

Impacts of macroalgal spores on the dynamics of adult macroalgae in a eutrophic estuary: High *versus* low hydrodynamic seasons and long-term simulations for global warming scenarios

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Abstract

A model describing macroalgal early life stages and adult dynamics was used to quantify the effects of non-adult forms on the productivity of adult macroalgae in a eutrophic estuary. Predictions indicate that during years with mild winters and low rainfall, spring blooms will occur at the expense of the growth and reproduction of overwintering adults and without the contribution of the spore bank. In these circumstances, there is a positive correlation between the intensity of the blooms and the biomass of overwintering adults until a maximum threshold value. On the contrary, in years with high rainfall and low or inexistent biomass of overwintering adults, the onset of adult's growth depends on the biomass of viable dormant spores, the growing season occurs later and adult productivity is very limited. Long-term predictions for climate change scenarios suggest that, in general, global warming will have adverse affects on *Ulva intestinalis* productivity, with the adults being more affected than the early life stages.

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1. Introduction

Green macroalgae belonging to Chlorophyta (e.g. *Ulva*, *Chaetomorpha*) have been identified as one of the most abundant group of the so-called “bloom” forming algae in coastal areas worldwide (e.g. Valiela et al., 1997; Raffaelli et al., 1998; Schramm, 1999; Cardoso et al., 2004). Due to their higher surface to volume (SA:V) ratios compared to rooted macrophytes, opportunistic green macroalgae have higher maximum uptake rates and lower half-saturation constants for nutrients, associated with a higher affinity for nitrogen (Hein et al., 1995). As a consequence, under nutrient surplus, opportunistic macroalgae tend to grow faster than primary producers with a more conservative

growing strategy (Pedersen and Borum, 1996). This type of mechanism often causes light limitation conditions for slower growing primary producers and, if such conditions persist, their standing stocks can be significantly decreased (e.g. Grall and Chauvoud, 2002; Raven and Taylor, 2003), which often has adverse impacts in the species richness and structure stability of the system (e.g. Norkko et al., 2000; Cardoso et al., 2004). In the last decades, a significant amount of work has examined adult green macroalgae populations, mostly due to their negative impacts in coastal areas worldwide (e.g. Boyer and Fong, 2005; Villares and Carballeira, 2003; Astill and Lavery, 2001). On the contrary, relatively fewer works have studied the processes affecting macroalgal early life stages (e.g. Worm and Lotze, 2006; Sousa et al., 2007). Macroalgal initial life stages are represented by several microscopic forms according to the adult's reproduction strategy. For example, *Ulva intestinalis* has different forms of reproduction: vegetative, asexual and sexual. Vegetative reproduction consists in

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separation from a parent plant of a vegetative component that latter develops into a new individual. Asexual reproduction occurs with an isomorphic alternation of haploid (gametophytes) and diploid (sporophyte) phases, which release biflagellate and motile gametes and quadriflagellate zoospores respectively; vegetative cells from zoospores and gametes can develop parthenogenetically. Sexual reproduction is anisogamic and involves fusion of male/female gametes, producing a zygote (2n) which grows into a sporophyte thallus. The zoospores from this thallus settle and germinate into male/female gametophytes (Fletcher, 1989; Poole and Raven, 1997).

The initial life forms of macroalgae can undergo a dormant stage represented by microscopic spores. Chapman (1986) defined the term “banks of microscopic forms” describing them as a combination of settled propagules, micro-recruits and microscopic life stages. These forms constitute an important overwintering mechanism in temperate ecosystems since they can promote algal recruitment in the following growth season (Schories, 1995; Lotze et al., 1999). Moreover, experimental evidence suggests that recruitment processes and factors affecting early life stages can determine the development and the dominance patterns of macroalgal blooms (Lotze and Worm, 2000). Although previous studies have suggested that spore survival may affect the growth of adult macroalgae (Schories, 1995; Lotze et al., 1999; Lotze and Worm, 2000; Worm et al., 2001), to our knowledge there are no works that have used a quantitative approach to this matter. Nevertheless, numerical models able to capture macroalgal microscopic-, juvenile- and adult-dynamics are suitable tools to address these subjects.

2. Objectives

The main objective of the present work was to use a macroalgal productivity model, describing both non-adult and adult dynamics, to quantify the contribution of algal early life stages (microscopic forms and juveniles <10 cm length) on adult productivity in years with distinct climate features. Based on a relatively long-term data series, the model was developed for *U. intestinalis* population at the Mondego estuary (western coast of Portugal). Furthermore, the model was also used to make long-term predictions of macroalgal productivity under scenarios of climate change caused by global warming. Observations suggest that global warming may have already triggered abrupt climate changes resulting in an altered probability of drought, large floods, tropical storm landfall and monsoon rainfall (Overpeck and Cole, 2006). In accordance with this, the model was used to make predictions for climate change scenarios as expected for temperate regions, namely, intensive rainfall, prolonged drought associated with temperature increase and sea-level rise.

3. Material and methods

3.1. Model conceptualization

A model able to predict the total productivity of *U. intestinalis* on the south arm of the Mondego estuary (western coast of Portugal) (Fig. 1) was previously used to assess the impacts of total macroalgal biomass, carbon (C)-, nitrogen (N)- and phosphorus (P)-loadings into the estuary and the adjacent coastal area (Martins et al.,

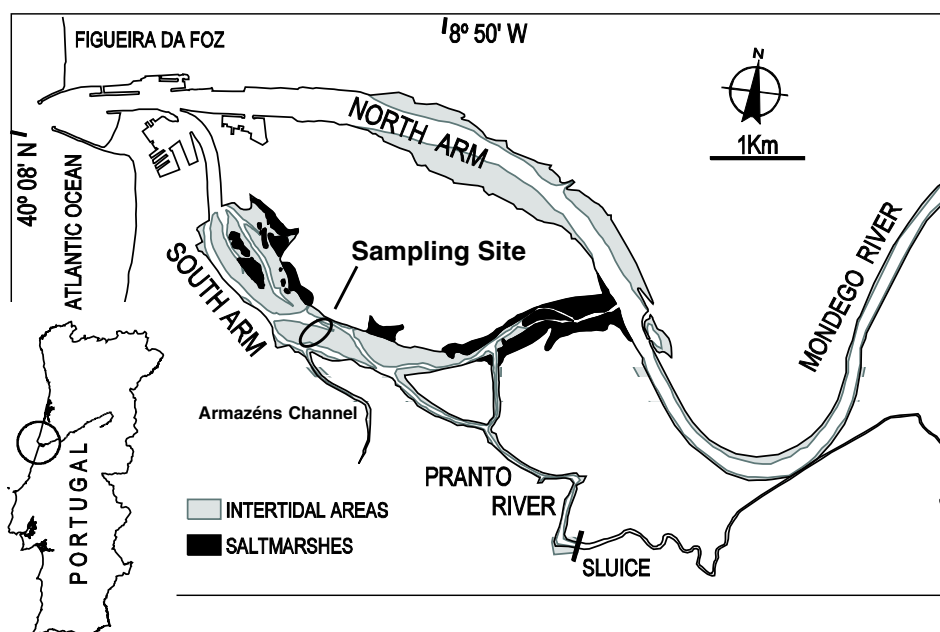


Fig. 1. The Mondego estuary with location of the sampling site used to collect data for the model's basic run.

