

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

Irene Martins ^{a,*}, R.J. Lopes ^b, A.I. Lillebø ^c, J.M. Neto ^a, M.A. Pardal ^a,
J.G. Ferreira ^d, J.C. Marques ^a

^a IMAR – Institute of Marine Research, Coimbra Interdisciplinary Centre, Department of Zoology, University of Coimbra, 3004-517 Coimbra, Portugal

^b CIBIO – Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, 4485-661 Vairão, Portugal

^c CESAM – Centro de Estudos do Ambiente e do Mar, University of Aveiro, 3810-193 Aveiro, Portugal

^d IMAR – Institute of Marine Research, Centre for Ecological Modelling, DCEA-FCT, Qta. Torre, 2829-516 Monte de Caparica, Portugal

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.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: *Enteromorpha*; Spores; Bathymetry; Model; Nutrient loading

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 under-

stand 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. Korpinen 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-Azcárate et al., 2003; Korpinen 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

* Corresponding author. Tel.: +351 239 834729; fax: +351 239 823603.
E-mail address: imartins@ci.uc.pt (I. Martins).

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, zoospores 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-

oso et al., 2004) and consumers (Lopes et al., 2000; Dolbeth 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; Patrício 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:

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

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

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

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

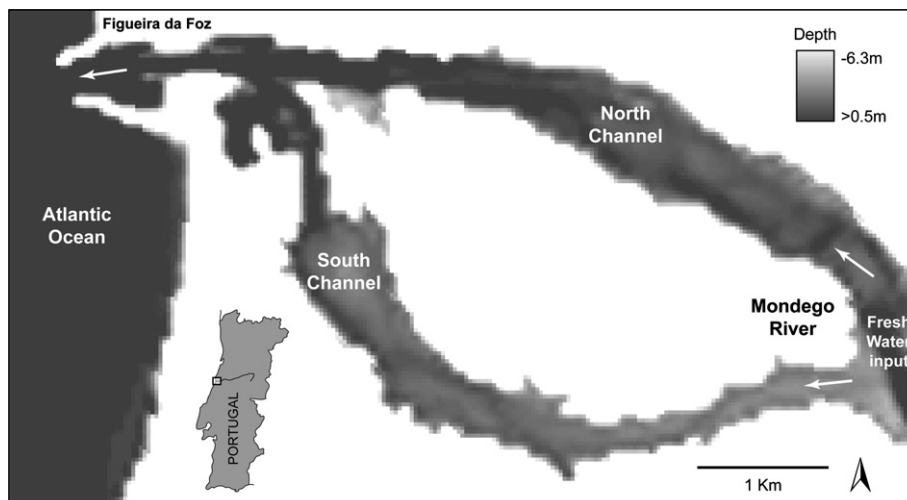


Fig. 1. Study area with bathymetry.

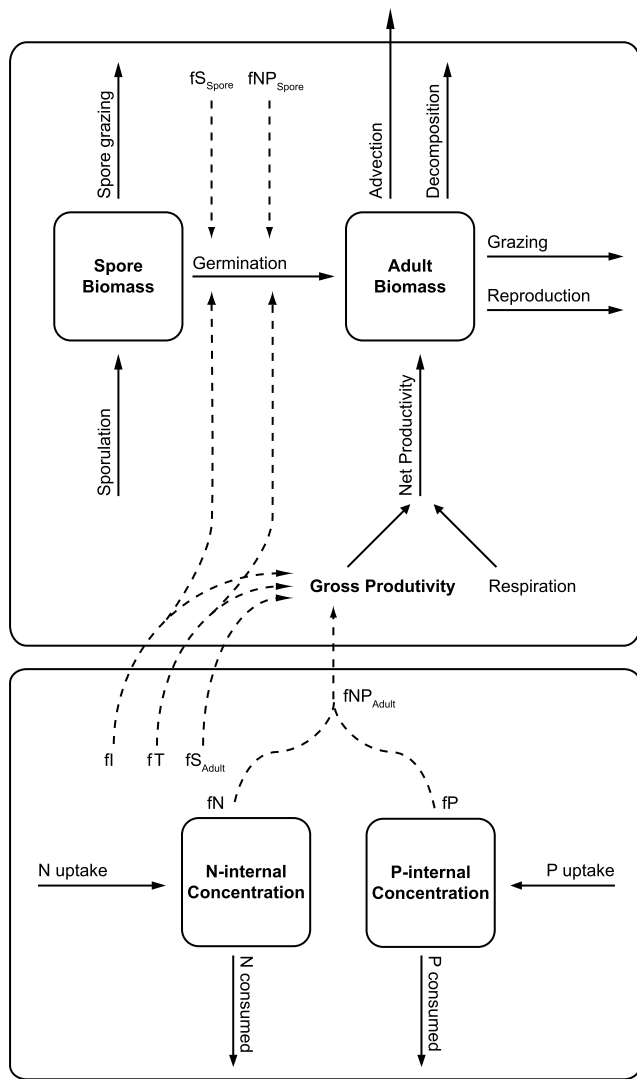


Fig. 2. Simplified conceptual diagram.

where S is spore biomass (mg C m^{-2}), A , adult biomass (g DW m^{-2}); N_{int} , internal nitrogen concentration ($\mu\text{mol N (g DW)}^{-1}$); P_{int} , internal phosphorus concentration ($\mu\text{mol P (g DW)}^{-1}$), Sp , sporulation ($\text{mg C m}^{-2} \text{d}^{-1}$); 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_{upt} , uptake of nutrient ($\mu\text{mol X (g DW)}^{-1} \text{d}^{-1}$); X_{cons} , consumed nutrient ($\mu\text{mol X (g DW)}^{-1} \text{d}^{-1}$); N , nitrogen ($\mu\text{mol l}^{-1}$), and P is phosphorus ($\mu\text{mol l}^{-1}$).

