



ELSEVIER

Available online at www.sciencedirect.com



Marine Pollution Bulletin xxx (2007) xxx–xxx

MARINE  
POLLUTION  
BULLETIN

www.elsevier.com/locate/marpolbul

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

Irene Martins <sup>a,\*</sup>, Ricardo J. Lopes <sup>b</sup>, A.I. Lillebø <sup>c</sup>, J.M. Neto <sup>a</sup>, M.A. Pardal <sup>a</sup>,  
João Gomes Ferreira <sup>d</sup>, João Carlos Marques <sup>a</sup>

<sup>a</sup> IMAR – Institute of Marine Research, Coimbra Interdisciplinary Centre, Department of Zoology, University of Coimbra, 3004-517 Coimbra, Portugal

<sup>b</sup> CIBIO – Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, 4485-661 Vairão, Portugal

<sup>c</sup> CESAM – Centro de Estudos do Ambiente e do Mar, University of Aveiro, 3810-193 Aveiro, Portugal

<sup>d</sup> IMAR – Institute of Marine Research, Centre for Ecological Modelling, DCEA-FCT, Qta. Torre, 2825-114 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 depth variations 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 blooming 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., in press). 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. 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 macroalgae, no references are made,

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

51 in general, to the processes that control macroalgal spore  
52 germination and their relation to adult macroalgae bio-  
53 mass. However, experimental work suggests that the  
54 recruitment processes and the factors affecting early life  
55 stages determine the development and the dominance pat-  
56 terns of macroalgal blooms (Lotze and Worm, 2000).  
57 Additionally, it seems that the development of green algal  
58 mats is initiated either by overwintering and regrowth of  
59 adult plants or by the formation of small propagules (veg-  
60 etative fragments, zoospores or zygotes) (Schories et al.,  
61 2000). Thus, it becomes clear that the full understanding  
62 of macroalgal dynamics and, consequently of the conse-  
63 quences of eutrophication processes, can only be achieved  
64 if both macroalgal adult individuals and microscopic life  
65 stages are taken into consideration (Sousa et al., in press).

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

## 72 2. Material and methods

### 73 2.1. Study site

74 The Mondego estuary is a warm-temperate system  
75 located on the west coast of Portugal, which consists of  
76 two different channels, north and south, separated by an  
77 alluvial island (Fig. 1). The north channel is deeper (5–  
78 10 m during high tide; tidal range 1–3 m), whilst the south  
79 channel is shallower (2–4 m during high tide, tidal range  
80 0.5–3.5 m). For a detailed characterisation of the system  
81 see e.g. Ferreira et al. (2002) and Lillebø et al. (2005).

82 During the 1980s and early 1990s, several studies  
83 assessed the ecological importance of the south channel  
84 (e.g. Marques et al., 1993) and during the 1990s, other  
85 works concluded about the ongoing eutrophication process  
86 and the impacts on established primary producers (Car-

87 doso et al., 2004) and consumers (Lopes et al., 2000; Dol-  
88 beth et al., 2003; Verdelhos et al., 2005). Modelling and  
89 theoretical approaches aiming to describe and understand  
90 the local effects of eutrophication from a holistic perspec-  
91 tive were also achieved (Martins and Marques, 2002;  
92 Pardal et al., 2004; Patrício et al., 2006).

93 The inter-annual variation of the biomass of opportu-  
94 nistic macroalgae (mainly represented by *Enteromorpha*)  
95 in the Mondego estuary is controlled by hydrodynamics,  
96 which in turn depends on precipitation and river manage-  
97 ment, according to the water requirements of paddy fields  
98 in the catchment (Martins et al., 2001). In dry years, char-  
99 acterized by decreased rainfall in late winter and spring, the  
100 biomass of *Enteromorpha* tends to increase significantly,  
101 frequently giving rise to a spring bloom (Pardal et al.,  
102 2000). In the present work, the definitions given in the  
103 ASSETS method for eutrophication assessment (Bricker  
104 et al., 2003) for Overall Eutrophic Condition (OEC) are  
105 used as follows: *high OEC* indicates significant expression  
106 of macroalgal symptoms of eutrophication (i.e. spring-  
107 early summer bloom), *low OEC* indicates low growth and  
108 biomass of *Enteromorpha*.

### 109 2.2. Model formulation

110 The model has four state variables: spore biomass  
111 ( $\text{mg C m}^{-2}$ ), adult biomass ( $\text{g DW m}^{-2}$ ), adult macroalgae  
112 N-internal concentration ( $\mu\text{mol N (g DW)}^{-1}$ ) and P-internal  
113 concentration ( $\mu\text{mol P (g DW)}^{-1}$ ) (Fig. 2). The state  
114 variables are defined as:

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

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

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

$$\frac{dP_{\text{int}}}{dt} = P_{\text{upt}} - P_{\text{cons}} \quad (4) \quad 116$$

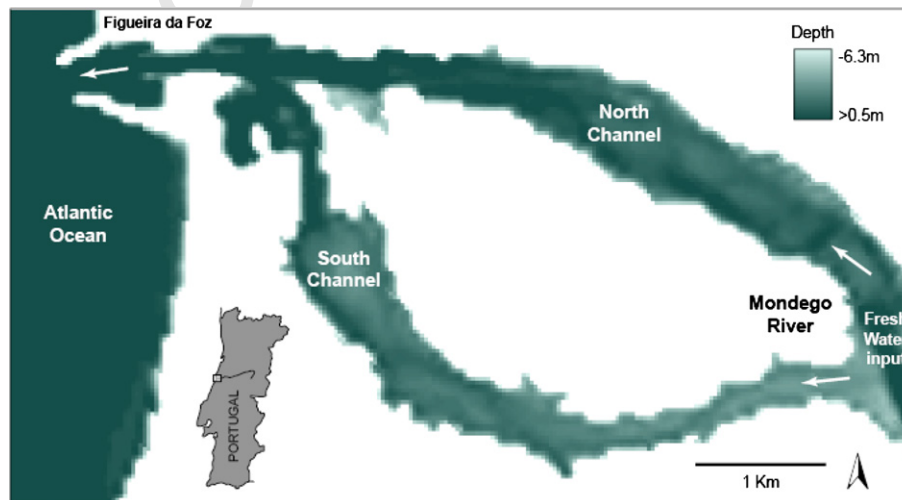


Fig. 1. Study area with bathymetry.

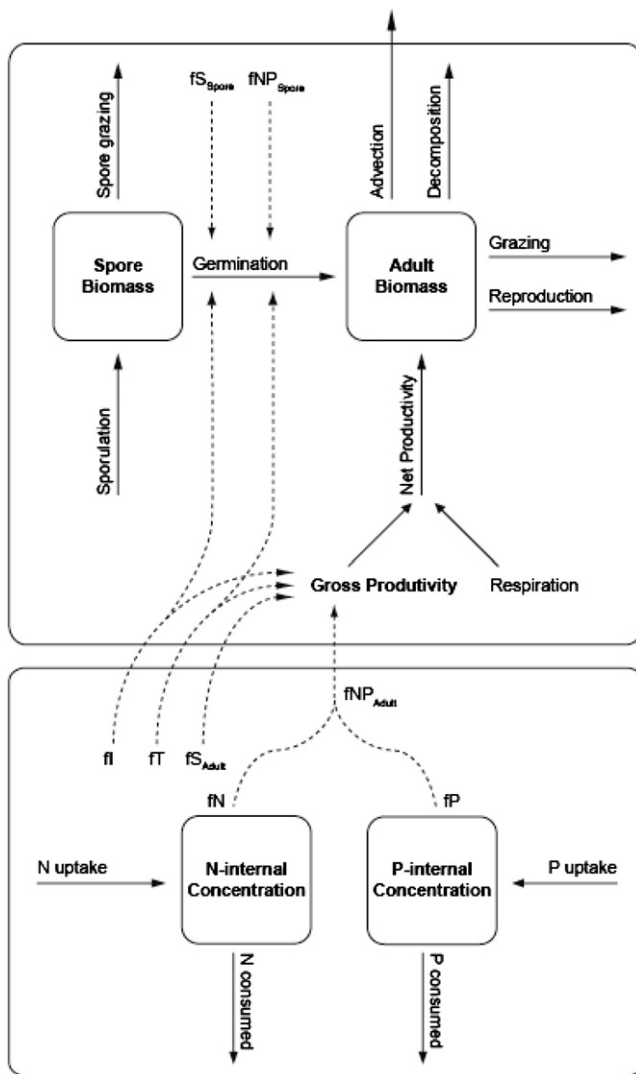


Fig. 2. Simplified conceptual diagram.

