MIGUEL ÂNGELO PARDAL
JOÃO CARLOS MARQUES
MANUEL AUGUSTO GRAÇA
Scientific Editors

Aquatic Ecology of the Mondego River Basin
Global Importance of Local Experience

Coimbra • Imprensa da Universidade

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Enteromorpha spp. (ULVALES: CHLOROPHYTA) GROWTH IN THE SOUTH ARM OF THE MONDEGO ESTUARY: FIELD GROWTH RATES WITH AND WITHOUT MACROFAUNAL GRAZER EFFECTS

Abstract

The aim of this study was to quantify field growth rates of *Enteromorpha* spp. and to compare macroalgal growth with and without macrofaunal grazer effects in the south arm of the Mondego estuary. From January 1996 to January 1997, *Enteromorpha* growth was characterised by null or very low values in winter and late autumn, which fitted to negative exponential models. In spring, macroalgal growth enhancement took place according to exponential models. During summer, although lower than in spring, *Enteromorpha* growth rates were positive with the exception of July. In spite of the growth enhancement observed in spring, average *Enteromorpha* growth rates were low for this time of the year. This was attributed to the significant input of freshwater to the south arm during winter and spring 1996. According to the results, *Enteromorpha* growth rates are positively correlated with salinity and negatively correlated with precipitation, which partially results from the dependency of salinity on precipitation. However, this dependency is only valid for certain periods of the year. The present results are inconclusive relatively to grazer effects on *Enteromorpha* growth, since macroinvertebrates were found inside both types of experimental devices.

Introduction

It is widely known that eutrophic conditions stimulate the growth of opportunistic primary producers. Higher surface to volume ratios (SA:V) of phytoplankton and ephemeral macroalgae (e.g. *Enteromorpha* spp.) determine high maximal uptake rates of nutrients, high initial slopes of photosynthesis versus irradiance and lower half-

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saturation constants for the uptake of nutrients (Hein et al. 1995, Valiela et al. 1997), which in turn determine high growth rates especially under nutrient enriched conditions.

On the other hand, it has been suggested that even under eutrophic conditions, grazing control may be an important factor regulating biomass accumulation of free-floating macroalgae, such as *Ulva* sp. and *Enteromorpha* sp. (Geertz-Hansen et al. 1993). Ultimately, the abundance and success of a given alga in a certain environment results from the balance between nutrient uptake, nutrient requirements, cell growth and loss rates due to grazing and physical processes (Hein et al. 1995).

In the Mondego estuary, eutrophication is characterised by significant accumulations of green macroalgae mainly *Enteromorpha* spp. (Marques et al. 1993, Pardal 1998, Lillebø et al. 1999, Martins et al. 1999). *Enteromorpha compressa* (L.) Greville and *Enteromorpha intestinalis* (L.) Link were identified as the most abundant species (Martins et al. 1999, Martins 2000). In fact, throughout the last decades *Enteromorpha* spp. became the dominant primary producer in the intertidal areas of south arm of the estuary. At the same time, there was a decrease in the area occupied by rooted macrophytes (especially *Zostera noltii*) (Pardal 1998, Martins 2000). The two processes may be related and may have resulted in the occurrence of less structured and more impoverished macrofaunal benthic communities in the south arm of the estuary (Lillebø et al. 1999, Pardal 1998, Pardal et al. 2000).

The general aim of the present work was to follow *Enteromorpha* spp. growth in the south arm of the Mondego estuary, throughout one year in order to detect the main external factors controlling it. In particularly, we tried to assess for macrofaunal grazer effects on *Enteromorpha* spp. growth.

Material and methods

Preparation of macroalgae for growth experiments

From January 1996 to January 1997, one experiment was run, every month, in an inner area of the south arm of the Mondego estuary (Fig. 1). Field work was always carried out during low-tide. One day before the beginning of the experiment, *Enteromorpha* spp. individuals were collected randomly on the intertidal muddy flats of the south arm of the estuary, placed in recipients containing estuarine water and carried to the lab. Forty healthy individuals were chosen, carefully washed with estuarine water and placed on kitchen paper inside a temperature-controlled room at 20°C, which allowed to remove the excess of water. After this procedure, macroalgal individuals were weighted for initial wet weight adjustment corresponding to 4-5 g of algal tissue. Each macroalgae portion was then placed inside identified experimental devices, consisting of semi-cylinder cages built in plexiglass (Fig. 2). The sides and bottom of 20 devices were surrounded by 0.5 mm mesh-size net to prevent grazers from enter, while sides and bottom of the other 20 devices were surrounded by 4 mm mesh-size net, which allowed grazers to enter (Fig. 2). The experimental devices