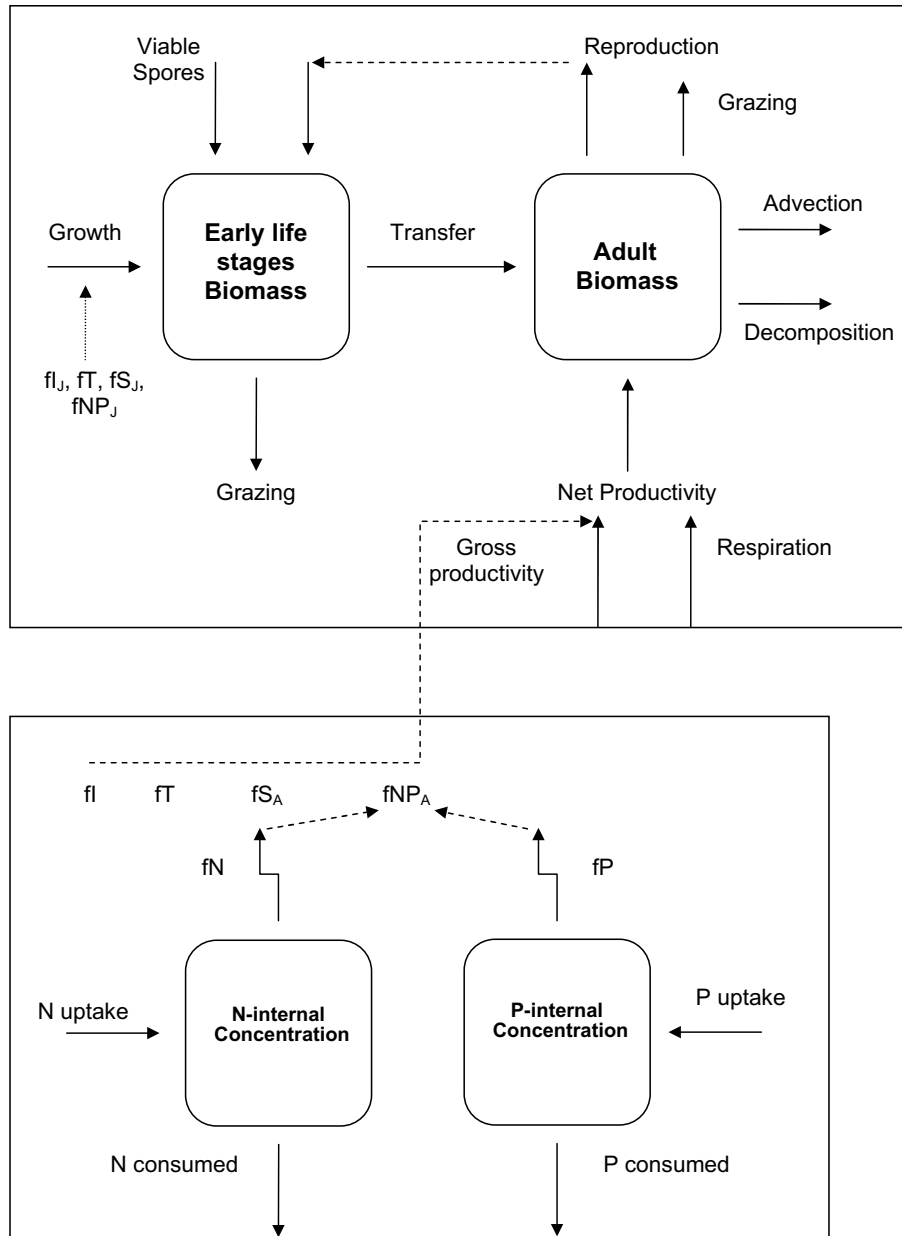


Fig. 2. Simplified conceptual diagram of the sub-model of macroalgal early life stages in connection with the sub-model of adult macroalgae developed by Martins et al. (2007).

2007). For a more detailed description of the Mondego estuary, see Martins et al. (2001), Lillebø et al. (2005), Neto et al. (2008). In the present work, the same model with a more detailed description of macroalgal early life stage dynamics is used to assess and quantify the effects of algal spores and juveniles on adult dynamics (Fig. 2).

We assumed that macroalgal early life stages include attached microscopic forms and macroscopic forms with <10 cm length (juveniles). All *U. intestinalis* individuals with length ≥10 cm were considered as adults. The equations used to describe early life stage dynamics are

described in detail in the next section. For details on the sub-models of *U. intestinalis* adults, light and tidal variations see Table 1 and Martins et al. (2007).

3.2. Biomass variation of macroalgal early life stages

The biomass variation of macroalgal early life stages was described by

$$\frac{dJ}{dt} = R_A + D + G_J - Z_J - T_A \tag{1}$$

Table 1
Main equations governing *U. intestinalis* adult-, light- and tidal-variation in the model

Equation	Definition	Observations
$\frac{dA}{dt} = P + T_A - Adv - Dec - Z_A - U$	Adult biomass variation	A – adults, P – net productivity, T_A – transfer from juveniles, Adv – advection, Dec – decomposition, Z_A – grazing on adults, U – sporulation
$P = GP - R$	Net productivity of adults	GP – gross productivity, R – respiration
$GP = Max_{GP} \cdot fI \cdot fT \cdot fS_A \cdot fNP_A$	Gross productivity of adults	Max_{GP} – maximum productivity rate, fI , fT , fS_A , fNP_A – limiting factors of light, temperature, salinity and nutrients
$\frac{dN_{int}}{dt} = N_{upt} - N_{cons}$	Nitrogen internal variation of adults	N_{upt} – nitrogen uptake, N_{cons} – nitrogen consumption
$\frac{dP_{int}}{dt} = P_{upt} - P_{cons}$	Phosphorus internal variation of adults	P_{upt} – phosphorus uptake, P_{cons} – phosphorus consumption
$PFD_z = PFD_0 \times e^{-kz}$	Photon flux density at depth	PFD at surface (PFD_0) was given by the Brock model (1981); k – light extinction coefficient, z – depth
$TidalHeight = \frac{HBM+HPM}{2} \cdot \cos\left(\frac{2\pi \cdot TIME}{TidePeriod}\right)$	Tidal height variation	HBM – low tide height; HPM – high tide height

For details, see Martins et al. (2007).

where J is the biomass of macroalgal early life stages, R_A the adult's reproduction, D the viable dormant spores, G_J

the growth, Z_J the grazing by macroinvertebrates, T_A the transfer to adults and t is the time.