117 where  $S$  is spore biomass ( $\text{g DW m}^{-2}$ ),  $A$ , adult biomass  
 118 ( $\text{g DW m}^{-2}$ );  $N_{\text{int}}$ , internal nitrogen concentration ( $\mu\text{mol N}$   
 119 ( $\text{g DW}^{-1}$ );  $P_{\text{int}}$ , internal phosphorus concentration  
 120 ( $\mu\text{mol P}$  ( $\text{g DW}^{-1}$ ),  $Sp$ , sporulation ( $\text{g DW m}^{-2} \text{d}^{-1}$ );  $G$ ,  
 121 germination ( $\text{d}^{-1}$ );  $Z_S$ , grazing on spores ( $\text{d}^{-1}$ );  $P$ , net pro-  
 122 ductivity ( $\text{d}^{-1}$ );  $Adv$ , advection ( $\text{d}^{-1}$ );  $D$ , decomposition  
 123 ( $\text{d}^{-1}$ );  $Z_A$ , grazing on adults ( $\text{d}^{-1}$ );  $U$ , reproduction ( $\text{d}^{-1}$ );  
 124  $X_{\text{upt}}$ , uptake of nutrient ( $\mu\text{mol X}$  ( $\text{g DW}^{-1} \text{d}^{-1}$ );  $X_{\text{cons}}$ ,  
 125 consumed nutrient ( $\mu\text{mol X}$  ( $\text{g DW}^{-1} \text{d}^{-1}$ ),  $N$ , nitrogen  
 126 ( $\mu\text{mol l}^{-1}$ ), and  $P$  is phosphorus ( $\mu\text{mol l}^{-1}$ ).

### 127 2.2.1. Spore biomass

128 It is assumed that spore biomass depends on three basic  
 129 processes: sporulation ( $S$ ), grazing by macroinvertebrates  
 130 ( $Z_S$ ) and germination ( $G$ ). In general, sporulation is defined  
 131 as the release of spores by adult macroalgae, which is a  
 132 process followed by significant mortality rates (Santelices,  
 133 1990). In the present work, sporulation is defined as the  
 134 concentration of spores present in the water column, which  
 135 are able to attach to a hard substrate ( $\text{mg C m}^{-2}$  converted

to  $\text{g DW m}^{-2}$  assuming a conversion factor of 0.4) and to  
 136 survive. This value was obtained experimentally in situ  
 137 from January 2004 to January 2005 (Sousa et al., unpub-  
 138 lished). Results showed that although *Enteromorpha* spores  
 139 were present all year round in the water column of the  
 140 Mondego, spore biomass was higher in spring and early  
 141 summer. However, no significant regressions were found  
 142 between the variation of spore biomass and environmental  
 143 factors. For this reason, in the model, sporulation is  
 144 defined as a data series in accordance with the values quan-  
 145 tified by Sousa et al. (unpublished). Additionally, it is also  
 146 assumed that the variation of spores in the water column  
 147 does not differ significantly between years.  
 148

149 Experimental evidence suggests that herbivores may  
 150 reduce *Enteromorpha* propagules by  $0.06\text{--}0.14 \text{ d}^{-1}$  (Lotze  
 151 and Worm, 2000). The maximum grazing rate on spores  
 152 ( $Z_{\text{maxS}}$ ) was set to  $0.14 \text{ d}^{-1}$  and grazer activity was consid-  
 153 ered temperature-dependent, which was described the func-  
 154 tion  $f(T)$  explained above (Eq. (8)). This is in accordance  
 155 with field data showing that amphipod grazers (e.g. *Melita*  
 156 sp., *Amphitoe* sp.) exhibit higher biomass values during  
 157 spring and summer (Pardal et al., 2000). Thus, the effects  
 158 of grazers on spores were defined by:

$$Z_S = Z_{\text{maxS}} \cdot f(T_{Z_S}) \quad (5) \quad 160$$

161 Spore germination was defined by:

$$G = G_{\text{max}} f(T) \cdot f(I) \cdot f(S_S) \cdot f(NP_S) \quad (6) \quad 163$$

164 where  $G_{\text{max}}$  is maximum spore germination rate ( $\text{d}^{-1}$ );  $f(T)$ ,  
 165 temperature limiting factor;  $f(I)$ , light limiting factor;  $f(S_S)$ ,  
 166 salinity limiting factor;  $f(NP_S)$ , nitrogen and phosphorus  
 167 limiting factor. Limiting factors;  $f(X)$ , vary between 0 and  
 168 1 corresponding to null and optimum conditions for germi-  
 169 nation, respectively. The germination rates of opportunistic  
 170 green macroalgae (*Ulva rigida* and *Enteromorpha intesti-*  
 171 *nalis*) were found to vary between 40% and 100% (Hoff-  
 172 mann and Camus, 1989). In accordance with this, maximum  
 173 spore germination rate was set at  $0.8 \text{ d}^{-1}$ . Spore germination  
 174 depends on light and temperature, which may be described  
 175 by a photoinhibition-type expression and by a temperature-  
 176 optimum curve, respectively, as in the case of adult macroalgal  
 177 growth (e.g. Martins and Marques, 2002). These variations are  
 178 shown in Eqs. (7) and (8), respectively:  
 179

$$f(I) = \frac{I}{I_S} \cdot e^{(1-\frac{I}{I_S})} \quad (7) \quad 181$$

182 where  $I$  is photon flux density ( $\mu\text{E m}^{-2} \text{s}^{-1}$ ), and  $I_S$  is opti-  
 183 mum photon flux density for *Enteromorpha* ( $\mu\text{E m}^{-2} \text{s}^{-1}$ )  
 184

$$f(T) = \exp \left[ -2.3 \cdot \left( \frac{T - T_{\text{opt}}}{T_x - T_{\text{opt}}} \right)^2 \right] \quad (8) \quad 186$$

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

192 The influence of salinity variation on *Enteromorpha*  
193 spore germination was experimentally assessed (Sousa  
194 et al., in press). The results indicate that spore germination  
195 is enhanced at 35 psu and decreases with decreasing salini-  
196 ties. This effect was described by:  
197

$$199 \quad f(S_S) = 1 - \left( \frac{S - S_{\text{optS}}}{S_{X_S} - S_{\text{optS}}} \right)^m \quad (9)$$

200 where  $S_{X_S} = S_{\text{minS}}$  and  $m = 2.5$  for  $S < S_{\text{optS}}$ ,  $S_{X_S} = S_{\text{maxS}}$   
201 and  $m = 2$  for  $S \geq S_{\text{optS}}$ ;  $S_{\text{opt}}$ , optimum salinity for growth  
202 (psu);  $S_{\text{min}}$ , lower salinity limit below which growth ceases  
203 (psu);  $S_{\text{max}}$  is upper salinity limit above which growth  
204 ceases (psu).