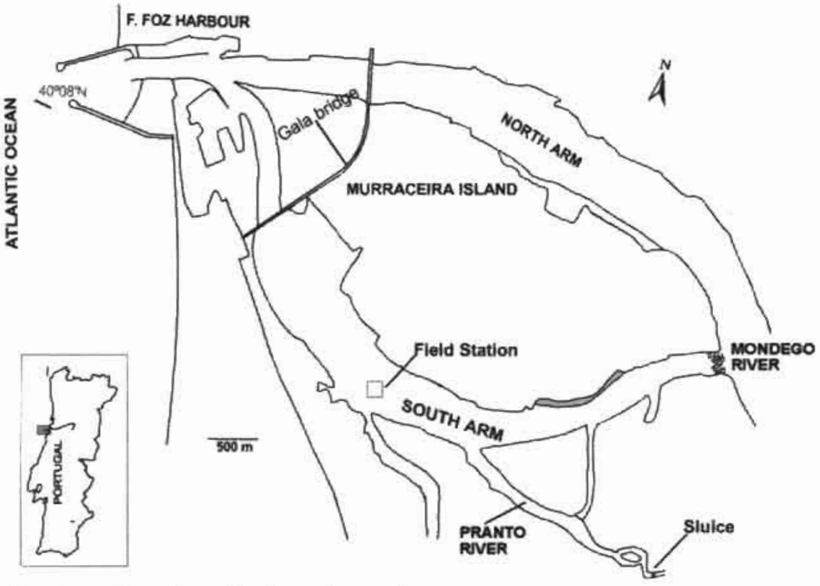

Figure 1. Experimental area located in the south arm of the Mondego estuary.

allowed sufficient water circulation and light penetration inside. Nevertheless under field conditions, the amount of light decreased with exposure time due to sediment deposition on device surfaces.

All experimental devices were carried out to the field and fixed by thin ropes to wood sticks buried in the sediment. Groups of five replicates of devices from both types were removed from the field after 5, 10, 15 and 20 days. In the laboratory, macroalgal individuals were carefully washed with estuarine water and weighted to final wet weight, following the water removal procedure already described.

For each sampling date, temperature (°C), salinity, dissolved oxygen (mg.l^{-1} and %) and pH data were measured *in situ* and water samples (approximately 250 ml) were collected to estimate dissolved inorganic nutrients (PO_4-P, NO_3-N, NO_2-N and NH_4-N). In the laboratory, water samples were filtered and analysed following Standard Methods (1992) procedures for orthophospate and N-compounds. Data on precipitation were obtained from the Geophysics Institute of the University of Coimbra and concern precipitation values measured at the city Coimbra.

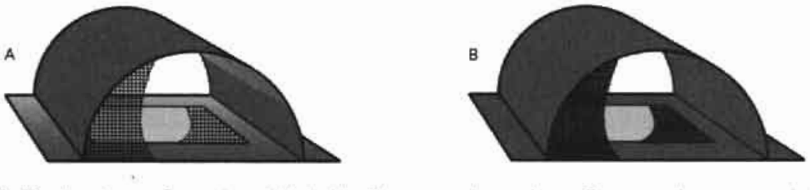

Figure 2. The two types of experimental "plexiglass" cages used to estimate *Enteromorpha* spp. growth: A) surrounded by 4 mm mesh size net to allow grazers entrance; B) surrounded by 0.5 mm mesh size net to prevent grazers entrance

Data analysis

Monthly growth rates of *Enteromorpha* spp. were calculated according with the exponential growth model:

$$W_t = W_0 \times e^{kt} \qquad (1)$$

W_t – *Enteromorpha* weight (g wet weight) at time t, W_0 – *Enteromorpha* initial weight (g wet weight), k – coefficient of specific growth (d^{-1}).

Enteromorpha weight data were ln transformed, which allowed the exponential curve to become a straight line. The slope of that line is k, i.e., *Enteromorpha* growth rate (Sokal and Rolf 1995; Zar 1999). After calculating *Enteromorpha* growth rates as the slopes of fitted regressions, the significance of regressions was tested by analysis of variance (ANOVA). Analysis of covariance (ANCOVA) was used to compare slopes (i.e. growth rates) and the Tukey test was used to detect significant differences between them.