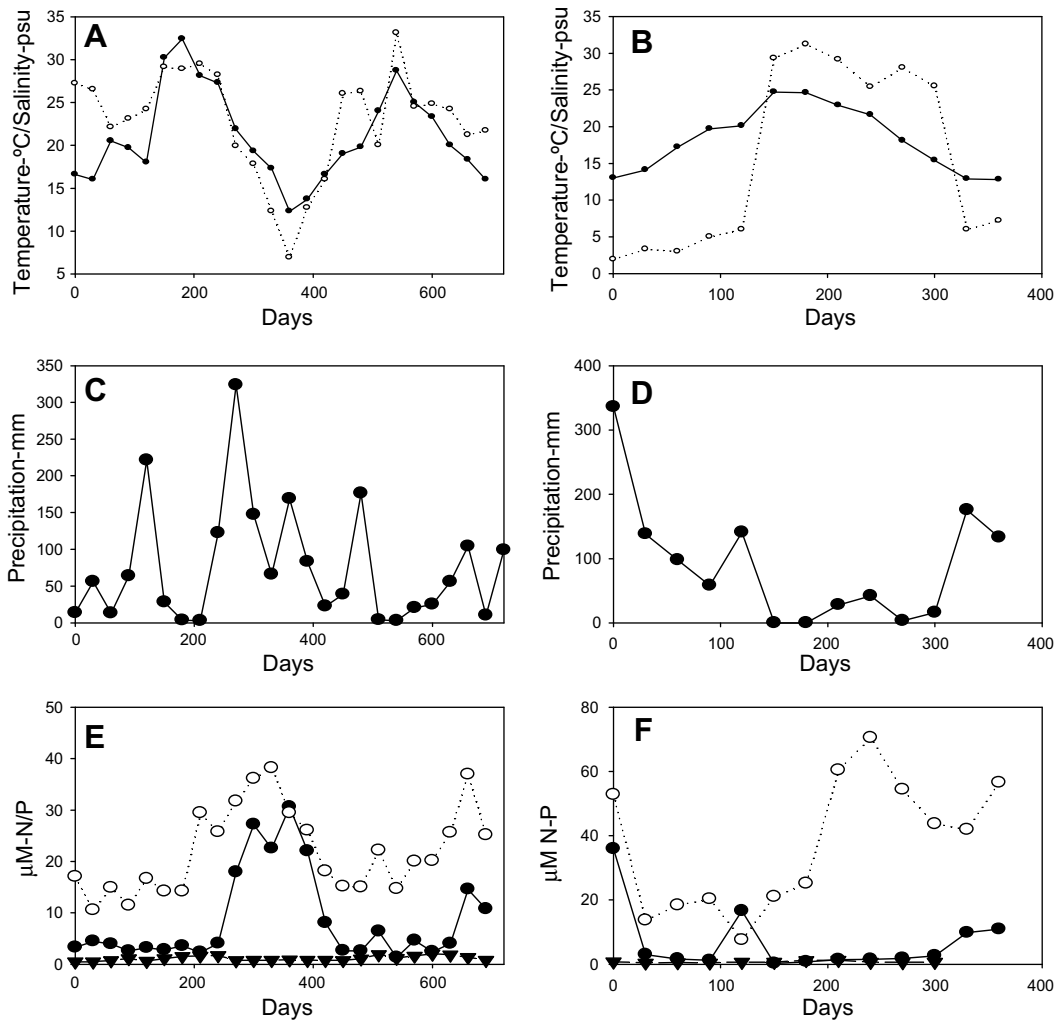


Fig. 3. Variation of external conditions in 1993–1994 (basic run): (A) temperature (—●—) and salinity (—○—), (C) precipitation, (E) $N-NH_4$ (—○—), $N-NO_3$ (—●—), $P-PO_4$ (—▼—) and during an unfavourable year: (B) temperature (—●—) and salinity (—○—), (D) precipitation and (F) $N-NH_4$ (—○—), $N-NO_3$ (—●—), $P-PO_4$ (—▼—).

3.2.1. New recruits resulting from reproduction of adult macroalgae

Adult macroalgae may allocate a significant amount of their biomass to the formation of zoospores and gametes, especially, during warmer months (Niesenbaum, 1988). For this reason reproduction was considered temperature dependent and the contribution of adult's reproduction to the production of new recruits (R_A) was described as

$$R_A = A \cdot \gamma \cdot R_{20} \cdot \theta^{(T-20)} \quad (2)$$

where A is the adult's biomass, R_{20} the adult's reproduction rate at 20 °C, T the temperature, θ the empirical coefficient and γ is the recruit's survival rate.

3.2.2. The contribution of dormant spores

As previously mentioned, *U. intestinalis* has a dormant life stage represented by microscopic spores, which can survive for some time in the sediments under adverse conditions (Schories and Reise, 1993). If external conditions are favourable, viable microscopic spores attach to substrata and germinate. In the model, these processes were represented by

$$D = B_D \cdot \lambda_{\max} \cdot fT \cdot fI_J \cdot fS_J \cdot fNP_J \quad (3)$$

where D is the viable spore's biomass, B_D the bank spore's biomass, λ_{\max} the maximum germination rate and fT , fI_J , fS_J and fNP_J are the temperature, light salinity and nutri-

ent limitation factors, respectively (described in the next section). The bank spore's biomass (B_D) used in the model was based on *in situ* quantifications (Sousa et al., unpublished) followed by calibration corresponding to 10 mg C m⁻².

3.2.3. The growth of early life forms

The growth of *Ulva*'s early life forms was described by

$$G_J = B_J \cdot \mu_{\max} \cdot fT \cdot fI_J \cdot fS_J \cdot fNP_J \quad (4)$$

where B_J is the biomass of *Ulva*'s early life forms, μ_{\max} the maximum growth rate and fT , fI_J , fS_J and fNP_J are the temperature, light salinity and nutrient limitation factors, respectively.

3.2.3.1. The effect of temperature. Experimental evidence suggests that *U. intestinalis* requires a temperature within the range 10–15 °C for germination (Lotze et al., 1999), although the maximum growth rate of *U. intestinalis* adults tends to occur at higher temperatures (Poole and Raven, 1997). This kind of variation is indicative of an optimum-type curve, which can be described by

$$fT = \exp \left[-2.3 \cdot \left(\frac{T - T_{\text{opt}}}{T_x - T_{\text{opt}}} \right)^2 \right] \quad (5)$$

Table 2

Definitions, values and source of the parameters used in the macroalgal early life stages sub-model

Symbol	Description	Units	Used value	Lit. range	Source
R_{20}	Adult's reproduction rate at 20 °C	d ⁻¹	0.01	Max. 0.6	Niesenbaum (1988)
θ	Empirical coefficient	–	1.047	1.01–1.2	EPA (1985)
μ_{\max}	Maximum growth rate	d ⁻¹	0.8	0.2–1.5	EPA (1985)
$G_{J\max}$	Maximum germination rate	d ⁻¹	0.8	0.4–1.0	Hoffmann and Camus (1989)
γ	Recruit's survival rate	d ⁻¹	0.1	–	Empirical and calibration
T_{opt}	Optimum temperature for germination and growth	°C	22	15–30	Based on values for adults – Poole and Raven (1997)
T_{\max}	Upper temperature for germination and growth	°C	35	–	Based on values for adults – Poole and Raven (1997)
T_{\min}	Lower temperature for germination and growth	°C	10	–	Based on values for adults – Poole and Raven (1997)
I_s	Optimum light intensity for photosynthesis	μmol E m ⁻² s ⁻¹	250	125–250	Kim and Lee (1996)
S_{opt}	Optimum salinity for germination and growth	psu	35	–	Sousa et al. (2007)
S_{\max}	Upper salinity for germination and growth	psu	45	–	In Poole and Raven (1997)
S_{\min}	Lower salinity for germination and growth	psu	10	0	In Poole and Raven (1997); Sousa et al. (2007)
N_{\max}	Maximum internal quota for nitrogen	μmol N (mg C) ⁻¹	12.85	–	Arhonditsis and Brett (2005)
P_{\max}	Maximum internal quota for phosphorus	μmol P (mg C) ⁻¹	0.81	–	Arhonditsis and Brett (2005)
N_{\min}	Minimum internal quota for nitrogen	μmol N (mg C) ⁻¹	5.7	–	Arhonditsis and Brett (2005)
P_{\min}	Minimum internal quota for phosphorus	μmol P (mg C) ⁻¹	0.258	–	Arhonditsis and Brett (2005)
N_{umax}	Maximum nitrogen uptake rate	μmol N (mg C) ⁻¹ d ⁻¹	11.42	–	Arhonditsis and Brett (2005)
P_{umax}	Maximum phosphorus uptake rate	μmol P (mg C) ⁻¹ d ⁻¹	0.29	–	Arhonditsis and Brett (2005)
KN	Half-saturation constant for nitrogen	μmol N l ⁻¹	3.214	–	Arhonditsis and Brett (2005)
KP	Half-saturation constant for phosphorus	μmol P l ⁻¹	0.322	–	Arhonditsis and Brett (2005)
Z_J	Grazing rate on young algae	d ⁻¹	0.23	0.06–0.14	Lotze and Worm (2000)
T_{optZ}	Optimum temperature for grazers	°C	22	–	Based on local macroinvertebrate biomass variation
T_{maxZ}	Upper temperature for grazers	°C	45	–	Based on local macroinvertebrate biomass variation
T_{minZ}	Lower temperature for grazers	°C	10	–	Based on local macroinvertebrate biomass variation

$T_x = T_{\min}$ for $T \leq T_{\text{opt}}$ and $T_x = T_{\max}$ for $T > T_{\text{opt}}$, where T_{opt} is the optimum temperature for germination and initial growth, T_{\min} the lower temperature limit below which germination and initial growth ceases and T_{\max} is the upper temperature limit above which germination and initial growth ceases.

3.2.3.2. The effect of light. Germlings of benthic algae seem to have lower light requirements than adults (e.g. Kim and Lee, 1996 and references therein), which may be related with the increase in the proportion of non-photosynthetic internal tissues during growth. Values reported in the literature indicate maximum photon flux densities between 125 and 250 $\mu\text{E m}^{-2} \text{s}^{-1}$ (Kim and Lee, 1996) and 600 $\mu\text{E m}^{-2} \text{s}^{-1}$ (Shellem and Josselyn, 1982; Beer and Shrage, 1987) for the production of algal juveniles and adults, respectively.