205 The effect of nutrients (N and P) on spore germination  
206 was described according to Eqs. (10) and (11), which reflect  
207 the dependency of spore growth on external nutrient con-  
208 centration, assuming an optimum N:P range of 12–16,  
209 and the “Liebig’s law of the minimum”:  
210

$$211 \quad \text{If } N : P \geq 12 \text{ and } N : P \leq 16 : f(\text{NP}_S) = 1$$

$$212 \quad \text{If } N : P < 12 : f(\text{NP}_S) = f(N_S) \quad (10)$$

$$212 \quad \text{If } N : P > 16 : f(\text{NP}_S) = f(P_S)$$

213 The uptake of nutrients by spores follows a simple Michaelis-  
214 Menten kinetics:  
215

$$217 \quad f(X_S) = VX_{\text{MaxS}} \cdot \frac{[X]}{[X] + KX_S} \quad (11)$$

218 where  $VX_{\text{MaxS}}$  is maximum uptake rate of nutrient X by  
219 spores ( $\mu\text{mol (g DW)}^{-1} \text{d}^{-1}$ ),  $KX_S$ , half-saturation constant  
220 for the uptake of the nutrient X by spores ( $\mu\text{mol (g DW)}^{-1}$ ),  
221 and X is nutrient concentration ( $\mu\text{mol l}^{-1}$ ).

222 Spore half-saturation constants and maximum uptake  
223 rates for P and N (Table 1) follow Jørgensen et al. (1991)  
224 and Lindenschmidt (2006).

#### 225 2.2.2. Adult macroalgal biomass

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

#### 230 2.2.3. Net productivity

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

$$234 \quad P = \text{GP} - R \quad (12)$$

235 where GP is gross productivity ( $\text{d}^{-1}$ ) and  $R$  is respiration  
236 ( $\text{d}^{-1}$ ), which were defined by Eqs. (13) and (14),  
237 respectively:  
238

$$240 \quad \text{GP} = \mu_{\text{max}} \cdot f(I) \cdot f(T) \cdot f(S) \cdot f(\text{NP}) \quad (13)$$

241 where  $f(T)$  and  $f(I)$  were previously described in Eqs. (8)  
242 and (9), respectively.  
243

$$245 \quad R = R_{\text{max20}} \cdot \theta^{(T-20)} \quad (14)$$

where  $R_{\text{max20}}$  is maximum respiration rate at 20 °C, and  $\theta$   
is empirical coefficient. 246 247

#### 248 2.2.4. Salinity

249 The influence of salinity on the growth of adult *Entero-*  
250 *morpha* ( $f(S)$ ) is based on the experimental work by Mar-  
251 tins et al. (1999) and described by:

$$253 \quad \text{For salinity } \geq 5 \quad f(S) = 1 - \left( \frac{S - S_{\text{opt}}}{S_x - S_{\text{opt}}} \right)^m \quad (15)$$

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

$$257 \quad \text{For salinity } < 5 \quad f(S) = \frac{S - S_{\text{min}}}{S_{\text{opt}} - S_{\text{min}}}$$

258  $S_{\text{opt}}$  is optimum salinity at which growth rate is maxi-  
259 mum (psu);  $S_{\text{min}}$ , lower salinity limit at which growth rate  
260 ceases (psu);  $S_{\text{max}}$  is upper salinity limit at which growth  
261 ceases (psu).

#### 262 2.2.5. Nutrients

263 It is assumed that the growth of adult macroalgae  
264 depends on their internal nitrogen (N) (Björnsäter and  
265 Wheeler, 1990) and internal phosphorus (P) concentra-  
266 tions. These dependencies were defined by:

$$268 \quad \text{If } N_{\text{int}} : P_{\text{int}} \geq 12 \text{ and } N_{\text{int}} : P_{\text{int}} \leq 16 : f(\text{NP}_A) = 1$$

$$269 \quad \text{If } N_{\text{int}} : P_{\text{int}} < 12 : f(\text{NP}_A) = f(N_A) \quad (16)$$

$$268 \quad \text{If } N_{\text{int}} : P_{\text{int}} > 16 : f(\text{NP}_A) = f(P_A)$$

$$270 \quad f(X) = \frac{X_{\text{int}} - X_{\text{min}}}{kqx + X_{\text{int}} - X_{\text{min}}} \quad (17)$$

271 where  $X_{\text{min}}$  is subsistence quota for nutrient X ( $\mu\text{mol X}$   
272 ( $\text{g DW)}^{-1}$ );  $kq$ , nutrient half-saturation constant for  
273 growth limitation ( $\mu\text{mol X (g DW)}^{-1}$ ),  $X - N_A$  or  $P_A$ .

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

$$278 \quad X_{\text{upt}} = \frac{X_{\text{imax}} - X_{\text{int}}}{X_{\text{imax}} - X_{\text{imin}}} \cdot \frac{V_{\text{max}} \cdot X_{\text{ext}}}{K_x + X_{\text{ext}}} \quad (18)$$

279 where  $X_{\text{int}}$  is internal nutrient concentration ( $\mu\text{mol X}$   
280 ( $\text{g DW)}^{-1}$ );  $X_{\text{imax}}$ , maximum internal concentration of  
281 nutrient ( $\mu\text{mol X (g DW)}^{-1}$ );  $X_{\text{imin}}$ , minimum internal con-  
282 centration of nutrient ( $\mu\text{mol X (g DW)}^{-1}$ );  $V_{\text{max}}$ , maximum  
283 uptake rate of nutrient ( $\mu\text{mol X (g DW)}^{-1} \text{d}^{-1}$ );  $K_x$ , half-  
284 saturation constant for the uptake of nutrient ( $\mu\text{mol X}$   
285 ( $\text{g DW)}^{-1}$ );  $X_{\text{ext}}$ , external concentration of nutrient ( $\mu\text{mol}$   
286  $X (\text{g DW)}^{-1}$ ); X, N ( $\text{NO}_3$  and  $\text{NH}_4$ ) and P ( $\mu\text{mol l}^{-1}$ ).

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

$$290 \quad X_{\text{cons}} = X_{\text{int}} \cdot X_{\text{requirement}} \quad (19)$$

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



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

Symbol	Description	Units	Used value	Literature range	Source
$\mu_{\max}$	Maximum growth rate at $T_{\text{opt}}$	$\text{d}^{-1}$	0.8	0.2–1.5	EPA (1985)
$R_{\max 20}$	Maximum respiration rate at 20 °C	$\text{d}^{-1}$	0.1	0.02–0.1	EPA (1985)
$\theta$	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 Shrage (1987)
$T_{\text{opt}}$	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	37	Maximum 42	Poole and Raven (1997)
$T_{\min}$	Lower temperature tolerance limit at which growth ceases	°C	10	Minimum –20	Poole and Raven (1997)
$S_{\text{opt}}$	Optimum salinity for growth	psu	18	18–22	Martins et al. (1999)
$S_{\max}$	Upper salinity tolerance limit at which growth ceases	psu	45	Maximum 95	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), Bendoricchio 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	Bendoricchio 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	Bendoricchio et al. (1994)
$K_{\text{NO}_3}$	Half-saturation constant for nitrate	$\mu\text{mol NO}_3 \text{l}^{-1}$	18	18	Bendoricchio et al. (1994)
$K_{\text{NH}_4}$	Half-saturation constant for ammonium	$\mu\text{mol NH}_4 \text{l}^{-1}$	20	14–43	Bendoricchio et al. (1994)
$P_{\max}$	Maximum internal quota for phosphorus	$\mu\text{mol P (g DW)}^{-1}$	126	Maximum 126	Bendoricchio et al. (1994)
$P_{\min}$	Minimum internal quota (subsistence quota) for phosphorus	$\mu\text{mol P (g DW)}^{-1}$	16	16–35	Bendoricchio 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	Bendoricchio et al. (1994)
$K_{\text{PO}_4}$	Half-saturation constant for phosphorus	$\mu\text{mol PO}_4 \text{l}^{-1}$	1	0.81–3.64	Bendoricchio et al. (1994)
$\text{dec}_{\max}$	Maximum decomposition rate	$\text{d}^{-1}$	0.025		Paalme et al. (2002)
$\text{Reprod}_{\text{rate}}$	Reproduction rate-amount of biomass lost by sporulation	$\text{d}^{-1}$	0.01		Niesenbaum (1988)
$\text{Germ}_{\max}$	Maximum germination	$\text{d}^{-1}$	0.8	0.4–1.0	Hoffmann and Camus (1989)
$\text{SporGraz}_{\text{rate}}$	Maximum macroinvertebrate grazing rate on spores	$\text{d}^{-1}$	0.14	0.06–0.14	Lotze and Worm (2000)
$T_{\text{opGrazSp}}$	Optimum temperature for grazers	°C	22	15–30	Pardal et al. (2000)
$T_{\max \text{GrazSp}}$	Upper temperature for grazers	°C	45	Maximum 42	Poole and Raven (1997)
$T_{\min \text{GrazSp}}$	Lower temperature for grazers	°C	10	Minimum –20	Poole and Raven (1997)
$S_{\text{optSp}}$	Optimum salinity for growth of spores	psu	35	18–22	Sousa et al. (in press)
$S_{\max \text{Sp}}$	Upper salinity for growth of spores	psu	45	Maximum 95	Poole and Raven (1997)
$S_{\min}$	Lower salinity for growth of spores	psu	10	0	Poole and Raven (1997) and Martins et al. (1999)
$V_{\max \text{NSp}}$	Maximum nitrogen uptake rate by spores	$\mu\text{mol N (g DW)}^{-1} \text{d}^{-1}$	0.6	1200–1406	Lindenschmidt (2006)
$K_{\text{NSp}}$	Spore half-saturation constant for nitrogen	$\mu\text{mol N l}^{-1}$	1.7857	17.85	Lindenschmidt (2006)
$V_{\max \text{PSP}}$	Maximum phosphorus uptake rate by spores	$\mu\text{mol PO}_4 \text{(g DW)}^{-1} \text{d}^{-1}$	0.14	178–844	Lindenschmidt (2006)
$K_{\text{PSP}}$	Spore half-saturation constant for phosphorus	$\mu\text{mol PO}_4 \text{l}^{-1}$	0.03225	0.81–3.64	Lindenschmidt (2006)