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 con-

verted 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 $0.06\text{--}0.14 \text{ d}^{-1}$ (Lotze and Worm, 2000). The maximum grazing rate on spores (Z_{maxS}) 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:

$$Z_S = Z_{\text{maxS}} \cdot f(T_{Z_S}) \quad (5)$$

Spore germination was defined by:

$$G = G_{\text{max}} f(T) \cdot f(I) \cdot f(S_S) \cdot f(NP_S) \quad (6)$$

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:

$$f(I) = \frac{I}{I_S} \cdot e^{(1-\frac{I}{I_S})} \quad (7)$$

where I is photon flux density ($\mu\text{E m}^{-2} \text{s}^{-1}$), and I_S is optimum photon flux density for *Enteromorpha* ($\mu\text{E m}^{-2} \text{s}^{-1}$)

$$f(T) = \exp \left[-2.3 \cdot \left(\frac{T - T_{\text{opt}}}{T_x - T_{\text{opt}}} \right)^2 \right] \quad (8)$$

where $T_x = T_{\text{min}}$ for $T \leq T_{\text{opt}}$ and $T_x = T_{\text{max}}$ for $T > T_{\text{opt}}$; T_{opt} , optimum temperature for growth ($^{\circ}\text{C}$); T_{min} , lower temperature limit below which growth ceases ($^{\circ}\text{C}$), and T_{max} is upper temperature limit above which growth ceases ($^{\circ}\text{C}$).

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:

$$f(S_S) = 1 - \left(\frac{S_S - S_{optS}}{S_{xS} - S_{optS}} \right)^m \quad (9)$$

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

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

$$\begin{aligned} \text{If } N : P \geq 12 \text{ and } N : P \leq 16 : f(NP_S) &= 1 \\ \text{If } N : P < 12 : f(NP_S) &= f(N_S) \\ \text{If } N : P > 16 : f(NP_S) &= f(P_S) \end{aligned} \quad (10)$$

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

$$f(X_S) = VX_{MaxS} \cdot \frac{[X]}{[X] + KX_S} \quad (11)$$

where VX_{MaxS} is maximum uptake rate of nutrient X by spores ($\mu\text{mol (g DW)}^{-1} \text{d}^{-1}$), KX_S , half-saturation constant for the uptake of the nutrient X by spores ($\mu\text{mol (g DW)}^{-1}$), 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 Jørgensen 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 , d^{-1}) is defined by:

$$P = GP - R \quad (12)$$

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

$$GP = \mu_{max} \cdot f(I) \cdot f(T) \cdot f(S) \cdot f(NP) \quad (13)$$

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

$$R = R_{max20} \cdot \theta^{(T-20)} \quad (14)$$

where R_{max20} is maximum respiration rate at 20 °C, and θ 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:

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

where $S_x = S_{min}$ and $m = 2.5$ for $S_A < S_{opt}$; $S_x = S_{max}$ and $m = 2$ for $S_A \geq S_{opt}$.

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

S_{opt} is optimum salinity at which growth rate is maximum (psu); S_{min} , lower salinity limit at which growth rate ceases (psu); S_{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:

$$\begin{aligned} \text{If } N_{int} : P_{int} \geq 12 \text{ and } N_{int} : P_{int} \leq 16 : f(NP_A) &= 1 \\ \text{If } N_{int} : P_{int} < 12 : f(NP_A) &= f(N_A) \\ \text{If } N_{int} : P_{int} > 16 : f(NP_A) &= f(P_A) \end{aligned} \quad (16)$$

$$f(X) = \frac{X_{int} - X_{imin}}{kqx + X_{int} - X_{imin}} \quad (17)$$

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

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

$$X_{upt} = \frac{X_{imax} - X_{int}}{X_{imax} - X_{imin}} \cdot \frac{V_{max} \cdot X_{ext}}{K_x + X_{ext}} \quad (18)$$

where X_{int} is internal nutrient concentration ($\mu\text{mol X (g DW)}^{-1}$); X_{imax} , maximum internal concentration of nutrient ($\mu\text{mol X (g DW)}^{-1}$); X_{imin} , minimum internal concentration of nutrient ($\mu\text{mol X (g DW)}^{-1}$); V_{max} , maximum uptake rate of nutrient ($\mu\text{mol X (g DW)}^{-1} \text{d}^{-1}$); K_x , half-saturation constant for the uptake of nutrient ($\mu\text{mol X (g DW)}^{-1}$); X_{ext} , external concentration of nutrient ($\mu\text{mol X (g DW)}^{-1}$); X , N (NO_3 and NH_4) and P ($\mu\text{mol l}^{-1}$).

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

$$X_{cons} = X_{int} \cdot X_{requirement} \quad (19)$$

where X_{int} is internal nutrient concentration ($\mu\text{mol X (g DW)}^{-1}$); $X_{requirement}$, amount of nutrient required for growth (d^{-1}). Daily nitrogen requirement rate for *Enteromorpha* was set at 45% of internal N d^{-1} , while the

