. In a study carried out in UK estuaries, Nedwell et al. (2002) found a significant correlation between the spring maximum chlorophyll a in coastal waters and the total annual estuarine load of TO\textsubscript{N}, ammonium and phosphate. Other studies also report the significant impacts of nutrients in the catchment on the water quality and biogeochemical processes estuarine and coastal waters (e.g. Sanders et al., 1997; Cao et al., 2005).

In years with high macroalgal growth (high OEC years), assuming that 40% of macroalgal biomass is decomposed within the system (Duarte and Cebrián, 1996), up to 89-times more macroalgae and, consequently C-, N- and P-bound to macroalgae are exported to the adjacent coastal areas compared to low OEC years. However, re-mineralization must occur before these nutrients are available to coastal phytoplankton.

Overall this study indicates that, in some periods opportunistic macroalgae act as important sinks of nutrients within the estuarine area and, consequently, significant amounts of nutrients bound to macroalgal tissue will be exported to the adjacent coastal areas. There will be a time-lag before these nutrients can beuptaken by coastal phytoplankton due to re-mineralization. On the contrary, in other periods, when macroalgal growth is very limited, large amounts of dissolved nutrients from domestic loads are directly released into the adjacent coastal area and may contribute to increased coastal phytoplankton growth. One aspect that can change this scenario is the significant presence of rooted-macrophytes (e.g. Zostera noltii) within the estuarine system. These primary producers have a more conservative growth strategy (sensu Pedersen and Borum, 1996) compared to ephemeral macroalgae and, thus, play a much more efficient role in the removal and recycling of nutrients.

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