On the other hand because adults of *U. intestinalis* are photoinhibited by increased photon flux densities (Häder

et al., 1999), a photoinhibition-type curve is frequently used to describe the light limitation factor of the adults (e.g. Bendoricchio et al., 1993; Martins and Marques, 2002). Although we found no specific references for *Ulva* sp. spores, photoinhibition of spores of other algae species has been observed under certain conditions, such as high irradiation intensities (Stibal et al., 2007) or UV-radiation (e.g. Huovinen et al., 2000; Wiencke et al., 2000; Bischof et al., 2006). Based on this, the effect of light on the growth of *U. intestinalis* early life stages was described by

$$f_{I_j} = \frac{I}{I_s} \cdot e^{(1-\frac{I}{I_s})} \quad (6)$$

where I is the photon flux density ($\mu\text{E m}^{-2} \text{s}^{-1}$) and I_s is the optimum photon flux density for *U. intestinalis* early life forms ($\mu\text{E m}^{-2} \text{s}^{-1}$).

3.2.3.3. The effect of salinity. Macroalgal recruitment tends to be lower at low temperatures and salinities (Flavier and Ziyigmark, 1993). In the case of *U. intestinalis*, spore

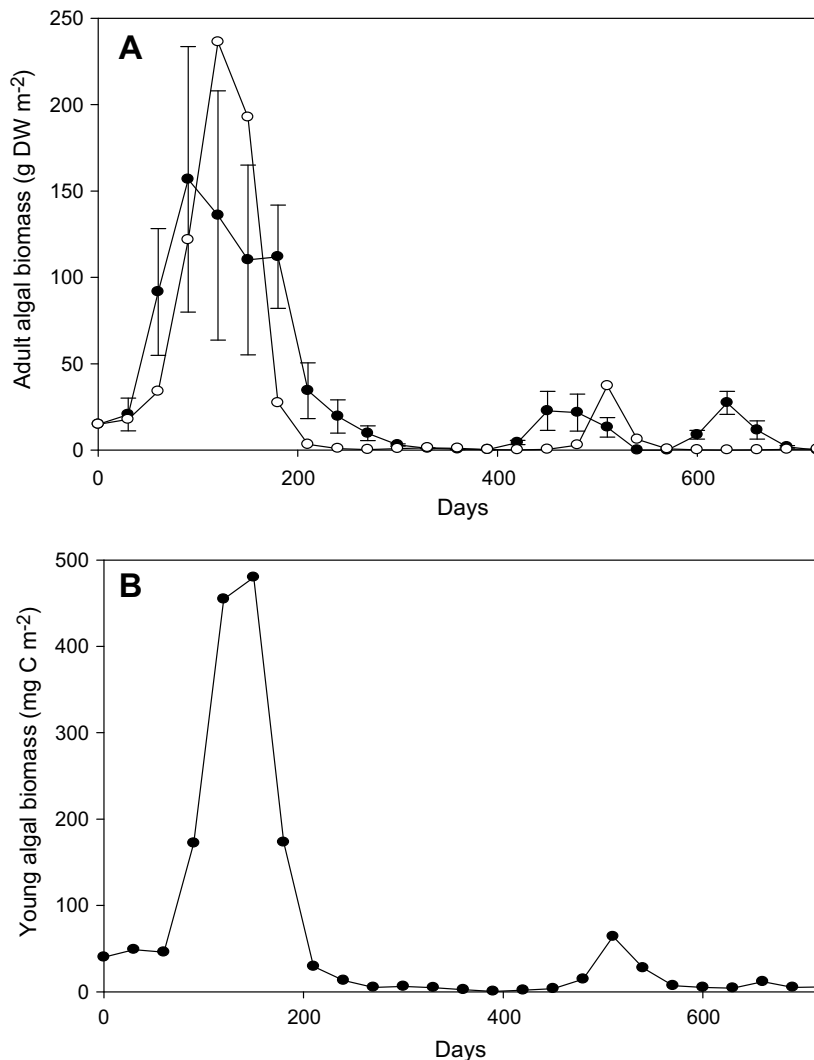


Fig. 4. Predicted (—○—) and observed (—●—) biomass variation \pm standard error of *U. intestinalis* adults (A) and predicted biomass of *U. intestinalis* early life stages (B) between 1993 and 1994 (basic run).

germination is enhanced at 35 psu and decreases with decreasing salinities (Sousa et al., 2007). Taking this into consideration, the effect of salinity on macroalgal early life stages was described as

$$fS_J = 1 - \left(\frac{S - S_{opt}}{S_x - S_{opt}} \right)^m \quad (7)$$

$S_x = S_{min}$ and $m = 2.5$ for $S < S_{opt}$ $S_x = S_{max}$ and $m = 2$ for $S \geq S_{opt}$ where S_{opt} is the optimum salinity for germination and initial growth, S_{min} the lower salinity limit below which germination and initial growth cease and S_{max} is the upper salinity limit above which germination and initial growth cease.

3.2.3.4. *The effect of nutrients.* The nutrient limitation factor was described accordingly with “Liebig’s law of the minimum” (e.g. EPA, 1985). Additionally, as the uptake by phytoplankton, the nutrient uptake by macroalgal

spores and juveniles was considered dependent on both external and internal nutrient concentrations (Arhonditsis and Brett, 2005):

$$fNP_J = \min \left\{ \frac{N_i - N_{min}}{N_{max} - N_{min}}, \frac{P_i - P_{min}}{P_{max} - P_{min}} \right\} \quad (8)$$

$$\frac{\partial N_i}{\partial t} = N_u \times N_r - G \cdot N_i, \quad \frac{\partial P_i}{\partial t} = P_u \times P_r - G \cdot P_i \quad (9)$$

$$N_u = N_{u_{max}} \frac{N}{N + KN}, \quad P_u = P_{u_{max}} \frac{P}{P + KP} \quad (10)$$

$$N_r = \frac{N_{max} - N_i}{N_{max} - N_{min}}, \quad P_r = \frac{P_{max} - P_i}{P_{max} - P_{min}} \quad (11)$$

where N_i is the internal nitrogen concentration, P_i the internal phosphorus concentration, $N_{u_{max}}$ the maximum uptake rate of nitrogen, $P_{u_{max}}$ the maximum uptake rate of phosphorus, KN the nitrogen half-saturation constant, KP the phosphorus half-saturation constant, N_{min} the minimum internal nitrogen quota, P_{min} the minimum internal