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

| Symbol | Description | Units | Value used | Literature range | Source |
|---------------------------------|---|---|------------|------------------|--|
| μ_{\max} | Maximum growth rate at T_{opt} | d^{-1} | 0.8 | 0.2–1.5 | EPA (1985) |
| $R_{\max 20}$ | Maximum respiration rate at 20 °C | d^{-1} | 0.1 | 0.02–0.1 | EPA (1985) |
| θ | Empirical coefficient | | 1.047 | 1.01–1.2 | EPA (1985) |
| I_s | Optimum light intensity for photosynthesis | $\mu\text{molE m}^{-2} \text{s}^{-1}$ | 600 | 500–1000 | Shellem and Josselyn (1982), Beer and Shragge (1987) |
| T_{opt} | Optimum temperature for growth | °C | 22 | 15–30 | Shellem and Josselyn (1982), Fitzgerald (1978) |
| T_{\max} | Upper temperature tolerance limit at which growth ceases | °C | 35 | – | Poole and Raven (1997) |
| T_{\min} | Lower temperature tolerance limit at which growth ceases | °C | 10 | – | Poole and Raven (1997) |
| S_{opt} | Optimum salinity for growth | psu | 18 | 18–22 | Martins et al. (1999) |
| S_{\max} | Upper salinity tolerance limit at which growth ceases | psu | 45 | – | Poole and Raven (1997) |
| S_{\min} | Lower salinity tolerance limit at which growth ceases | psu | 0 | 0 | Poole and Raven (1997) and Martins et al. (1999) |
| N_{\min} | Minimum internal quota (subsistence quota) for nitrogen | $\mu\text{mol N (g DW)}^{-1}$ | 500 | 499–1717 | Solidoro et al. (1997) |
| N_{\max} | Maximum internal quota for nitrogen | $\mu\text{mol N (g DW)}^{-1}$ | 3000 | 1928–4285 | Solidoro et al. (1997), Bendricchio et al. (1994) |
| kq | Nitrogen half-saturation constant for growth | $\mu\text{mol N (g DW)}^{-1}$ | 1786 | Maximum 1786 | EPA (1985) |
| $V_{\max \text{NO}_3}$ | Maximum nitrate uptake rate | $\mu\text{mol NO}_3 \text{(g DW)}^{-1} \text{d}^{-1}$ | 1200 | 1200–1406 | Bendricchio et al. (1994) |
| $V_{\max \text{NH}_4}$ | Maximum ammonium uptake rate | $\mu\text{mol NH}_4 \text{(g DW)}^{-1} \text{d}^{-1}$ | 1500 | 3428–8913 | Bendricchio et al. (1994) |
| K_{NO_3} | Half-saturation constant for nitrate | $\mu\text{mol NO}_3 \text{l}^{-1}$ | 18 | 18 | Bendricchio et al. (1994) |
| K_{NH_4} | Half-saturation constant for ammonium | $\mu\text{mol NH}_4 \text{l}^{-1}$ | 20 | 14–43 | Bendricchio et al. (1994) |
| P_{\max} | Maximum internal quota for phosphorus | $\mu\text{mol P (g DW)}^{-1}$ | 126 | Maximum 126 | Bendricchio et al. (1994) |
| P_{\min} | Minimum internal quota (subsistence quota) for phosphorus | $\mu\text{mol P (g DW)}^{-1}$ | 16 | 16–35 | Bendricchio et al. (1994) |
| $V_{\max \text{PO}_4}$ | Maximum phosphorus uptake rate | $\mu\text{mol PO}_4 \text{(g DW)}^{-1} \text{d}^{-1}$ | 96 | 178–844 | Bendricchio et al. (1994) |
| K_{PO_4} | Half-saturation constant for phosphorus | $\mu\text{mol PO}_4 \text{l}^{-1}$ | 1 | 0.81–3.64 | Bendricchio et al. (1994) |
| dec_{\max} | Maximum decomposition rate | d^{-1} | 0.025 | Maximum 0.65 | Paalme et al. (2002) |
| $\text{Reprod}_{\text{rate}}$ | Reproduction rate-amount of biomass lost by sporulation | d^{-1} | 0.01 | Maximum 0.6 | Niesenbaum (1988) |
| Germ_{\max} | Maximum germination | d^{-1} | 0.8 | 0.4–1.0 | Hoffmann and Camus (1989) |
| $\text{SporGraz}_{\text{rate}}$ | Maximum macroinvertebrate grazing rate on spores | d^{-1} | 0.14 | 0.06–0.14 | Lotze and Worm (2000) |
| T_{opGrazSp} | Optimum temperature for grazers | °C | 22 | 15–30 | Pardal et al. (2000) |
| $T_{\max \text{GrazSp}}$ | Upper temperature for grazers | °C | 35 | – | Poole and Raven (1997) |
| $T_{\min \text{GrazSp}}$ | Lower temperature for grazers | °C | 10 | – | Poole and Raven (1997) |
| S_{optSp} | Optimum salinity for growth of spores | psu | 35 | – | Sousa et al. (2007) |
| $S_{\max \text{Sp}}$ | Upper salinity for growth of spores | psu | 45 | – | Poole and Raven (1997) |
| S_{\min} | Lower salinity for growth of spores | psu | 10 | 0 | Sousa et al. (2007) |
| $V_{\max \text{NSp}}$ | Maximum nitrogen uptake rate by spores | $\mu\text{mol N (g DW)}^{-1} \text{d}^{-1}$ | 4568 | – | Lindenschmidt (2006) |
| K_{NSp} | Spore half-saturation constant for nitrogen | $\mu\text{mol N l}^{-1}$ | 1.7857 | – | Lindenschmidt (2006) |
| $V_{\max \text{PSp}}$ | Maximum phosphorus uptake rate by spores | $\mu\text{mol PO}_4 \text{(g DW)}^{-1} \text{d}^{-1}$ | 116 | – | Lindenschmidt (2006) |
| K_{PSp} | Spore half-saturation constant for phosphorus | $\mu\text{mol PO}_4 \text{l}^{-1}$ | 0.03225 | – | Lindenschmidt (2006) |

phosphorus requirement was set at 25% of internal-P d^{-1} . Nitrogen requirement rate was based on the range 37.3 and 7.4 $\text{mg N (g DW)}^{-1} \text{d}^{-1}$ 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-

pared to N and that the depletion of P appears to occur faster than N-depletion due to different types of internal pools (Björnsäter 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 ($Z_{\max A}$) 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)):

$$Z_A = Z_{\max A} \cdot f(T) \quad (20)$$

2.2.7. Sporulation

Macroalgae may allocate a significant amount of their biomass to the formation of zoospores and gametes (Niesenbaum, 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°C is considered and sporulation is defined by:

$$Sp = Sp_{\max} \cdot \theta^{(T-20)} \quad (21)$$

where θ 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:

$$D = D_{r\max} \theta^{(T-20)} \quad (22)$$

Decomposition rate ($D_{r\max}$) at 20°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 *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 $10\% \text{ d}^{-1}$ 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 macroalgal 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°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°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 , $\mu\text{E m}^{-2} \text{ s}^{-1}$ -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:

$$\text{PFD}_z = \text{PFD}_0 \times e^{-kz} \quad (23)$$

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

Based on values estimated *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 ($>50 \text{ g DW m}^{-2}$), the value of k is considered biomass-dependent to account for self-shading:

$$k = \begin{cases} 2 \dots (\text{Sluice} = 0, \text{AdultBiomass} < 50) \\ 5.59 \dots (\text{Sluice} = 1, \text{AdultBiomass} < 50) \\ 2 + (0.01 \times \text{AdultBiomass}) \dots (\text{Sluice} = 0, \text{AdultBiomass} \geq 50) \\ 5.59 + (0.01 \times \text{AdultBiomass}) \dots (\text{Sluice} = 1, \text{AdultBiomass} \geq 50) \end{cases} \quad (24)$$