The t-test was used to compare *Enteromorpha* growth rates with and without grazer effects, after checking for normality (Kolmogorov test) and for homogeneity of variances (Bartlett test). Correlation between growth rates and physicochemical parameters was assessed by Pearsons' correlation coefficient and the significance of the correlation was assessed by an F-test (Zar 1999). MICROSOFT EXCEL 97 and STATGRAPHICS software packages were used to perform all statistical analysis.

Results

In winter and late autumn, *Enteromorpha* weight variation inside both types of devices was well fitted to negative exponential models (Figs 3 and 4). In spring and August, *Enteromorpha* weight variation without grazer effects was well described by positive exponential models (Fig. 3), which was not the case of *Enteromorpha* spp. weight variation with grazers (Fig. 4). In both situations (with and without grazers), the weight variation of *Enteromorpha* in July was poorly fitted to exponential models (Fig. 3 and Fig. 4).

Enteromorpha spp. specific growth rates without grazers ranged from –0.33 to 0.063 d^{-1} in January 1996 and June/August, respectively. Macroalgal growth in the presence of grazers ranged from –0.38 to 0.13 d^{-1} in January and May, respectively (Fig. 5). Higher growth rates occurred in spring and also in August, while in July *Enteromorpha* had a negative growth rate (Fig. 5).

Monthly growth rates were significantly different when compared to each other (ANCOVA, $P<0.05$). *Enteromorpha* growth in January and February 1996 was significantly different from growth in any other month (Tukey test, $P<0.001$) (Tables 1 and 2).

No significant differences were found between *Enteromorpha* spp. growth rates with and without grazer effects (t test, $P>0.05$). Additionally, macroinvertebrates were found inside both type of experimental devices. Table 3 shows the most representative taxa and their relative abundance inside experimental devices.

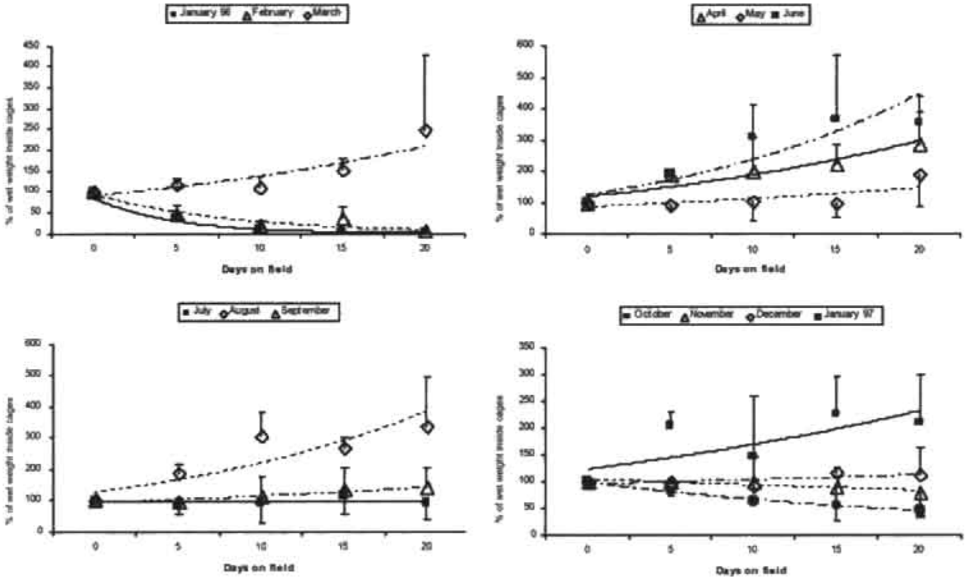

Figure 3. Variation of *Enteromorpha* spp. wet weight (%) inside experimental cages without grazers. R^2 between data and exponential models in March, April, May and June were 0.80, 0.85, 0.52 and 0.83, respectively.