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

and *Ulva lactuca*, respectively (Pedersen and Borum, 298  
 1996), and assuming that nitrogen represents 3.25% of 299  
 macroalgal dry weight (Neto, 2004). Phosphorus require- 300

301 ment rate was achieved by calibration and taking into con-  
302 sideration that P represents a lower % of macroalgal dry  
303 weight compared to N and that, apparently, the depletion  
304 of P occurs faster than N-depletion due to different types  
305 of internal pools (Björnsäter and Wheeler, 1990).

#### 306 2.2.6. Herbivory

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

$$315 Z_A = Z_{\max A} \cdot f(T) \quad (20)$$

#### 316 2.2.7. Sporulation

317 Macroalgae may allocate a significant amount of their  
318 biomass to the formation of zoospores and gametes (Nie-  
319 senbaum, 1988), specially during warmer months, when  
320 the percentage of reproductive biomass may reach 60%.  
321 To account for this adult biomass loss process, the model  
322 considers a maximum reproduction rate of  $0.01 \text{ d}^{-1}$  at  
323  $20^\circ\text{C}$  defined by:

$$325 Sp = Sp_{\max} \cdot \theta^{(T-20)} \quad (21)$$

326 where  $\theta$  is empirical coefficient.

#### 327 2.2.8. Decomposition

328 Decomposition is another important loss process, par-  
329 ticularly when during intensive growing periods, macroal-  
330 gae accumulate in layers where growth rate decreases  
331 exponentially through the canopy (Vergara et al., 1998).  
332 In this situation, the upper layers remain photosyntheti-  
333 cally active, whereas the deeper layers undergo decomposi-  
334 tion due to extreme self-shading (Hernández et al., 1997).  
335 Due to spring and summer high air and water tempera-  
336 tures, this process may be particularly significant in  
337 warm-temperate estuaries such as the Mondego estuary.  
338 Thus, decomposition was described by:

$$340 D = D_{\max} \theta^{(T-20)} \quad (22)$$

341 Decomposition rate ( $D_{\max}$ ) at  $20^\circ\text{C}$  was calibrated to  
342  $0.025 \text{ d}^{-1}$ , which is in accordance to a decomposition rate  
343 of 65% during 28 days for *Cladophora glomerata* obtained  
344 by Paalme et al. (2002).

#### 345 2.2.9. Advection

346 In estuaries and other coastal systems with significant  
347 hydrodynamics, the loss of macroalgae and other macro-  
348 phytes to the ocean is a process with significant impacts  
349 on the mass balance of plant biomass and nutrients within  
350 these systems (Flindt et al., 1997; Salomonsen et al., 1997).  
351 The present model does not explicitly simulate hydrody-  
352 namics. However, based on predicted macroalgal produc-  
353 tion 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 pro-  
ductivity 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  
 $20^\circ\text{C}$  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 temper-  
ature in  $5^\circ\text{C}$ . 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 real values for the Mondego estuary. Photon  
flux density at surface ( $\text{PFD}_0$ ,  $\mu\text{E m}^{-2} \text{ s}^{-1}$ -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  $z$  ( $\text{PFD}_z$ ) was  
calculated according to the Lambert–Beer equation:

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

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

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 con-  
trolled 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:

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

404 In estuaries, the immersion depth of ephemeral macroalgae  
 405 and other attached macrophytes is regulated by tides. Tidal  
 406 height was simulated using the basic harmonic constituents,  
 407 where HBM and HPM are low tide and high tide  
 408 heights, respectively, and vary according to the spring neap  
 409 oscillation. The depth (*Depth*) of any individual is spatial-  
 410 and time-dependent, since it depends both on the bathym-  
 411 etry of the point where the individual is located and on tidal  
 412 height:

$$414 \text{ TidalHeight} = \frac{\text{HBM} + \text{HPM}}{2} \cdot \cos\left(\frac{2 \cdot \pi \cdot \text{TIME}}{\text{TidePeriod}}\right) \quad (25)$$

$$\text{HBM} = \text{If.SpringNeapOscillation} \geq 0 \dots$$

$$\text{THEN} \dots 0.2 + \text{SpringNeapOscillation} \quad (26)$$

$$416 \text{ ELSE} \dots 0.2 - \text{SpringNeapOscillation}$$

$$\text{HPM} = \text{If} \dots \text{SpringNeapOscillation} \geq 0 \dots$$

$$\text{Then} \dots 3.7 - \text{SpringNeapOscillation} \quad (27)$$

418 Else 3.7 + SpringNeapOscillation  
 419 where 0.2 and 3.7 m correspond to the maximum tidal  
 420 range in the south channel of the Mondego estuary:

$$422 \text{ Depth} = \text{TidalHeight} - \text{Bathymetry} \quad (28)$$

### 423 2.3. From modelling to GIS

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

434 Model results were obtained at the scale of 1 m<sup>2</sup> and  
 435 subsequently upscaled to the system using a bathymetric  
 436 map and GIS (ArcGis 9.1, ESRI, USA). Global calcula-  
 437 tions were obtained for the whole area of the south channel  
 438 of the Mondego estuary (136.5 ha). Furthermore, since  
 439 *Enteromorpha* show a patchy distribution within the sys-  
 440 tem, the variation of the area covered with adult algae  
 441 throughout time estimated in situ (Lopes et al., 2006) was  
 442 considered and used to perform global calculations.

443 Estimations of *Enteromorpha* internal N and P are based  
 444 on values obtained, in situ, from January 1999 to January  
 445 2001 and correspond to 3.25% and 0.11% of dry weight,  
 446 respectively (Neto, 2004). The considered macroalgae inter-  
 447 nal C content was 29% of dry weight (Duarte, 1992).

### 448 2.4. Calibration, sensitivity and statistical analysis

449 Parameter calibration was achieved by optimisation  
 450 algorithms. Sensitivity analysis was performed in accor-  
 451 dance to Jørgensen (1994). To assess for model reliability,  
 452 model predictions for adult biomass at depth +1.8 m were

453 compared with real data of *Enteromorpha* biomass quanti-  
 454 fied in the south channel of the Mondego estuary between  
 455 January 1993 and January 1997, in a field station located at  
 456 +1.8 m. Model II-regression was used to compare predic-  
 457 tions with observations. This regression model is recom-  
 458 mended whenever both variables are subject to error  
 459 (Sokal and Rohlf, 1995). The significance of the regression  
 460 was tested by analysis of variance (ANOVA), since it is the  
 461 only means of testing it in model II-regression (Fowler  
 462 et al., 1998). ANOVA was also used to assess for differ-  
 463 ences between macroalgal biomass in different years.