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:

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

$$\text{HBM} = \text{If SpringNeapOscillation} \geq 0 \\ \text{THEN } 0.2 + \text{SpringNeapOscillation} \quad (26)$$

$$\text{ELSE } 0.2 - \text{SpringNeapOscillation}$$

$$\text{HPM} = \text{If SpringNeapOscillation} \geq 0 \\ \text{THEN } 3.7 - \text{SpringNeapOscillation} \quad (27)$$

$$\text{ELSE } 3.7 + \text{SpringNeapOscillation}$$

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 were 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 Jørgensen (1994). To assess for model reliability, model predictions for adult biomass at depth +1.8 m were compared with real data of *Enteromorpha* biomass quanti-

fied 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.

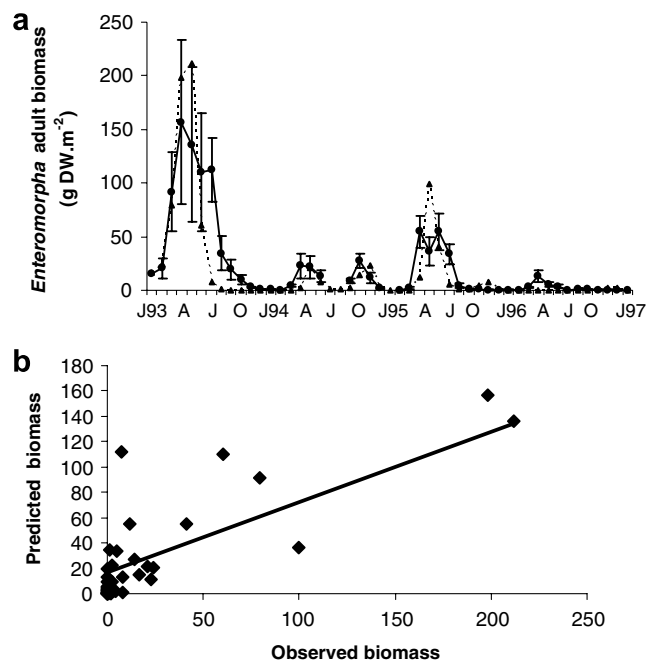


Fig. 3. Predicted (---) and observed (—) biomass variation \pm standard error of adult *Enteromorpha* (g DW m⁻²) at +1.8 m (a). Model II-regression between observed and predicted values (b).

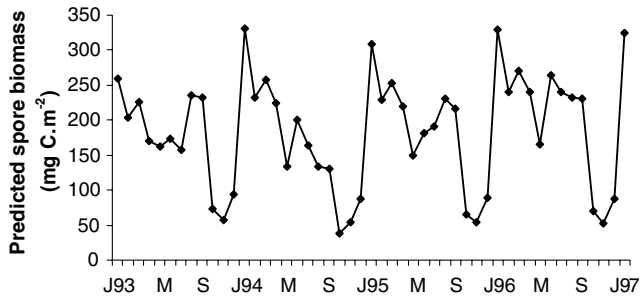


Fig. 4. Predicted spore biomass (mg C m^{-2}) variation at +1.8 m.

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).

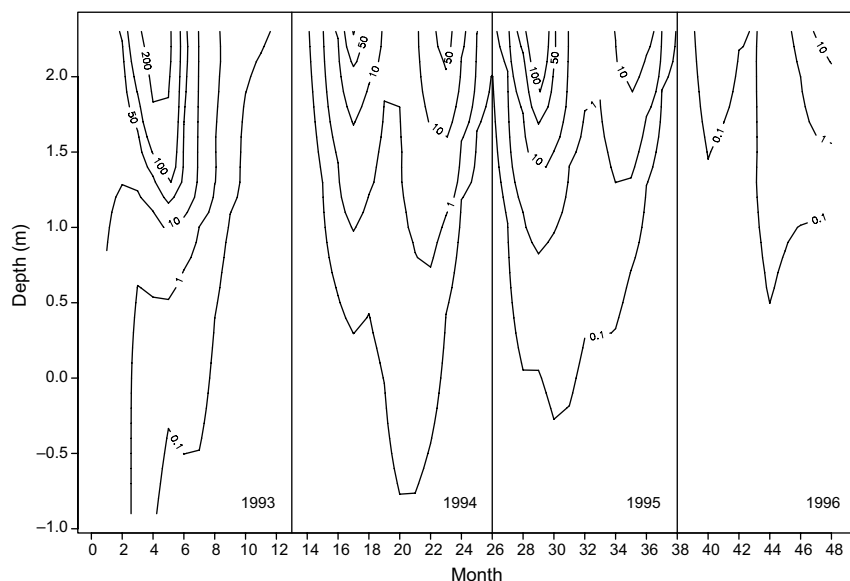


Fig. 5. Variation of *Enteromorpha* adult biomass (g DW m^{-2}) with depth during the study period.