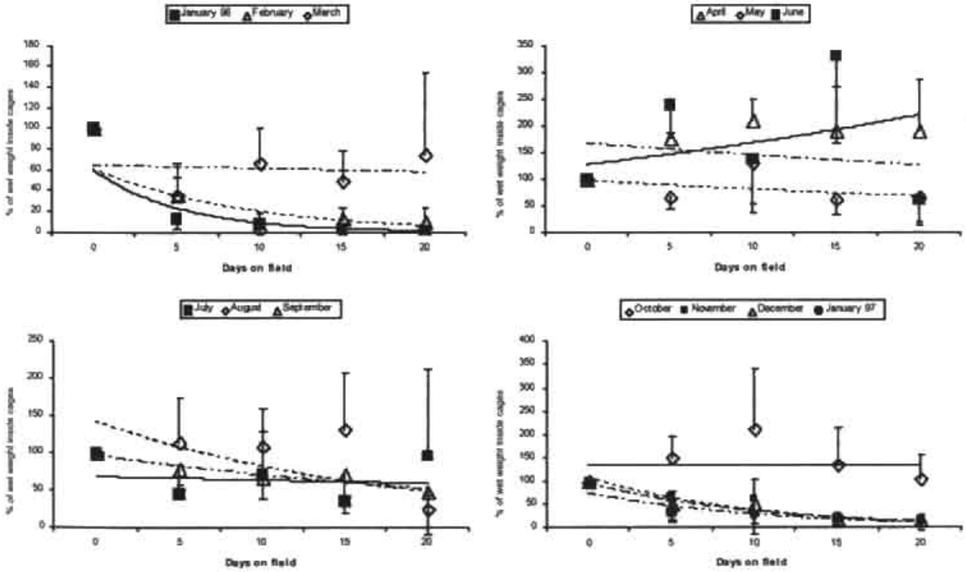

Figure 4. Variation of *Enteromorpha* spp. wet weight (%) inside experimental cages with grazers. R^2 between data and exponential models in March, April, May and June were 0.01, 0.54, 0.19 and 0.033, respectively

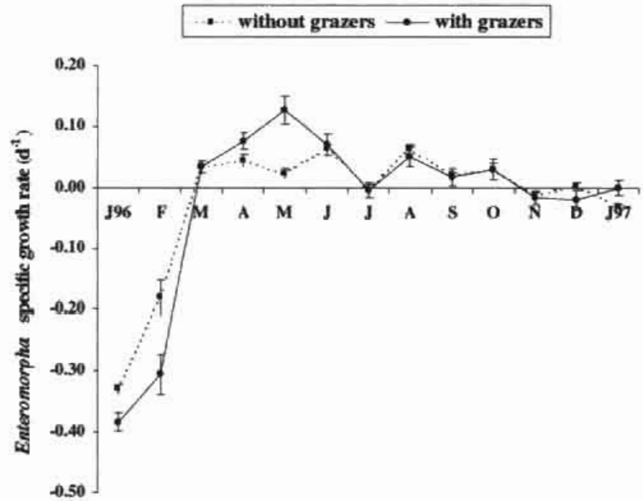

Figure 5. Variation of *Enteromorpha* spp. growth rate (d^{-1}) without and with grazer effects ± standard error

		Jan-96	Feb-96	Mar-96	Apr-96	May-96	Jun-96	Jul-96	Aug-96	Sep-96	Oct-96	Nov-96	Dec-96	Jan-97
	slopes	-0.332	-0.182	0.033	0.044	0.023	0.063	-0.005	0.063	0.020	0.029	-0.014	0.002	-0.031
Jan-96	-0.332	-												
Feb-96	-0.182	S***	-											
Mar-96	0.033	S***	S***	-										
Apr-96	0.044	S***	S***	NS	-									
May-96	0.023	S***	S***	NS	NS	-								
Jun-96	0.063	S***	S***	NS	NS	NS	-							
Jul-96	-0.005	S***	S***	NS	S*	NS	S***	-						
Aug-96	0.063	S***	S***	NS	NS	NS	NS	S***	-					
Sep-96	0.020	S***	S***	NS	NS	NS	NS	NS	NS	-				
Oct-96	0.029	S***	S***	NS	NS	NS	NS	NS	NS	NS	-			
Nov-96	-0.014	S***	S***	NS	S**	NS	S***	NS	S***	NS	NS	-		
Dec-96	0.002	S***	S***	NS	NS	NS	S***	NS	S***	NS	NS	NS	-	
Jan-97	-0.031	S***	S***	S***	S***	S***	S***	NS	S***	S*	S***	NS	NS	-