### 3. Results

464 Predicted adult algal biomass variation followed the  
 465 same pattern as observed biomass variation (Fig. 3). Nev-  
 466 ertheless, there are some deviations between the two sets of  
 467 values, particularly, during spring 1993, when the model  
 468 tends to overestimate macroalgal biomass and from June  
 469 onwards, when the predicted values are lower than obser-  
 470 vations. Such discrepancies are not unusual considering  
 471 that observed values correspond to a medium-term time  
 472 series of field data, which is affected by numerous stochas-  
 473 tic effects. Nevertheless, the regression between observed  
 474 and predicted values is highly significant (ANOVA,  
 475  $F_{1,41} = 85$ ,  $P < 0.001$ ,  $r^2 = 0.68$ ) (Fig. 3).

476 The predicted variation of *Enteromorpha* spore biomass  
 477 is very similar during the four studied years and, although  
 478 spore biomass presents seasonal fluctuations, they are pres-  
 479 ent all year round within the water column (minimum =  
 480 0.093 g DW m<sup>-2</sup>) (Fig. 4), which is in agreement with field  
 481 measurements.  
 482

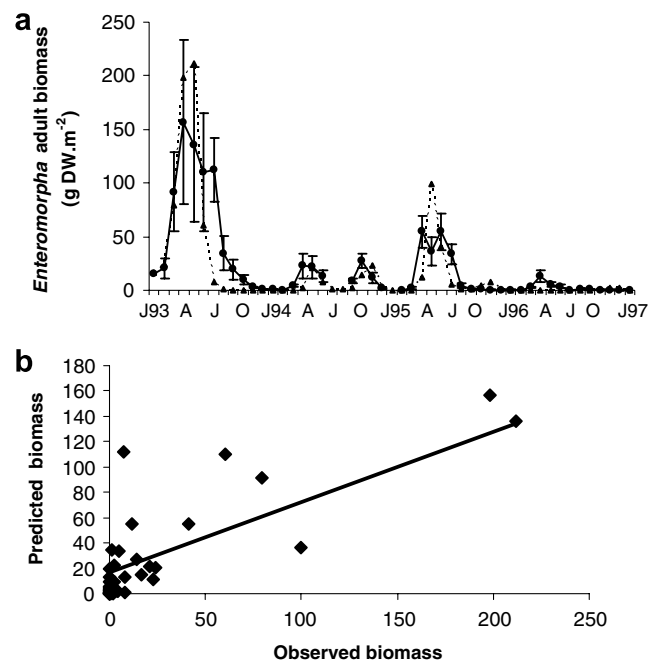


Fig. 3. Predicted (---) and observed (—) biomass variation  $\pm$  standard error of adult *Enteromorpha* (g DW m<sup>-2</sup>) at +1.8 m (a). Model II-regression between observed and predicted values (b).

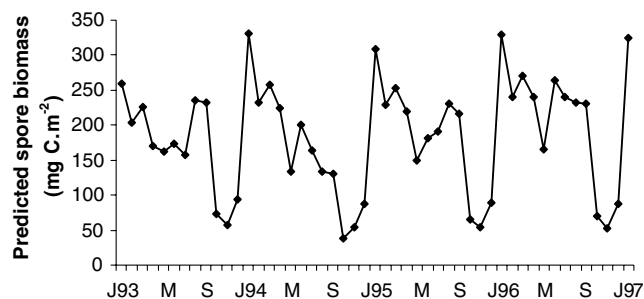


Fig. 4. Predicted spore biomass ( $\text{mg C m}^{-2}$ ) variation at +1.8 m.

483 Adult algal biomass was significantly different  
 484 (ANOVA,  $P < 0.05$ ) between the four studied years. Max-  
 485 imum predicted adult biomass at +1.8 m for 1993, 1994,  
 486 1995 and 1996 was 256.23, 14.06, 50.95 and  
 487 8.41  $\text{g DW m}^{-2}$ , respectively (Fig. 5). This clearly indicates  
 488 that 1993 was the most favourable year to macroalgal  
 489 growth, whilst 1996 was the least favourable. In 1995,  
 490 *Enteromorpha* presented the second highest biomass value  
 491 but the maximum depth distribution was lower than in  
 492 1994, which suggests the occurrence of increased light lim-  
 493 itation conditions for macroalgal growth between 1993 and  
 494 1996.

495 The results also indicate that algal growth is very sensi-  
 496 tive to depth variations and that, according to prevailing  
 497 conditions, it varies differently in different seasons and in  
 498 different years. In 1993, from autumn until spring, the bio-  
 499 mass of *Enteromorpha* increased exponentially from the  
 500 highest (−0.9 m) to the lowest depth (+2.3 m), while in  
 501 1996 the increase was only linear. In general during spring  
 502 (April–May) and early autumn (October), macroalgal bio-  
 503 mass increased exponentially towards the lowest depth,  
 504 whilst in summer, this pattern of variation changed and  
 505 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 sug-  
 gested 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 Mond-  
 ego 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 signifi-  
 cant. 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 nutri-  
 ents 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  $\text{kg N yr}^{-1}$   
 (Alvera-Azcárate et al., 2003), the amount of N retained  
 in the system during high OEC years (1993) corresponds  
 to 156,631 inhabitants, while in low OEC years (1996)  
 the value decreases to 1763 inhabitants (Table 2).

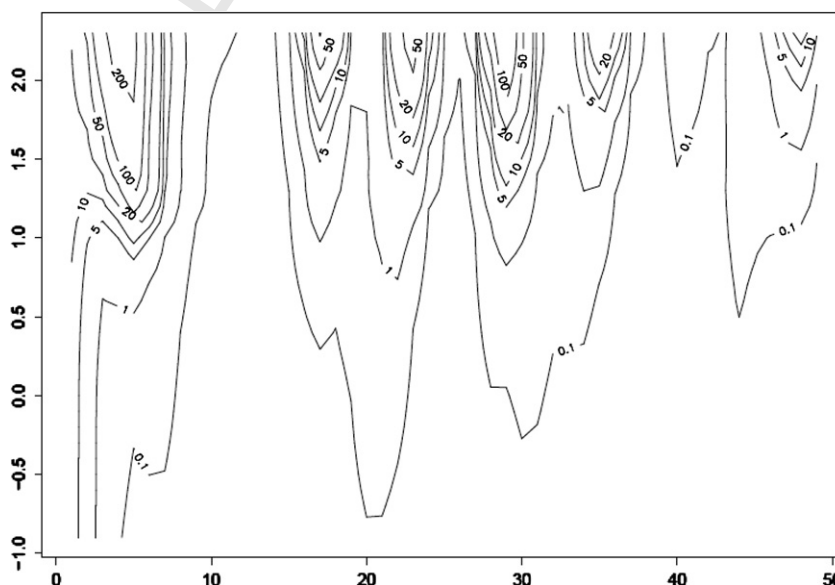


Fig. 5. Variation of *Enteromorpha* adult biomass ( $\text{g DW m}^{-2}$ ) with depth during the study period.