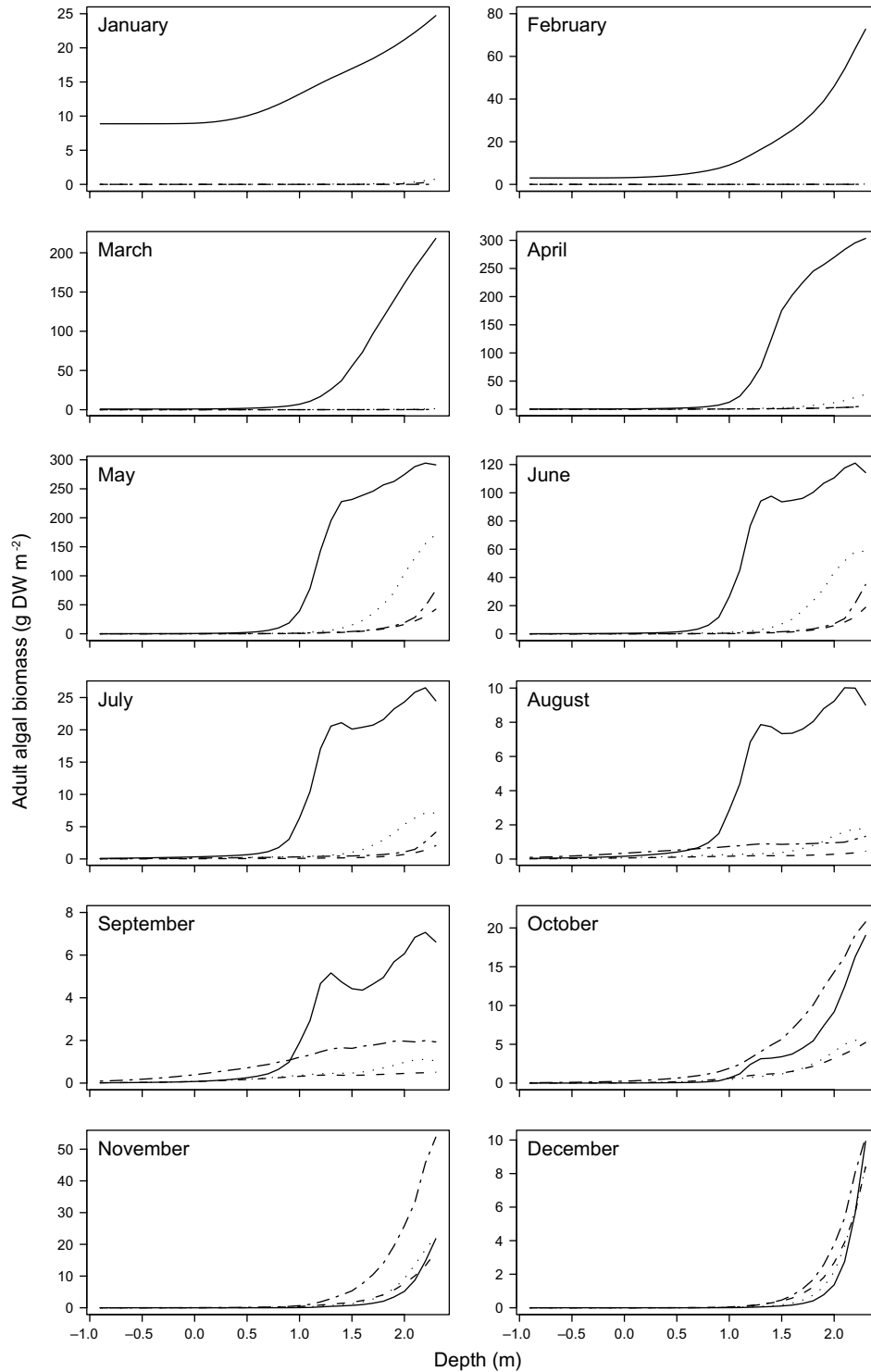


Fig. 6. Predicted monthly variation of *Enteromorpha* adult biomass (g DW m⁻²) with depth during the four different years: — 1993, 1995, -.-.- 1994, --- 1996.

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

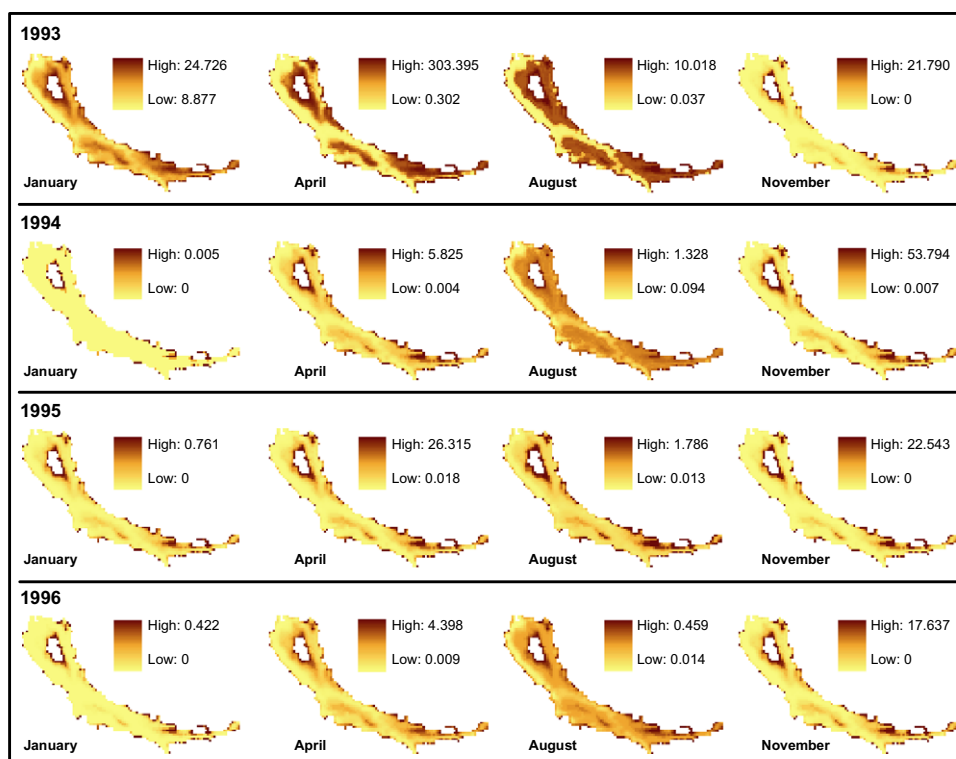


Fig. 7. Bathymetric distribution of *Enteromorpha* biomass (g DW m^{-2}) at the south channel of the Mondego estuary during winter (average of January, February and March), spring (average of April, May and June) summer (average of July, August and September) and autumn (average of October, November and December) in the four studied years.