Table 1. Tukey test results from monthly *Enteromorpha* spp. growth without grazers. NS-not significant, S-significant (*$p<0.05$, **$p<0.01$, ***$p<0.001$)

		Jan-96	Feb-96	Mar-96	Apr-96	May-96	Jun-96	Jul-96	Aug-96	Sep-96	Oct-96	Nov-96	Dec-96	Jan-97
	slopes	-0.384	-0.305	0.034	0.076	0.127	0.070	-0.004	0.051	0.017	0.030	-0.017	-0.021	-0.001
Jan-96	-0.384	-												
Feb-96	-0.305	NS	-											
Mar-96	0.034	S***	S***	-										
Apr-96	0.076	S***	S***	NS	-									
May-96	0.127	S***	S***	S**	NS	-								
Jun-96	0.070	S***	S***	NS	NS	NS	-							
Jul-96	-0.004	S***	S***	NS	NS	S***	NS	-						
Aug-96	0.051	S***	S***	NS	NS	NS	NS	NS	-					
Sep-96	0.017	S***	S***	NS	NS	S***	NS	NS	NS	-				
Oct-96	0.030	S***	S***	NS	NS	S**	NS	NS	NS	NS	-			
Nov-96	-0.017	S***	S***	NS	S**	S***	S*	NS	NS	NS	NS	-		
Dec-96	-0.021	S***	S***	NS	S***	S***	S***	NS	NS	NS	NS	NS	-	
Jan-97	-0.001	S***	S***	NS	S*	S***	S*	NS	NS	NS	NS	NS	NS	-

Table 2. Tukey test results from monthly *Enteromorpha* spp. growth with grazers. NS-not significant, S-significant (*$p<0.05$, **$p<0.01$, ***$p<0.001$)

Table 3. Relative percentage of macrofaunal species inside the two types of experimental cages

Taxa	Genus and species
Molusca: Gastropoda, Bivalvia	*Hydrobia ulvae*-45 % *Cerastoderma edule*-1.7 %, *Scrobicularia plana*-3 %
Arthropoda: Crustacea Isopoda Amphipoda Decapoda	*Cyathura carinata*-0.5 %, *Sphaeroma* spp.-0.11 %, *Idotea* spp.-0.19 % *Melita palmata*-34.5 %, *Amphitoe* spp.-0.2 %, *Gammarus* spp.-0.1 % *Carcinus maenas*-10.3 %, *Crangon crangon*-3 %, *Palaemon* spp.-1.3 %

High precipitation occurred in winter and spring of 1996, which was accompanied by low salinity values, particularly, from January 1996 to May and again in December 1996 and January 1997 (Fig. 6). In fact, throughout 1996, salinity was strongly dependent on precipitation (Fig. 7).

Enteromorpha growth was positively correlated with salinity (F 0.05(2),11,11, r=0.61, P<0.05) (Fig. 8a) and negatively correlated with precipitation (F 0.05(2),11,11, r= -0.65, P<0.05) (Fig. 8b).

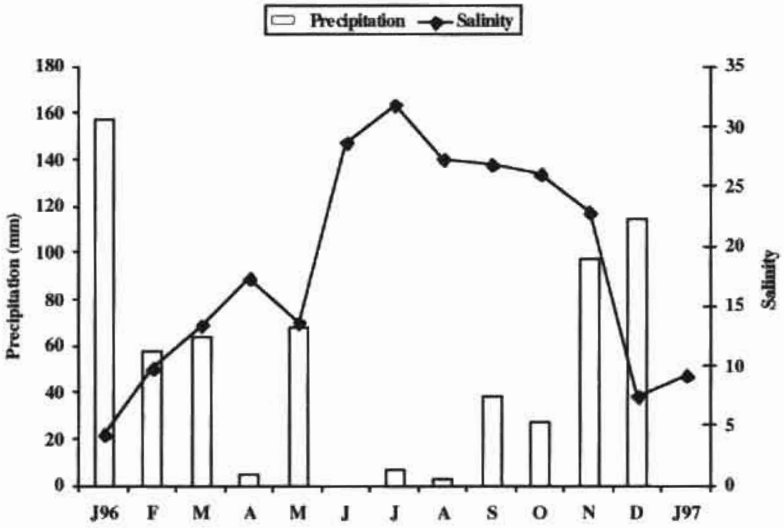

Figure 6. Variation of precipitation (mm) and salinity throughout the study period