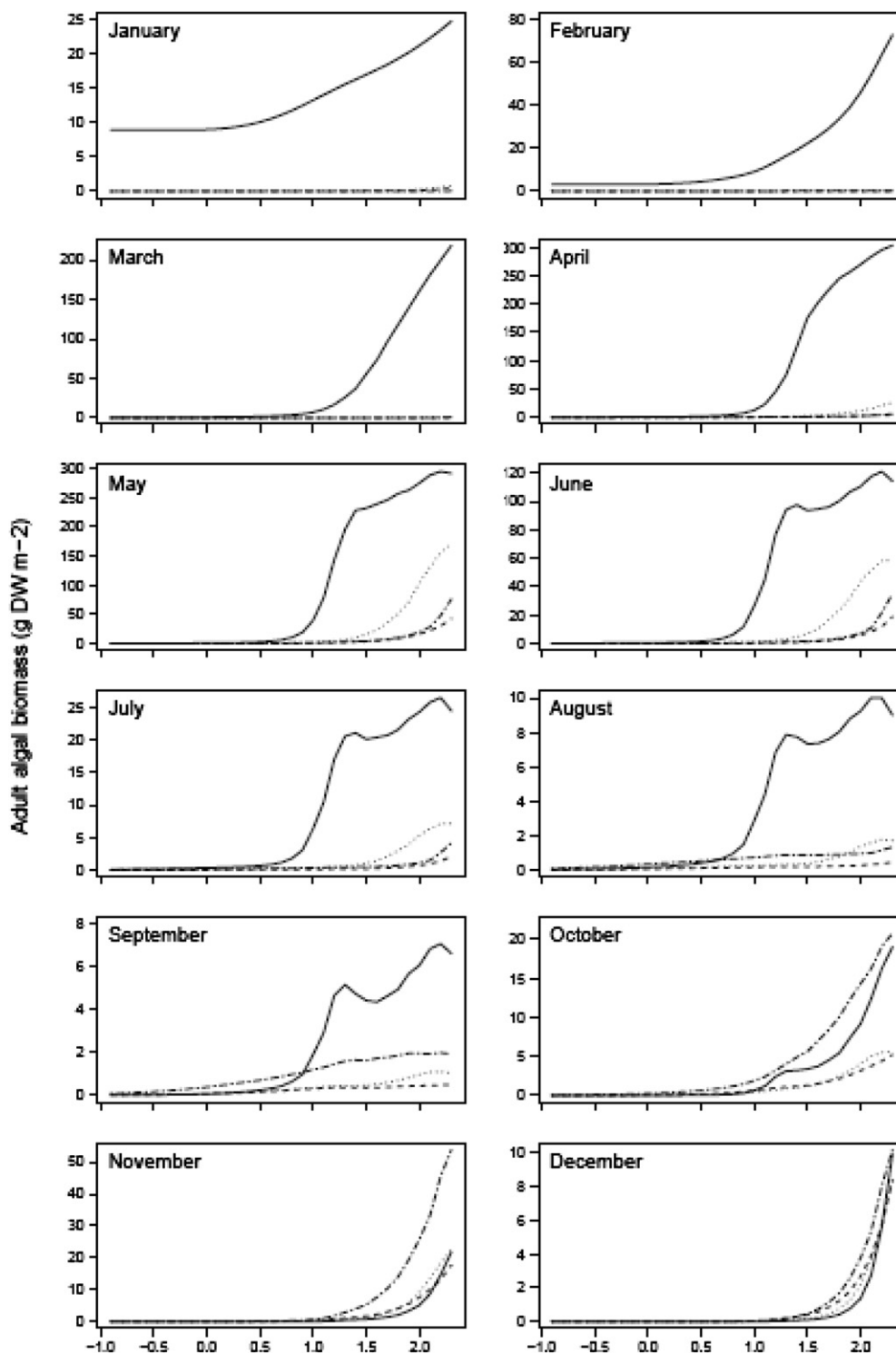


Fig. 6. Predicted monthly variation of *Enteromorpha* adult biomass ( $\text{g DW m}^{-2}$ ) with depth during the four different years: — 1993, ..... 1995, -.-.- 1994, --- 1996.

#### 542 4. Discussion

543 The present model describes quite accurately the annual  
 544 variation of opportunistic macroalgal biomass in a temperate  
 545 mesotidal estuary for a significant period of time (January  
 546 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 macroalgae biomass in nature. Additionally the present work is, to our knowledge, the first model that describes macroalgal spore

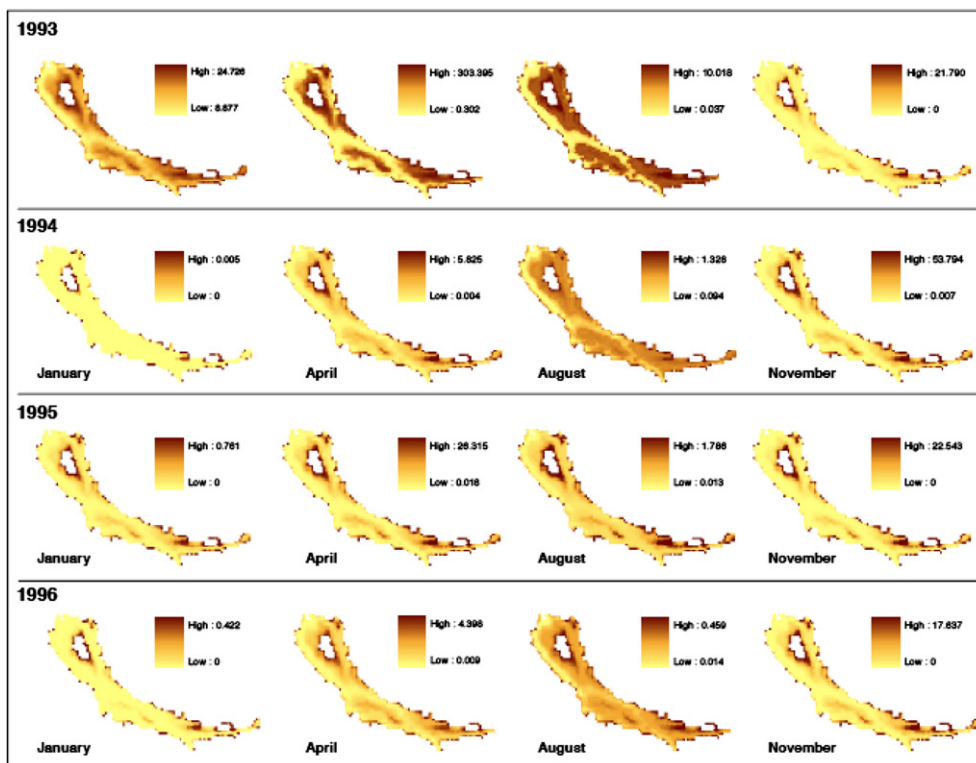


Fig. 7. Bathymetric distribution of *Enteromorpha* biomass ( $\text{g DW m}^{-2}$ ) at the south channel of the Mondego estuary during winter (average of January, February and March), spring (average of April, May and June) summer (average of July, August and September) and autumn (average of October, 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  $4.4 \text{ kg N yr}^{-1}$  (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.

553 dynamics and its relationships with adult macroalgae, which is undoubtedly a more complete approach to  
 554 describe algal dynamics, since frequently factors affecting  
 555 early life stages determine the development and the domi-  
 556 nance patterns of macroalgal blooms (Lotze and Worm,  
 557 2000). According with simulations, although the contribu-  
 558 tion of spore biomass is relatively low compared to adult  
 559 biomass, spore dynamics has a significant impact on adult  
 560

561 biomass, particularly during low OEC years. Specific and  
 562 detailed analysis of the effects of spore dynamics on adult  
 563 growth and biomass are reported elsewhere (Martins  
 564 et al., unpublished).

565 The present results indicate that there are significant  
 566 spatial variations within the same system regarding macro-  
 567 algal growth. In the present model, spatial variability is due  
 568 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. On contrary, 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, at intertidal areas, bathymetry is only one of the factors contributing to the patchy distribution of macroalgae and, consequently, to the patchiness display 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 amount 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 previously been 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., 2002), 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  $\text{TO}_x\text{N}$ , 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-bounded to macroalgae are exported to the adjacent coastal areas compared to low OEC years. However, remineralization 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 bounded to macroalgal tissue will be exported to the adjacent coastal areas. There will be a time-lag before these nutrients can be uptake 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.