Table 2

Classification of the studied years according to the Assessment of Estuarine Trophic Status (ASSETS) methodology related to the Overall Eutrophic Condition (OEC) (Bricker et al., 2003)

| Annual total values | 1993 | 1994 | 1995 | 1996 |
|--|----------|------------|------------|---------|
| ASSETS classification of eutrophication status | High OEC | Medium OEC | Medium OEC | Low OEC |
| Produced <i>Enteromorpha</i> biomass (ton DW) | 21,205 | 1430 | 2472 | 239 |
| Internal-C (ton) | 6150 | 415 | 717 | 69 |
| Internal-N (ton) | 689 | 47 | 80 | 8 |
| Internal-P (ton) | 23 | 1.6 | 2.7 | 0.26 |
| Exported <i>Enteromorpha</i> (ton DW) | 12,723 | 858 | 1483 | 143 |
| C-exported (ton) | 3688 | 249 | 430 | 42 |
| N-exported (ton) | 414 | 28 | 48 | 4.7 |
| P-exported (ton) | 14 | 0.94 | 1.6 | 0.16 |
| PEQ (population equivalents) | 156,631 | 10,562 | 18,257 | 1763 |
| PEQ: Number of inhabitants | 2.38 | 0.16 | 0.28 | 0.026 |
| N-internal requirement: N-domestic load | 13.5 | 0.91 | 1.57 | 0.15 |
| P-internal requirement: P-domestic load | 1.01 | 0.07 | 0.12 | 0.01 |

Predicted biomass of adult *Enteromorpha*, C-, N- and P-internal content, exported biomass and exported-C, -N and -P. Assumed PEQ was 4.4 kg N yr^{-1} (Alvera-Azcárate et al., 2003). The number of inhabitants in the watershed of the Mondego estuary is about 65,700 with an annual domestic load of 51 ton of N and 23 ton of P.

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 bio-

mass, 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

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_xN, 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 be uptaken 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.

Acknowledgments

The present work was supported by The Portuguese Foundation for Science and Technology (FCT) through a post-doc grant to I. Martins (SFRH/BPD/5665/2001). The authors acknowledge all researchers and technicians from IMAR-CIC that were indirectly involved in data acquisition through field and/or laboratory work.

References

- Albrecht, A.S., 1998. Soft bottom versus hard rock: community ecology of macroalgae on intertidal mussel beds in the Wadden Sea. *Journal of Experimental Marine Biology and Ecology* 229, 85–109.
- Alvera-Azcárate, A., Ferreira, J.G., Nunes, J.P., 2003. Modelling eutrophication in mesotidal and macrotidal estuaries. The role of intertidal seaweeds. *Estuarine Coastal and Shelf Science* 56 (1), 1–10.
- Baird, M.E., Walker, S.J., Wallace, B.B., Webster, I.T., Parslow, J.S., 2003. The use of mechanistic descriptions of algal growth and zooplankton grazing in an estuarine eutrophication model. *Estuarine Coastal and Shelf Science* 56 (3–4), 685–695.
- Beer, S., Shragge, B., 1987. Photosynthetic carbon metabolism in *Enteromorpha compressa* (Chlorophyta). *Journal of Phycology* 23, 580–584.
- Bell, E.C., 1993. Photosynthetic response to temperature and desiccation of the intertidal alga *Mastocarpus papillatus*. *Marine Biology* 117, 337–346.
- Bell, E.C., 1995. Environmental and morphological influences on thallus temperature and desiccation of the intertidal alga *Mastocarpus papillatus* Kützting. *Journal of Experimental Marine Biology and Ecology* 191, 29–55.
- Bendoricchio, G., Coffaro, G., Di Luzio, M., 1993. Modelling the photosynthetic efficiency for *Ulva rigida* growth. *Ecological Modelling* 67, 221–232.
- Bendoricchio, G., Coffaro, G., De Marchi, C., 1994. A trophic model for *Ulva rigida* in the Lagoon of Venice. *Ecological Modelling* (75/76), 485–496.
- Björnsäter, B.R., Wheeler, P.A., 1990. Effect of nitrogen and phosphorus supply on growth and tissue composition of *Ulva fenestrata* and *Enteromorpha intestinalis* (Ulvales, Chlorophyta). *Journal of Phycology* 26, 603–611.
- Bricker, S.B., Ferreira, J.G., Simas, T., 2003. An integrated methodology for assessment of estuarine trophic status. *Ecological Modelling* 169, 39–60.