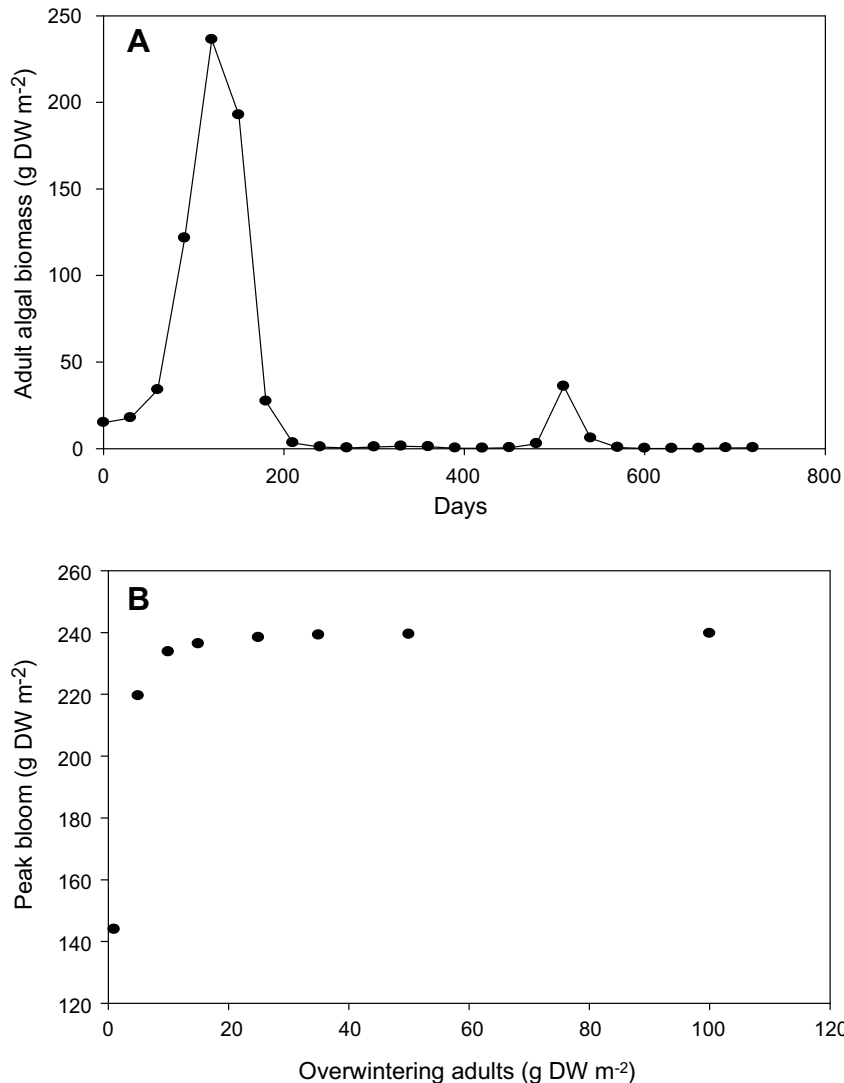


Fig. 5. Predicted biomass of *U. intestinalis* adults during a favourable period and without the contribution of spores (A). Relationship between the biomass of overwintering adults and the maximum adult biomass reached during the spring bloom (peak bloom) in a favourable year (B).

phosphorus quota, N_{\max} the maximum internal nitrogen quota, P_{\max} the maximum internal phosphorus quota, N the nitrogen external concentration and P is the phosphorus external concentration.

3.2.4. Grazing on macroalgal early life stages

Herbivory is a process with very significant impacts on algal early life stages and has been reported as reducing algal juveniles at rates varying from 0.06 to 0.14 d⁻¹ (Worm and Chapman, 1998; Lotze and Worm, 2000; Worm and Lotze, 2006). According to this, the effect of grazers was described as

$$Z_J = B_J \cdot Z_r \cdot f(T_{Z_J}) \tag{12}$$

where B_J is the biomass of *Ulva*'s early life forms, Z_r the grazing rate on macroalgal early life stages and $f(T_{Z_J})$ is the temperature limiting factor of grazers.

3.2.5. Transfer to adults

The maximum growth rate of macroalgal early life forms can reach 0.8 d⁻¹ (Hoffmann and Camus, 1989). On the other hand, on a laboratorial setup using limiting light conditions for macroalgal growth, the average growth of *U. intestinalis* spores at 20 and 35 psu was estimated as 0.25 ± 0.11 d⁻¹ (Sousa et al., 2007). Taking this range into consideration, it was assumed that microscopic forms take approximately 12 days to achieve the adult size (10 cm length). The time lag between the microscopic and the adult phase was taken into consideration through the specific expression “DELAY”, included in STELLA software. Through calibration, the amount of early life forms being transferred to adults per day was set at 1%.

3.3. Simulations

The model's basic run includes temperature, salinity, nutrients (dissolved inorganic nitrogen and phosphorus)

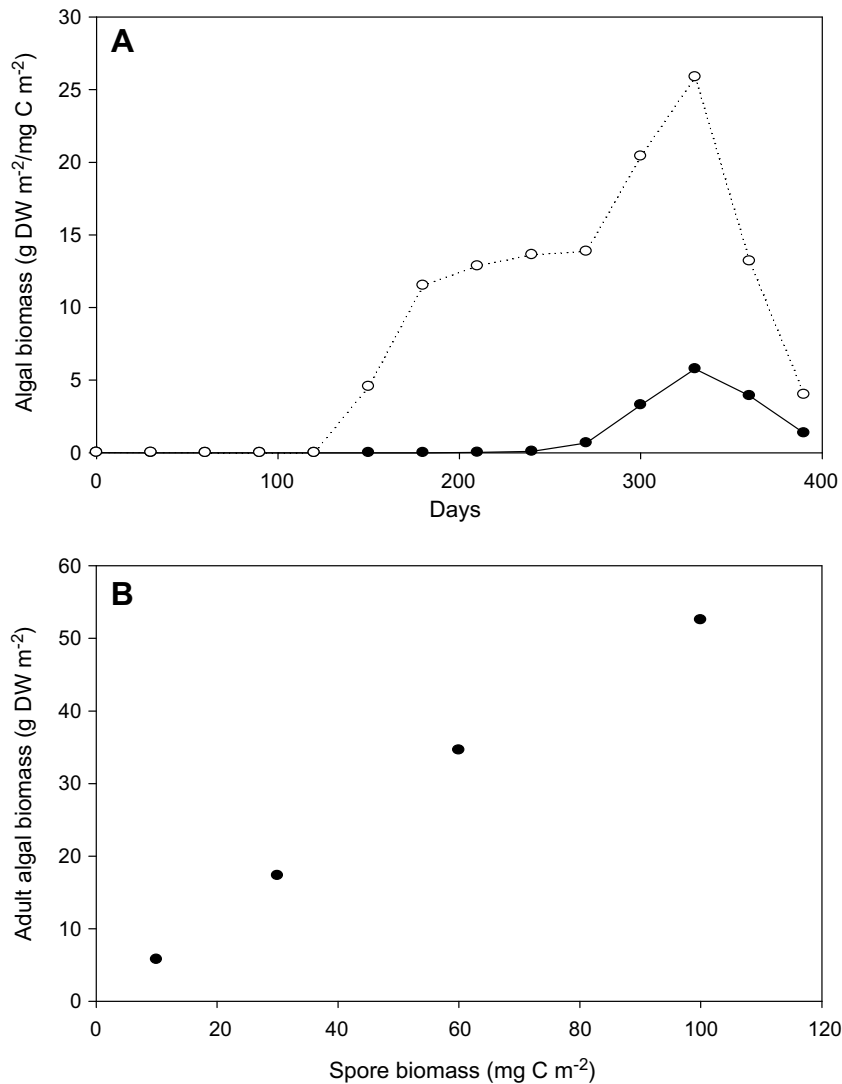


Fig. 6. Predicted biomass of *U. intestinalis*' adults (—●—) and early life stages (young) (—○—) under unfavourable conditions (A). Relationship between the biomass of spores stored in the spore's bank and the maximum adult biomass attained in an unfavourable year (B).

and precipitation values corresponding to the variation observed in a sampling site located at the Mondego estuary, between January 1993 and January 1994 (Figs. 3A and B). According to the *Assessment of Estuarine Trophic Status* methodology (ASSETS – Bricker et al., 2003) related to the *overall eutrophic condition* (OEC), 1993 and 1994 were classified as high OEC and medium OEC, respectively (Martins et al., 2007) and, consequently, represent favourable conditions for macroalgal growth. On the contrary, 1996 was classified as low OEC (Martins et al., 2007). Therefore, in the present work, the variations of external conditions registered for 1996 were used to simulate the scenario of *unfavourable conditions*. Parameter def-

inition and values are shown in Table 2. In every run, the initial simulation time corresponds to January. Based on available data for the Mondego estuary (e.g. Lillebø et al., 2005; Sousa et al., 2007), state variable initial values in the basic run were set at 40 mg C m^{-2} and 15 g DW (dry weight) m^{-2} , for algal juveniles and adults, respectively. For unfavourable conditions, the initial values of the state variables were set at 0 mg C m^{-2} and 0.01 g DW m^{-2} , for algal juveniles and adults, respectively, based on the assumption that – under these conditions – there are no overwintering adults or juveniles in January. Global warming scenarios were run with state variable's initial values equal to the basic run and corresponded to three different scenarios: (1) Intense rainfall during winters and springs followed by dry summers; (2) Prolonged drought with no increase on the average temperature and with a increase of 2°C and 4°C on the average water temperature; (3) Sea-level increase of 1 m per century according to ice sheet collapse predictions (Overpeck and Cole, 2006) associated to the expansion of ocean water (IPCC, 2007). For all runs, the initial simulation time corresponds to January and the DT is 30 days.