## 5. Uncited reference

Martins et al. (2005).

## 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* Kützinger. *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.

- 682 Bricker, S.B., Ferreira, J.G., Simas, T., 2003. An integrated methodology  
683 for assessment of estuarine trophic status. *Ecological Modelling* 169,  
684 39–60.
- 685 Brock, T.D., 1981. Calculating solar radiation for ecological studies.  
686 *Ecological Modelling* 14, 1–19.
- 687 Cao, W., Hong, H., Yue, S., 2005. Modelling agricultural nitrogen  
688 contributions to the Jiulong River estuary and coastal water. *Global*  
689 *and Planetary Change* 47, 111–121.
- 690 Cardoso, P.G., Pardal, M.A., Lillebø, A.I., Ferreira, S.M., Raffaelli, D.,  
691 Marques, J.C., 2004. Dynamic changes in seagrasses assemblages  
692 under eutrophication and implications for recovery. *Journal of*  
693 *Experimental Marine Biology and Ecology* 302, 233–248.
- 694 Dolbeth, M., Pardal, M.A., Lillebø, A.I., Azeiteiro, U., Marques, J.C.,  
695 2003. Short- and long-term effects of eutrophication on the secondary  
696 production of an intertidal macrobenthic community. *Marine Biology*  
697 143 (6), 1229–1238.
- 698 Duarte, C.M., 1992. Nutrient concentration of aquatic plants: patterns  
699 across species. *Limnological Oceanography* 37 (4), 882–889.
- 700 Duarte, C.M., Cebrián, J., 1996. The fate of marine autotrophic  
701 production. *Limnological Oceanography* 41 (8), 1758–1766.
- 702 EPA – Environmental Protection Agency, USA, 1985. Rates, constants,  
703 and kinetics. Formulations in surface water quality modelling, 2nd ed.,  
704 455pp.
- 705 Ferreira, J.G., Ramos, L., 1989. A model for the estimation of annual  
706 production rates of macrophyte algae. *Aquatic Botany* 33, 53–70.
- 707 Ferreira, J.G., Simas, T., Schifferegger, K., Lencart-Silva, J., 2002. In:  
708 Identification of Sensitive Areas and Vulnerable Zones in Four  
709 Portuguese Estuaries, vol. I. INAG-Instituto da Água, IMAR-Insti-  
710 tute of Marine Research.
- 711 Ferreira, J.G., Bricker, S.B., Simas, T.C., in press. Application and  
712 sensitivity testing of a eutrophication assessment method on coastal  
713 systems in the United States and European Union. *Journal of*  
714 *Environmental Management*.
- 715 Fitzgerald, W.J., 1978. Environmental parameters influencing the growth  
716 of *Enteromorpha clathrata* (Roth) J. Ag. in the intertidal zone on  
717 Guam. *Botanica Marina* 21, 207–220.
- 718 Flindt, M.R., Salomonsen, J., Carrer, M., Bocci, M., Kamp-Nielsen, L.,  
719 1997. Loss, growth and transport dynamics of *Chaetomorpha aerea*  
720 and *Ulva rigida* in the Lagoon of Venice during an early summer field  
721 campaign. *Ecological Modelling* 102, 133–141.
- 722 Fowler, J., Cohen, L., Jarvis, P., 1998. *Practical Statistics for Field*  
723 *Biology*, second ed. Wiley, New York, 259pp.
- 724 Giannotti, A.L., McGlathery, K., 2001. Consumption of *Ulva lactuca*  
725 (Chlorophyta) by the omnivorous mud snail *Ilyanassa obsoleta* (Say).  
726 *Journal of Phycology* 37, 209–215.
- 727 Hernández, I., Peralta, G., Pérez-Lloréns, J.L., Vergara, J.J., Niell, F.X.,  
728 1997. Biomass and dynamics of growth of *Ulva* species in Palmones  
729 river estuary. *Journal of Phycology* 33, 764–772.
- 730 Hoffmann, A.J., Camus, P., 1989. Sinking rates and viability of spores  
731 from benthic algae in central Chile. *Journal of Experimental Marine*  
732 *Biology and Ecology* 126, 281–291.
- 733 Jørgensen, S.E., 1994. *Fundamentals of Ecological Modelling*, second ed.  
734 Elsevier, Amsterdam, 628pp.
- 735 Jørgensen, S.E., Nielsen, S.N., Jørgensen, L.A., 1991. *Handbook of*  
736 *Ecological Parameters and Ecotoxicology*. Elsevier, Amsterdam.
- 737 Korpinen, P., Kiirikki, M., Koponen, J., Peltoniemi, H., Sarkkula, J.,  
738 2004. Evaluation and control of eutrophication in Helsinki sea area  
739 with the help of a nested 3D-ecohydrodynamic model. *Journal of*  
740 *Marine Systems* 45, 255–265.
- 741 Kraufvelin, P., Salovius, S., Christie, H., Moy, F.E., Karez, R., Pedersen,  
742 M.F., 2006. Eutrophication-induced changes in benthic algae affect the  
743 behaviour and fitness of the marine amphipod *Gammarus locusta*.  
744 *Aquatic Botany* 84 (3), 199–209.
- 745 Lillebø, A.I., Flindt, M.R., Pardal, M.A., Martins, I., Neto, J.M.,  
746 Marques, J.C., 2002. Nutrient dynamics in the intertidal pools of the  
747 Mondego estuary. II. Seasonal efflux of PO<sub>4</sub>-P and NH<sub>4</sub>-N in bare  
748 bottom and vegetated pools. In: Pardal, M.A., Marques, J.C., Graça,  
M.A. (Eds.), *Aquatic Ecology of the Mondego River Basin. Global*  
749 *Importance of Local Experience*. Imprensa da Universidade, Coimbra,  
750 751
- Lillebø, A.I., Neto, J.M., Martins, I., Verdelhos, T., Leston, S., Cardoso,  
752 P.G., Ferreira, S.M., Marques, J.C., Pardal, M.A., 2005. Management  
753 of a shallow temperate estuary to control eutrophication: the effect of  
754 hydrodynamics on the system's loading. *Estuarine Coastal and Shelf*  
755 *Science* 65, 697–707.
- Lindenschmidt, K.-E., 2006. The effect of complexity on parameter  
756 sensitivity and model uncertainty in river water quality modelling.  
757 *Ecological Modelling* 190, 72–86.
- Lopes, R.J., Pardal, M.A., Marques, J.C., 2000. Impact of macroalgae  
759 blooms and wader predation on intertidal macroinvertebrates –  
760 experimental evidence in the Mondego estuary (Portugal). *Journal of*  
761 *Experimental Marine Biology and Ecology* 249, 165–179.
- Lopes, R.J., Pardal, M.A., Múrias, T., Cabral, J.A., Marques, J.C., 2006.  
763 Influence of macroalgal mats on abundance and distribution of dunlin  
764 *Calidris alpina* in estuaries: a long-term approach. *Marine Ecology*  
765 *Progress Series* 323, 11–20.
- 766
- 767 Lotze, H.K., Worm, B., 2000. Variable and complementary effects of  
768 herbivores on different life stages of bloom-forming macroalgae.  
769 *Marine Ecology Progress Series* 200, 167–175.
- 770 Marques, J.C., Maranhão, P., Pardal, M.A., 1993. Human impact  
771 assessment on the subtidal macrobenthic community structure in the  
772 Mondego Estuary (Western Portugal). *Estuarine Coastal and Shelf*  
773 *Science* 37, 403–419.
- 774 Martins, I., Marques, J.C., 2002. A model for the growth of opportunistic  
775 macroalgae (*Enteromorpha* sp.) in tidal estuaries. *Estuarine Coastal*  
776 *and Shelf Science* 55 (2), 247–257.
- 777 Martins, I., Oliveira, J.M., Flindt, M.R., Marques, J.C., 1999. The effect  
778 of salinity on the growth rate of the macroalgae *Enteromorpha*  
779 *intestinalis* (Chlorophyta) in the Mondego estuary (west Portugal).  
780 *Acta Oecologica* 20, 259–265.
- 781 Martins, I., Pardal, M.A., Lillebø, A.I., Flindt, M.R., Marques, J.C.,  
782 2001. Hydrodynamics as a major factor controlling the occurrence of  
783 green macroalgal blooms in a eutrophic estuary: a case study on the  
784 influence of precipitation and river management. *Estuarine Coastal*  
785 *and Shelf Science* 52, 165–177.
- 786 Martins, I., Flindt, M.R., Pardal, M.A., Lillebø, A.I., Oliveira, J.M.,  
787 Marques, J.C., 2002. Nutrient dynamics in the intertidal pools of the  
788 Mondego estuary. III. The importance of nutrient effluxes to macro-  
789 algal growth (*Enteromorpha* sp.). In: Pardal, M.A., Marques, J.C.,  
790 Graça, M.A. (Eds.), *Aquatic Ecology of the Mondego River Basin.*  
791 *Global Importance of Local Experience*. Imprensa da Universidade,  
792 Coimbra.
- 793 Martins, I., Neto, J.M., Fontes, M.G., Marques, J.C., Pardal, M.A., 2005.  
794 Seasonal variation in short-term survival of *Zostera noltii* transplants  
795 in a declining meadow in Portugal. *Aquatic Botany* 82 (2), 132–142.
- 796 Matta, J.L., Chapman, D.J., 1995. Effects of light, temperature and  
797 desiccation on the net emersed productivity of the intertidal macroalga  
798 *Colpomenia peregrina* Sauv. (Hamel). *Journal of Experimental Marine*  
799 *Biology and Ecology* 189, 13–27.
- 800 Nedwell, D.B., Dong, L.F., Sage, A., Underwood, G.J.C., 2002. Varia-  
801 tions of the nutrient loads to the mainland UK estuaries: correlation  
802 with catchment areas, urbanization and coastal eutrophication.  
803 *Estuarine Coastal and Shelf Science* 54, 951–970.
- 804 Neto, J.M.M., 2004. Nutrient enrichment in a temperate macro-tidal  
805 system. Scenario analysis and contribution to coastal management,  
806 Ph.D. Thesis, University of Coimbra, Portugal.
- 807 Niesenbaum, R.A., 1988. The ecology of sporulation by the macroalga  
808 *Ulva lactuca* L. (Chlorophyceae). *Aquatic Botany* 32, 155–166.
- 809 Nobre, A.M., Ferreira, J.G., Newton, A., Simas, T., Icely, J.D., Neves, R.,  
810 2005. Management of coastal eutrophication: Integration of field data,  
811 ecosystem-scale simulations and screening models. *Journal of Marine*  
812 *Systems* 56, 375–390.
- 813 Paalme, T., Kukk, H., Kotta, J., Orav, H., 2002. “In vitro” and “in situ”  
814 decomposition of nuisance macroalgae *Cladophora glomerata* and  
815 *Pilayella littoralis*. *Hydrobiologia* (475/476), 469–476.