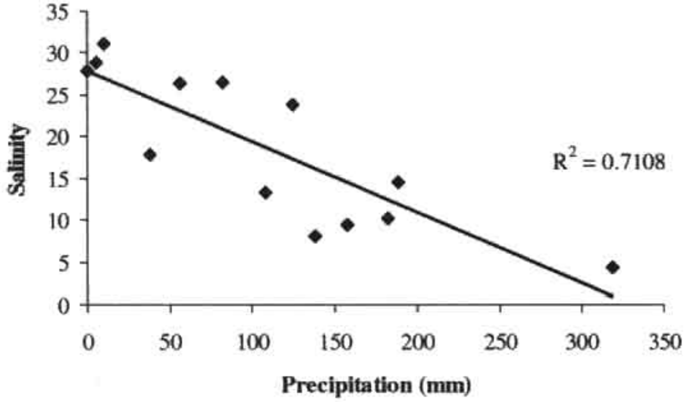

Figure 7. Relationship between salinity and precipitation (mm) in the Mondego estuary during 1996

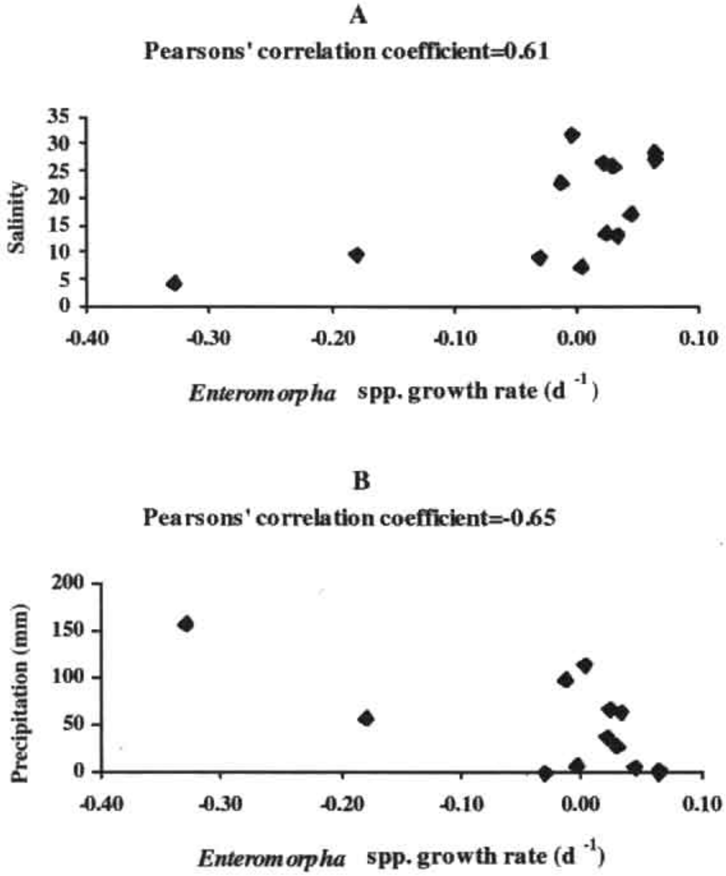

Figure 8. *Enteromorpha* spp. growth rate (d^{-1}) *versus* salinity (A) and *versus* precipitation (mm) (B).

Discussion

The yearly growth variation of *Enteromorpha* spp., over the study period, followed the typical variation of Ulvaceae populations in the Northern Hemisphere (e.g. Hull 1987, Sfriso 1995, Schories 1995, Hernández et al. 1997). During winter, Ulvales vanish or become reduced to few adult individuals in more sheltered areas, whereas in spring and summer macroalgal growth is enhanced, usually originating the development of significant amounts of biomass (Pregnall and Rudy 1985, Everett 1994, Schories 1995). However, while macroalgal populations from northern Europe usually start to grow in May (Schories and Reise 1993, Kolbe et al. 1995), in the Mondego estuary, *Enteromorpha* spp. started to grow in March. The earlier growth enhancement of *Enteromorpha* in the Mondego estuary probably reflects differences in light and temperature conditions between northern and southern Europe.