Table 3
Sensitivity analysis for a favourable and an unfavourable year

Parameters	Favourable year		Unfavourable year	
	Adults	Juveniles	Adults	Juveniles
B_{D+}	0	0.09	1	1
B_{D-}	0	0.09	1	1
Z_{J+}	-0.01	-0.92	-0.89	-1.08
Z_{J-}	-0.25	-13	-7.32	-35
$\lambda+$	0	0.09	1	1
$\lambda-$	0	0.1	1	1
$\mu+$	0.01	1.55	0.4	0.88
$\mu-$	0	0.52	0.24	0.44
Adv+	-0.2	-0.15	-0.47	-0.13
Adv-	-0.53	-0.47	-0.64	-0.17
Z_{A+}	-0.46	-0.33	-1.33	-0.38
Z_{A-}	-1.13	-0.91	-4.45	-1.24
Dec +	-0.67	-0.51	-1.60	-0.45
Dec -	-2.57	-1.97	-10.57	-2.83
R_{20+}	-0.32	0.53	-0.98	-0.12
R_{20-}	-0.75	0.57	-2.05	0.01

B_D – biomass of dormant spores, Z_J – grazing rate on juveniles, λ – germination rate, μ – growth rate, Adv – advection rate of adults, Z_A – grazing rate on adults, Dec – decomposition rate of adults, U – reproduction rate.

3.4. Calibration, sensitivity and statistical analysis

Parameter calibration was achieved by optimisation algorithms, followed by comparison of predicted and observed adult biomass variation between January 1993 and January 1994, to assess for model reliability. Model II regression was used to compare predicted and observed *U. intestinalis* biomass variation, whilst the significance of the regression was tested by ANOVA.

Sensitivity analysis was performed in accordance with Jørgensen (1994). To assess for the sensitivity of the state variables in different years, sensitivity analysis was performed under favourable and unfavourable external conditions.

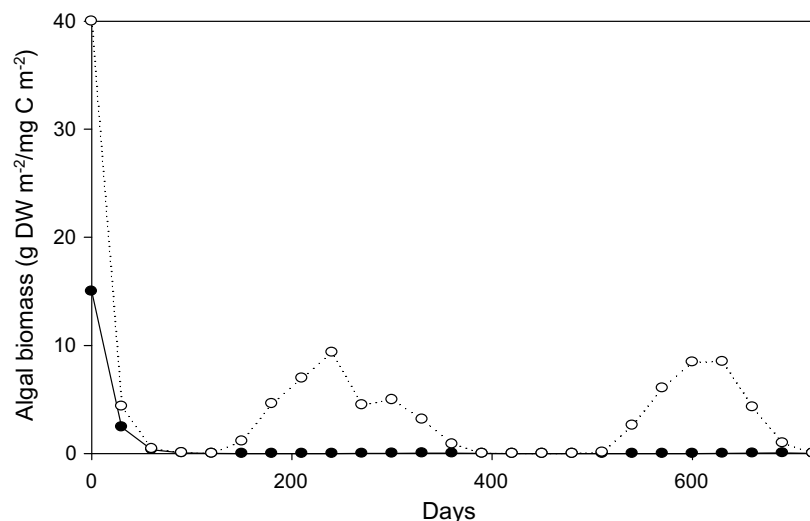


Fig. 7. Predicted biomass of *U. intestinalis* adults (—●—) and early life stages (young) (—○—) during scenarios of intense rainfall.

4. Results

In general, the predicted biomass of adult macroalgae follows the same variation as the observed biomass (Fig. 4A). The regression between the two sets of data is significant (ANOVA, $F_{1,22} = 42$, $P < 0.001$, $r^2 = 0.65$) and, thus, the model was considered valid to address the initial questions.

According to simulations, for 1993–1994, the biomass of young macroalgae follows the same pattern of variation as adult macroalgae, reaching a maximum value of 480 mg C m^{-2} during spring of 1993 (Fig. 4B).

According to predictions, in years characterized by the occurrence of favourable external conditions during winter and spring, spring blooms will take place even without the contribution of the spore bank (Fig. 5A). Under favourable external conditions, a biomass of 1 g DW m^{-2} in winter can promote a spring bloom of $\sim 144 \text{ g DW m}^{-2}$ in spring and the peak of the spring bloom increases linearly with the adult overwintering biomass until 5 g DW m^{-2}

(Fig. 5B). Beyond this threshold, the peak bloom tends to stabilise for further increases of the adult overwintering biomass (Fig. 5B). On the contrary, during years presenting unfavourable conditions to algal growth, the total annual productivity of *U. intestinalis* also depends on the biomass accumulated as spores, particularly, if there are no overwintering adults or very few. In these circumstances, *U. intestinalis* exhibits a very low and later growth peak (Fig. 6A), which increases linearly with the biomass stored in the spore bank (Fig. 6B).

Results from the sensitivity analysis show that, as expected, adults and early life forms of *U. intestinalis* are more sensitive to parameter changes in unfavourable years compared to favourable ones. Particularly, grazing rates and decomposition are extremely sensitive parameters during unfavourable years (Table 3).

Simulations suggest that intense rainfall in winter and spring followed by dry summers have dramatic impacts on *U. intestinalis* populations, with the adults being more affected than the juveniles (Fig. 7).

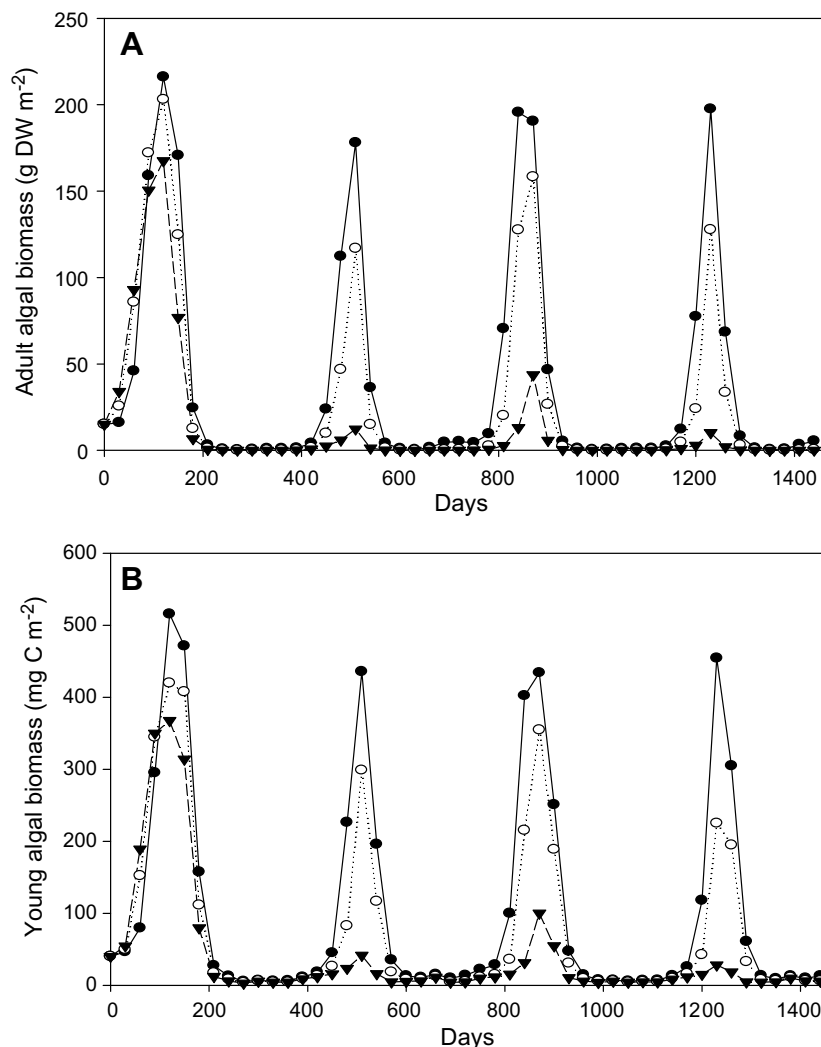


Fig. 8. Predicted biomass of *U. intestinalis* adults (A) and early life forms (young) (B) for scenarios of prolonged drought without temperature increase (—●—), with a 2 °C temperature increase (—○—) and a 4 °C temperature increase (—▼—).