- 816 Pardal, M.A., Marques, J.C., Metelo, I., Lillebø, A.I., Flindt, M.R., 2000. 848  
817 Impact of eutrophication on the life cycle, population dynamics and 849  
818 production of *Amphitoe valida* (Amphipoda) along an estuarine spatial 850  
819 gradient (Mondego estuary, Portugal). *Marine Ecology Progress Series* 851  
820 196, 207–219. 852  
821 Pardal, M.A., Cardoso, P.G., Sousa, J.P., Raffaelli, D., 2004. Assessing 853  
822 environmental quality: a novel approach. *Marine Ecology Progress* 854  
823 *Series* 267, 1–8. 855  
824 Patrício, J., Ulanowicz, R., Pardal, M.A., Marques, J.C., 2006. Ascen- 856  
825 dency as an ecological indicator for environmental quality assessment 857  
826 at the ecosystem level: a case study. *Hydrobiologia* 555, 19–30. 858  
827 Pedersen, M.F., Borum, J., 1996. Nutrient control of algal growth in 859  
828 estuarine waters. Nutrient limitation and the importance of nitrogen 860  
829 requirements and nitrogen storage among phytoplankton and species 861  
830 of macroalgae. *Marine Ecology Progress Series* 142, 261–272. 862  
831 Raffaelli, D.G., Raven, J.A., Poole, L.J., 1998. Ecological impact of green 863  
832 macroalgal blooms. *Oceanography and Marine Biology: An Annual* 864  
833 *Review* 36, 97–125. 865  
834 Raffaelli, D., Bell, E., Weithoff, G., Matsumoto, A., Cruz-Motta, J.J., 866  
835 Kershaw, P., Parker, R., Parry, D., Jones, M., 2003. (Review) The ups 867  
836 and downs of benthic ecology: considerations of scale, heterogeneity 868  
837 and surveillance for benthic-pelagic coupling. *Journal of Experimental* 869  
838 *Marine Biology and Ecology* 285–286, 191–203. 870  
839 Rivers, J., Peckol, P., 1995. Summer decline of *Ulva lactuca* (Chlorophyta) 871  
840 in a eutrophic embayment: interactive effects of temperature and 872  
841 nitrogen availability?. *Journal of Phycology* 31 223–228. 873  
842 Salomonsen, J., Flindt, M.R., Geertz-Hansen, O., 1997. Significance of 874  
843 advective transport of *Ulva lactuca* for a biomass budget on a shallow 875  
844 water location. *Ecological Modelling* 102, 129–132.  
845 Sanders, R., Klein, C., Jickells, T., 1997. Biogeochemical nutrient cycling  
846 in the Upper Great Ouse Estuary, Norfolk, UK. *Estuarine Coastal and*  
847 *Shelf Science* 44, 543–555.
- Santelices, B., 1990. Patterns of reproduction, dispersal and recruitment in 848  
seaweeds. *Oceanography and Marine Biology: An Annual Review* 28, 849  
177–276. 850
- Schories, D., Anibal, J., Chapman, A.S., Herre, E., Isaksson, I., Lillebø, 851  
A.I., Pihl, L., Reise, K., Sprung, M., Thiel, M., 2000. Flagging greens: 852  
hydrobiid snails as substrata for the development of green algal mats 853  
(*Enteromorpha* spp.) on tidal flats of North Atlantic coasts. *Marine* 854  
*Ecology Progress Series* 199, 127–136. 855
- Shellem, B.H., Josselyn, M.N., 1982. Physiological ecology of *Enteromor-* 856  
*pha clathrata* (Roth) Grev. on a salt marsh mudflat. *Botanica Marina* 857  
25, 541–549. 858
- Simas, T., Nunes, J.P., Ferreira, J.G., 2001. Effects of global climate 859  
change on coastal salt marshes. *Ecological Modelling* 139, 1–15. 860
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, third ed. Freeman, New York. 861
- Solidoro, C., Brando, V.E., Dejak, C., Franco, D., Pastres, R., Pecelik, 862  
G., 1997. Long-term simulations of population dynamics of *Ulva* 863  
*rigida* in the lagoon of Venice. *Ecological Modelling* 102, 259–272. 864
- Sousa, A.I., Martins, I., Lillebø, A.I., Flindt, M.R., Pardal, M.A., in 865  
press. Influence of salinity, nutrients and light on the germination and 866  
growth of *Enteromorpha* sp. spores. *Journal of Experimental Marine* 867  
*Biology and Ecology*. 868
- Verdelhos, T., Neto, J.M., Marques, J.C., Pardal, M.A., 2005. The effect 869  
of eutrophication abatement on the bivalve *Scrobicularia plana*. 870  
*Estuarine Coastal and Shelf Science* 63, 261–268. 871
- Vergara, J.J., Sebastián, M., Pérez-Lloréns, J.L., Hernández, I., 1998. 872  
Photoacclimation of *Ulva rigida* and *U. rotundata* (Chlorophyta) 873  
arranged in canopies. *Marine Ecology Progress Series* 165, 283–292. 874  
875