- Brock, T.D., 1981. Calculating solar radiation for ecological studies. *Ecological Modelling* 14, 1–19.
- Cao, W., Hong, H., Yue, S., 2005. Modelling agricultural nitrogen contributions to the Jiulong River estuary and coastal water. *Global and Planetary Change* 47, 111–121.
- Cardoso, P.G., Pardal, M.A., Lillebø, A.I., Ferreira, S.M., Raffaelli, D., Marques, J.C., 2004. Dynamic changes in seagrasses assemblages under eutrophication and implications for recovery. *Journal of Experimental Marine Biology and Ecology* 302, 233–248.
- Dolbeth, M., Pardal, M.A., Lillebø, A.I., Azeiteiro, U., Marques, J.C., 2003. Short- and long-term effects of eutrophication on the secondary production of an intertidal macrobenthic community. *Marine Biology* 143 (6), 1229–1238.
- Duarte, C.M., 1992. Nutrient concentration of aquatic plants: patterns across species. *Limnological Oceanography* 37 (4), 882–889.
- Duarte, C.M., Cebrián, J., 1996. The fate of marine autotrophic production. *Limnological Oceanography* 41 (8), 1758–1766.
- EPA – Environmental Protection Agency, USA, 1985. Rates, constants, and kinetics. Formulations in surface water quality modelling, 2nd ed., 455pp.
- Ferreira, J.G., Ramos, L., 1989. A model for the estimation of annual production rates of macrophyte algae. *Aquatic Botany* 33, 53–70.
- Ferreira, J.G., Simas, T., Nobre, A., Silva, M.C., Schifferegger, K., Lencart-Silva, J., 2003. Identification of sensitive areas and vulnerable zones in transitional and coastal Portuguese systems. Application of the United States National Estuarine Eutrophication Assessment to the Minho, Lima, Douro, Ria de Aveiro, Mondego, Tagus, Sado, Mira, Ria Formosa and Guadiana systems. IMAR/INAG, 2003. <<http://www.eutro.org>>.
- Ferreira, J.G., Bricker, S.B., Simas, T.C., 2007. Application and sensitivity testing of a eutrophication assessment method on coastal systems in the United States and European Union. *Journal of Environmental Management* 82, 433–445.
- Fitzgerald, W.J., 1978. Environmental parameters influencing the growth of *Enteromorpha clathrata* (Roth) J. Ag. in the intertidal zone on Guam. *Botanica Marina* 21, 207–220.
- Flindt, M.R., Salomonsen, J., Carrer, M., Bocci, M., Kamp-Nielsen, L., 1997. Loss, growth and transport dynamics of *Chaetomorpha aerea* and *Ulva rigida* in the Lagoon of Venice during an early summer field campaign. *Ecological Modelling* 102, 133–141.
- Fowler, J., Cohen, L., Jarvis, P., 1998. *Practical Statistics for Field Biology*, second ed. Wiley, New York, 259pp.
- Giannotti, A.L., McGlathery, K., 2001. Consumption of *Ulva lactuca* (Chlorophyta) by the omnivorous mud snail *Ilyanassa obsoleta* (Say). *Journal of Phycology* 37, 209–215.
- Hernández, I., Peralta, G., Pérez-Lloréns, J.L., Vergara, J.J., Niell, F.X., 1997. Biomass and dynamics of growth of *Ulva* species in Palmones river estuary. *Journal of Phycology* 33, 764–772.
- Hoffmann, A.J., Camus, P., 1989. Sinking rates and viability of spores from benthic algae in central Chile. *Journal of Experimental Marine Biology and Ecology* 126, 281–291.
- Jørgensen, S.E., 1994. *Fundamentals of Ecological Modelling*, second ed. Elsevier, Amsterdam, 628pp.
- Jørgensen, S.E., Nielsen, S.N., Jørgensen, L.A., 1991. *Handbook of Ecological Parameters and Ecotoxicology*. Elsevier, Amsterdam.
- Korpinen, P., Kiirikki, M., Koponen, J., Peltoniemi, H., Sarkkula, J., 2004. Evaluation and control of eutrophication in Helsinki sea area with the help of a nested 3D-ecohydrodynamic model. *Journal of Marine Systems* 45, 255–265.
- Kraufvelin, P., Salovius, S., Christie, H., Moy, F.E., Karez, R., Pedersen, M.F., 2006. Eutrophication-induced changes in benthic algae affect the behaviour and fitness of the marine amphipod *Gammarus locusta*. *Aquatic Botany* 84 (3), 199–209.
- Lillebø, A.I., Flindt, M.R., Pardal, M.A., Martins, I., Neto, J.M., Marques, J.C., 2002. Nutrient dynamics in the intertidal pools of the Mondego estuary. II. Seasonal efflux of PO₄-P and NH₄-N in bare bottom and vegetated pools. In: Pardal, M.A., Marques, J.C., Graça, M.A. (Eds.), *Aquatic Ecology of the Mondego River Basin. Global Importance of Local Experience*. Imprensa da Universidade, Coimbra.
- Lillebø, A.I., Neto, J.M., Martins, I., Verdelhos, T., Leston, S., Cardoso, P.G., Ferreira, S.M., Marques, J.C., Pardal, M.A., 2005. Management of a shallow temperate estuary to control eutrophication: the effect of hydrodynamics on the system's loading. *Estuarine Coastal and Shelf Science* 65, 697–707.
- Lindenschmidt, K.-E., 2006. The effect of complexity on parameter sensitivity and model uncertainty in river water quality modelling. *Ecological Modelling* 190, 72–86.
- Lopes, R.J., Pardal, M.A., Marques, J.C., 2000. Impact of macroalgae blooms and wader predation on intertidal macroinvertebrates – experimental evidence in the Mondego estuary (Portugal). *Journal of Experimental Marine Biology and Ecology* 249, 165–179.
- Lopes, R.J., Pardal, M.A., Múrias, T., Cabral, J.A., Marques, J.C., 2006. Influence of macroalgal mats on abundance and distribution of dunlin *Calidris alpina* in estuaries: a long-term approach. *Marine Ecology Progress Series* 323, 11–20.
- Lotz, H.K., Worm, B., 2000. Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae. *Marine Ecology Progress Series* 200, 167–175.
- Marques, J.C., Maranhão, P., Pardal, M.A., 1993. Human impact assessment on the subtidal macrobenthic community structure in the Mondego Estuary (Western Portugal). *Estuarine Coastal and Shelf Science* 37, 403–419.
- Martins, I., Marques, J.C., 2002. A model for the growth of opportunistic macroalgae (*Enteromorpha* sp.) in tidal estuaries. *Estuarine Coastal and Shelf Science* 55 (2), 247–257.
- Martins, I., Oliveira, J.M., Flindt, M.R., Marques, J.C., 1999. The effect of salinity on the growth rate of the macroalgae *Enteromorpha intestinalis* (Chlorophyta) in the Mondego estuary (west Portugal). *Acta Oecologica* 20, 259–265.
- Martins, I., Pardal, M.A., Lillebø, A.I., Flindt, M.R., Marques, J.C., 2001. Hydrodynamics as a major factor controlling the occurrence of green macroalgal blooms in a eutrophic estuary: a case study on the influence of precipitation and river management. *Estuarine Coastal and Shelf Science* 52, 165–177.
- Martins, I., Flindt, M.R., Pardal, M.A., Lillebø, A.I., Oliveira, J.M., Marques, J.C., 2002. Nutrient dynamics in the intertidal pools of the Mondego estuary. III. The importance of nutrient effluxes to macroalgal growth (*Enteromorpha* sp.). In: Pardal, M.A., Marques, J.C., Graça, M.A. (Eds.), *Aquatic Ecology of the Mondego River Basin. Global Importance of Local Experience*. Imprensa da Universidade, Coimbra.
- Matta, J.L., Chapman, D.J., 1995. Effects of light, temperature and desiccation on the net emersed productivity of the intertidal macroalga *Colpomenia peregrina* Sauv. (Hamel). *Journal of Experimental Marine Biology and Ecology* 189, 13–27.
- Nedwell, D.B., Dong, L.F., Sage, A., Underwood, G.J.C., 2002. Variations of the nutrient loads to the mainland UK estuaries: correlation with catchment areas, urbanization and coastal eutrophication. *Estuarine Coastal and Shelf Science* 54, 951–970.
- Neto, J.M.M., 2004. Nutrient enrichment in a temperate macro-tidal system. Scenario analysis and contribution to coastal management, Ph.D. Thesis, University of Coimbra, Portugal.
- Niesenbaum, R.A., 1988. The ecology of sporulation by the macroalga *Ulva lactuca* L. (Chlorophyceae). *Aquatic Botany* 32, 155–166.
- Nobre, A.M., Ferreira, J.G., Newton, A., Simas, T., Icely, J.D., Neves, R., 2005. Management of coastal eutrophication: Integration of field data, ecosystem-scale simulations and screening models. *Journal of Marine Systems* 56, 375–390.
- Paalme, T., Kukk, H., Kotta, J., Orav, H., 2002. “In vitro” and “in situ” decomposition of nuisance macroalgae *Cladophora glomerata* and *Pilayella littoralis*. *Hydrobiologia* (475/476), 469–476.
- Pardal, M.A., Marques, J.C., Metelo, I., Lillebø, A.I., Flindt, M.R., 2000. Impact of eutrophication on the life cycle, population dynamics and production of *Amphitoe valida* (Amphipoda) along an estuarine spatial