The occurrence of dry winters and summers favours macroalgae populations as long as temperature values are kept similar to those observed in 1993–1994. However, long-term simulations of dry conditions associated to increases of the average temperature have negative impacts on *U. intestinalis* population. *U. intestinalis* populations located at the intertidal area, more precisely at +1.8 m, exhibit an average decrease of ~30 and 66% on productivity for increases of 2 °C and 4 °C, respectively, compared to simulations with no temperature increase (Fig. 8).

Predictions for sea-level rise suggest that *U. intestinalis* will exhibit significant decreases on productivity, particularly, for bathymetries $\leq +2$ m. According to simulations for a sea level rise of 1 m, *U. intestinalis* will not subsist at bathymetries $\leq +2$ m, whilst at a bathymetry of +2.3 m, *U. intestinalis* productivity decreases about 84% compared to the values quantified in 1993–1994 (Fig. 9). In this scenario, *U. intestinalis* will disappear from about ~81% of the actual intertidal area (between -0.9 m and

+1.8 m) but it will persist in ~19% of the actual intertidal area corresponding to bathymetries ranging from +1.9 m to +2.3 m (Fig. 10). However, if sea level rise (1 m) is accompanied by an increase on the average water temperature, the productivity of *U. intestinalis* located at +2.3 m tends to decrease with increasing temperatures (Fig. 11).

5. Discussion

The present results confirm previous studies which indicate that, even at eutrophied coastal areas, the growth of opportunistic macroalgae is highly variable and depends on several factors. Besides the abiotic parameters (e.g. precipitation, salinity, water current) identified as key-factors on the regulation of the inter-annual variation of *U. intestinalis* on the Mondego estuary (Martins et al., 2001), the present work suggests that biotic factors, namely, the amount of macroalgae spores can also play an important role on the yearly growth and productivity of opportunistic

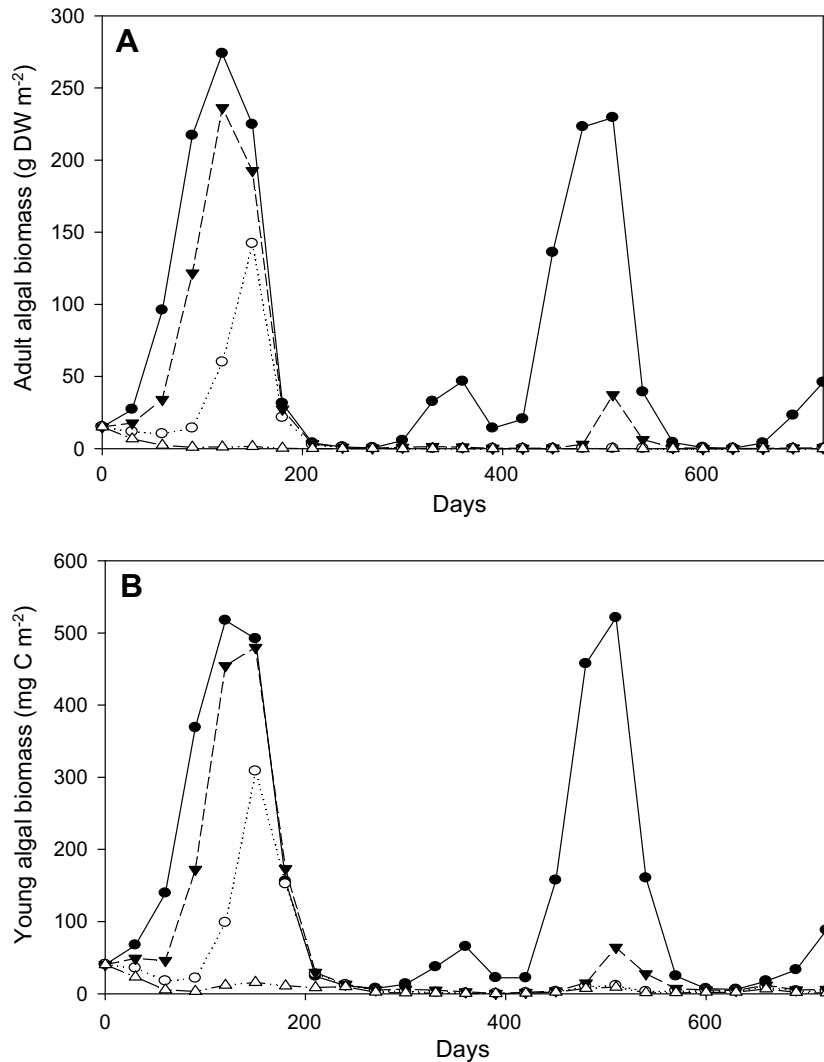


Fig. 9. Comparison of the biomass variation of *U. intestinalis*'s adults (A) and early life forms (young) (B) between scenarios with and without sea level rise and at different bathymetries. +2.3 m without sea level rise (—●—), +1.8 m without sea level rise (---▼---), +2.3 m with 1 m sea level rise (---○---), +1.8 m with 1 m sea level rise (—△—).

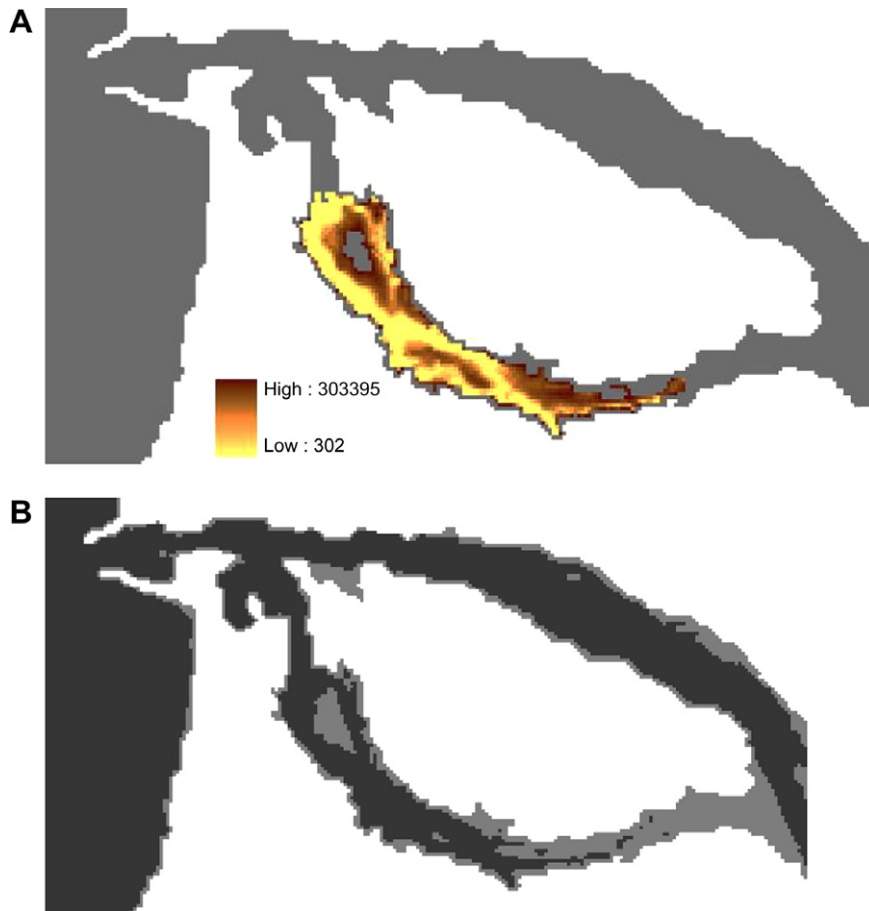


Fig. 10. Comparison between predictions of the bathymetric distribution of *U. intestinalis* adults in April 1993 (A): high – 304 g DW m⁻², low – 0.302 g DW m⁻² and scenarios of sea level rise (1 m) (B) at the south channel of the Mondego estuary: dark grey – areas where *U. intestinalis* will not subsist, Light grey – areas where *U. intestinalis* can still grow (see text for explanation).