However, the quantified *Enteromorpha* growth rates (maximum values of 6 % and 13 % d^{-1} without and with grazers, respectively) are low when compared with other populations of Ulvales, some of them located further north. For example, in the Venice Lagoon, *Ulva* sp. presents growth rates of 23 % d^{-1} (Sfriso 1995), while in the Roskilde Fjord (Denmark), *Ulva* sp. growth may range between 4-20 % d^{-1} (Geertz-Hansen et al. 1993). In spite of an earlier improvement of temperature and light conditions, *Enteromorpha* growth in 1996 at the south arm of the Mondego estuary was comparatively low. On the other hand, the winter and spring of 1996 were quite rainy.

This situation is in agreement with the finding that, the amount of freshwater flowing through the south arm of the estuary is an important factor controlling macroalgal growth (Martins et al. 2001). The amount of freshwater in the south arm depends on precipitation and on river management practices. High freshwater discharge to the system causes significant decreases in salinity values and increases in the light extinction coefficient and in the water currents (Martins et al. 2001). Furthermore, because the freshwater is highly enriched in inorganic nitrogen, mostly nitrate (Pardal 1998, Martins 2000, Martins et al. 2001), it may also contribute for a potential P-limitation of primary producers. The combined effect of all these factors seems to determine *Enteromorpha* growth and standing crop in a given year (Martins et al. 1999, Martins et al. 2001).

In the winter and spring of 1996 precipitation was quite high, about 811 mm. On the other hand, the low salinity values quantified between January and May 1996 suggest that, the upstream sluices remained opened for long periods, which determined significant freshwater flow to the south arm of the estuary. This also agrees with the observed positive correlation between *Enteromorpha* growth and salinity and with the negative correlation between macroalgal growth and precipitation. In 1996, since it was a very rainy year and the sluices remained opened for long periods, salinity was strongly dependent on precipitation. Nevertheless, this is not always the case because it may rain and still the sluices may be kept closed (Martins et al. 2001).

The decrease in *Enteromorpha* spp. growth observed in July may be related with environmental conditions at that time of the year. Frequently, summer is reported as a nutrient limiting period of the year, which consequently may restrict macroalgal growth (e.g. Rivers and Peckol 1995, Pedersen 1995, Pedersen and Borum 1996). On the other hand, in lower latitudes, the limitation of macroalgal growth during summer has also been attributed to temperature and photon flux density (PFD), which may act synergistically to suppress the photosynthetic capacity of emersed macroalgae. (Pregnall and Rudy 1985, Rivers and Peckol 1995). Actually, desiccation stress has been suggested as the main cause of the summer decline of southern European populations of Ulvales (Hernández et al. 1997, Aníbal 1998). In the Mondego estuary, temperatures easily increase to 25°C during summer, while photon flux densities can reach 2000 µmol photon m^{2}.s^{-1} (Martins 2000). Considering that photosynthetic saturation of *Enteromorpha* spp. takes place between 500 and 1000 µmol photon m^{2}.s^{-1} (Shellem and Josselyn 1982, Beer and Shragge 1987), *Enteromorpha* photoinhibition may be a common process in the Mondego estuary during summer, especially during diurnal low tides. However, this process requires further investigation, since August growth rates were relatively high considering the obtained results.

In spring, *Enteromorpha* weight variation inside devices with grazers was more irregular than growth without grazers and, it seldom fitted a positive exponential model. This situation may be the result of some disturbance caused by the animals. On the other hand, the highest average growth rate of *Enteromorpha* spp. occurred within cages with grazers. Moreover, some of the animals (e.g. *Crangon crangon*, *Carcinus maenas* and Palaemonidae) found inside experimental devices are known to macerate and ingest *Enteromorpha* directly (Warwick et al. 1982). However, since such macroinvertebrates were found inside both types of experimental devices, it is not possible to draw conclusions relatively to the effects of grazers on *Enteromorpha* spp. growth.

Other studies, carried out in the south arm of the Mondego estuary (Pardal 1998, Pardal et al. 2000), have established clear relationships between the biomass of macroalgae and the abundance of some macroinvertebrate (e.g. *Amphitoe* spp., *Melita palmata*). The highest densitiy and biomass of such species was observed in the place where green macroalgae biomass was higher, which may reflect some kind of feeding dependency (Pardal 1998, Pardal et al. 2000). According with this and if indeed these anfipods graze on *Enteromorpha* spp. then, they can not ultimately prevent spring macroalgal blooms to take place. Perhaps that, as suggested by Valiela et al. (1997), the potential control of macroalgae by grazers is likely only in estuaries subject to low rates of N loading, which is not the case of the Mondego estuary.

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