- gradient (Mondego estuary, Portugal). Marine Ecology Progress Series 196, 207–219.
- Pardal, M.A., Cardoso, P.G., Sousa, J.P., Raffaelli, D., 2004. Assessing environmental quality: a novel approach. Marine Ecology Progress Series 267, 1–8.
- Patrício, J., Ulanowicz, R., Pardal, M.A., Marques, J.C., 2006. Ascendancy as an ecological indicator for environmental quality assessment at the ecosystem level: a case study. Hydrobiologia 555, 19–30.
- Pedersen, M.F., Borum, J., 1996. Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. Marine Ecology Progress Series 142, 261–272.
- Poole, L.J., Raven, J.A., 1997. The biology of *Enteromorpha*. In: Round, F.E., Chapman, D.J. (Eds.), Progress in Phycological Research, vol. 12, Biopress Ltd, 123 pp.
- Raffaelli, D.G., Raven, J.A., Poole, L.J., 1998. Ecological impact of green macroalgal blooms. Oceanography and Marine Biology: An Annual Review 36, 97–125.
- Raffaelli, D., Bell, E., Weithoff, G., Matsumoto, A., Cruz-Motta, J.J., Kershaw, P., Parker, R., Parry, D., Jones, M., 2003. (Review) The ups and downs of benthic ecology: considerations of scale, heterogeneity and surveillance for benthic-pelagic coupling. Journal of Experimental Marine Biology and Ecology 285–286, 191–203.
- Rivers, J., Peckol, P., 1995. Summer decline of *Ulva lactuca* (Chlorophyta) in a eutrophic embayment: interactive effects of temperature and nitrogen availability?. Journal of Phycology 31 223–228.
- Salomonsen, J., Flindt, M.R., Geertz-Hansen, O., 1997. Significance of advective transport of *Ulva lactuca* for a biomass budget on a shallow water location. Ecological Modelling 102, 129–132.
- Sanders, R., Klein, C., Jickells, T., 1997. Biogeochemical nutrient cycling in the Upper Great Ouse Estuary, Norfolk, UK. Estuarine Coastal and Shelf Science 44, 543–555.
- Santelices, B., 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanography and Marine Biology: An Annual Review 28, 177–276.
- Schories, D., Anibal, J., Chapman, A.S., Herre, E., Isaksson, I., Lillebø, A.I., Pihl, L., Reise, K., Sprung, M., Thiel, M., 2000. Flagging greens: hydrobiid snails as substrata for the development of green algal mats (*Enteromorpha* spp.) on tidal flats of North Atlantic coasts. Marine Ecology Progress Series 199, 127–136.
- Shellem, B.H., Josselyn, M.N., 1982. Physiological ecology of *Enteromorpha clathrata* (Roth) Grev. on a salt marsh mudflat. Botanica Marina 25, 541–549.
- Simas, T., Nunes, J.P., Ferreira, J.G., 2001. Effects of global climate change on coastal salt marshes. Ecological Modelling 139, 1–15.
- Sokal, R.R., Rohlf, F.J., 1995. Biometry, third ed. Freeman, New York.
- Solidoro, C., Brando, V.E., Dejak, C., Franco, D., Pastres, R., Pecelik, G., 1997. Long-term simulations of population dynamics of *Ulva rigida* in the lagoon of Venice. Ecological Modelling 102, 259–272.
- Sousa, A.I., Martins, I., Lillebø, A.I., Flindt, M.R., Pardal, M.A., 2007. Influence of salinity, nutrients and light on the germination and growth of *Enteromorpha* sp. spores. Journal of Experimental Marine Biology and Ecology 341, 142–150.
- Verdelhos, T., Neto, J.M., Marques, J.C., Pardal, M.A., 2005. The effect of eutrophication abatement on the bivalve *Scrobicularia plana*. Estuarine Coastal and Shelf Science 63, 261–268.
- Vergara, J.J., Sebastián, M., Pérez-Lloréns, J.L., Hernández, I., 1998. Photoacclimation of *Ulva rigida* and *U. rotundata* (Chlorophyta) arranged in canopies. Marine Ecology Progress Series 165, 283–292.