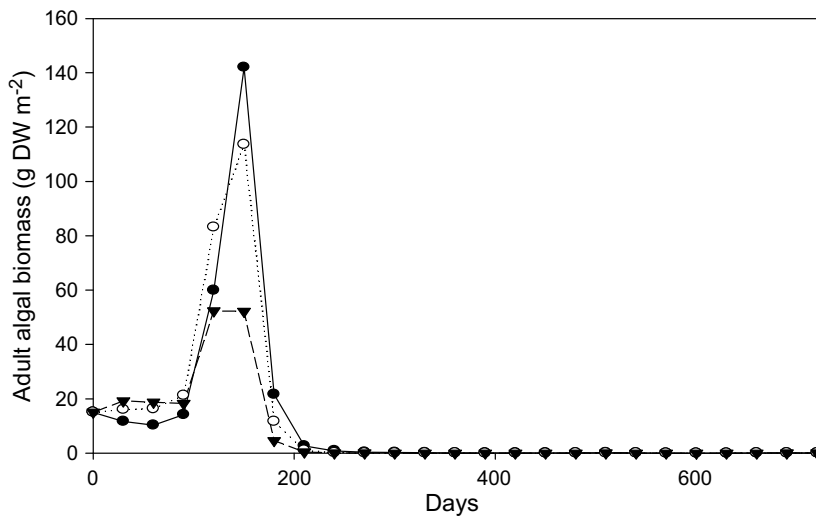


Fig. 11. Predicted biomass variation of *U. intestinalis*' adults at +2.3 m for scenarios of sea level rise (1 m) without temperature increase (–●–), with a 2 °C temperature increase (–○–) and a 4 °C temperature increase (–▼–).

algae. According to the present model, in unfavourable years – when adult macroalgae do not persist throughout winter or are present in very low amounts – the onset of

U. intestinalis growth occurs at the expense of microscopic spores. Furthermore, the growing season does not take place in spring but later on in the year (beginning of

Table 4

Overwintering adults, existence of spring blooms, impact of spores on adults and numerical predictions for favourable and unfavourable external conditions

External conditions	Persistence of adults during winter	Spring adult bloom	Impact of spores on adults	Numerical predictions
Favourable: low hydrodynamics	Yes	Yes	Not significant	5 g DW m ⁻² of adults in January ↓ ~200 g DW m ⁻² of adults in May
Unfavourable: high hydrodynamics	No	No The growing season takes place later in the year	Highly significant The onset of adult growth depends on microscopic spores	10 mg C m ⁻² of spores ↓ ~6 g DW m ⁻² of adults in autumn

Favourable: low rainfall, high salinity, low currents, low light extinction; unfavourable: high rainfall, low salinity, high currents, high light extinction coefficients.

autumn) and adult productivity is very limited (Table 4). According to simulations, in these circumstances, adult macroalgal productivity increases linearly with the biomass of spores accumulated in the dormant bank, which is in accordance with previously reported experimental evidence (e.g. Santelices et al., 1995; Lotze et al., 1999). Thus, the present results indicate that, under unfavourable conditions, *U. intestinalis* productivity is strongly dependent on the biomass accumulated in the spore bank. Although little research has focused on the viability of macroalgal spores accumulated in the sediments, experimental evidence suggest that spores are still viable after remaining in the sediments for 10 months but their viability decreases over time (Schories, 1995). Taking this and the present results into consideration, it is reasonable to assume that, during unfavourable years, the productivity of adult macroalgae will also depend on the timing that optimal conditions take to arise. The latter these conditions occur, the less adult biomass will be accumulated in the system due to lower amounts of viable spores.

On the contrary, during favourable years – when external conditions allow the persistence of adults of *U. intestinalis* during winter – predictions suggest that spring growth can take place independently of the spore bank (Table 4) and that, in these circumstances, macroalgal productivity increases linearly with the biomass of overwintering adults until a certain threshold value is reached (~5 g DW m⁻²). Above this threshold, the peak bloom stabilises which is related to light limitation conditions caused by self-shading. This process is accounted in the model (Martins et al., 2007).

Predictions for climate change scenarios suggest that *U. intestinalis* will be adversely affected by the occurrence of persistent and intense rainfall in the winter and spring, which is related with the adverse impacts that several external factors, such as low salinity, high light extinction coefficients, high *N:P* ratios and high current velocities have on the growth of *U. intestinalis* early life stages (Sousa et al., 2007) and on the growth and transport of adults (Martins et al., 1999, 2001; Kamer and Fong, 2001; Neto et al., 2008). In this scenario, the highest sensitivity of adults

compared to algal juveniles is related with the significant advection of adult macroalgae from the system, which occurs whenever high rainfall associated to significant freshwater discharges to the system take place (Neto et al., 2008). Due to their smaller size, attached spores and juveniles are not so vulnerable to drifting out of the system as adult macroalgae.

If drought periods are associated with water temperature increases, predictions indicate that, although less dramatically than in the former scenario, *U. intestinalis* will also decrease its productivity at the Mondego estuary. This is due to the effect of desiccation on young and adult macroalgae (e.g. Matta and Chapman, 1995), which is described and taken into account in the model (Martins et al., 2007). In accordance to most climate change scenarios which predict an increase in the average global temperature (IPCC, 2007), in the present work, we have only considered scenarios of temperature increase. However, the occurrence of climate feedbacks (positive or negative) may increase the complexity of temperature responses to global warming (EPA, <<http://www.epa.gov/climate-change/science/futuretc.html>>).

A sea level rise of 1 m – as expected to occur in one century if the ice sheet collapse predictions are confirmed (Overpeck and Cole, 2006) – will cause a significant decrease on *U. intestinalis* productivity at the Mondego estuary due to the general increase of depth and the consequent decrease of light reaching macroalgal surface. According to predictions, in this situation due to light limitation, *U. intestinalis* will disappear from ~81% of the actual intertidal area (between -0.9 m and +1.8 m) but it will persist in ~19% of the actual intertidal area corresponding to bathymetries ranging from +1.9 m to +2.3 m. However for simulations where sea level rise is accompanied by temperature increases, the productivity of *U. intestinalis* located at higher bathymetries will decrease with increasing temperatures, mostly, due to desiccation.

In general, the present results reflect the correct incorporation into the model of processes related to algal early life

stages and adult dynamics and their dependency on external environmental conditions.

In conclusion, the present work corroborates the idea that hydrodynamics control macroalgae productivity at shallow mesotidal estuaries. During low hydrodynamic conditions, adults of *U. intestinalis* persist in the system throughout winter and, during spring, macroalgal blooms are likely to happen without the contribution of dormant spores. On the contrary, under high hydrodynamic conditions, adult macroalgae drift out the system and external conditions do not favour the growth of persistent individuals. As a consequence, macroalgae productivity will be extremely limited and strongly dependent on the biomass of dormant spores. Predictions for global warming scenarios suggest that, in general, *U. intestinalis* will be adversely affected due to light limitation, desiccation and advection. In certain scenarios, the productivity of *U. intestinalis* will be strongly dependent on the viability and growth of microscopic forms and juveniles since adults tend to be more sensitive to high hydrodynamics and sea level rise.

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