



Hydrodynamics as a Major Factor Controlling the Occurrence of Green Macroalgal Blooms in a Eutrophic Estuary: A Case Study on the Influence of Precipitation and River Management

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Received 24 April 2000 and accepted in revised form 30 August 2000

Data on the variation of physicochemical parameters, biomass and growth of green macroalgae (mostly *Enteromorpha*) collected between January 1993 and January 1997 in the Mondego Estuary (western coast of Portugal) was analysed with the aim to identify the factors that control opportunistic macroalgal abundance in the system.

The annual biomass of *Enteromorpha* spp. is strongly dependent on the amount of fresh water that enters the system during winter and spring. In turn, the input of fresh water is regulated by precipitation and by river management practices. The optimization of the rice crops from the upstream valley depends on their water level, which determines the number of days and hours per day during which sluice gates remain open in winter and spring. River flow has significant impacts on salinity, N:P ratios, current velocities and light extinction coefficients within the system. The interaction of all these factors controls macroalgal growth and biomass loss processes.

In winters and springs during which sluice gates are often closed due to water deficiency of the rice fields (dry winter and spring or dry winter followed by rainy spring), little fresh water enters the system and consequently, salinity remains high, N:P ratios around 20, light penetration increases, and current velocities fall. These conditions facilitate macroalgal fixation, enhance their growth and spring blooms occur. On the contrary, during winters and springs when fresh water is in excess of rice fields' needs (rainy winters and springs), sluice gates remain open for long periods of time. High input of fresh water to the system causes salinity and light penetration to decrease, while N:P ratios and current velocities increase. These conditions contribute both to reduced *Enteromorpha* growth and higher loss of macroalgal biomass from the system to the ocean.

The present work shows that the inter-annual variation of macroalgal biomass in the Mondego Estuary is controlled by hydrodynamics, which in turn depends on precipitation and on river management, according with the water needs of the upstream rice crop.

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Keywords: eutrophication; *Enteromorpha*; hydrodynamics; river management; precipitation; rice crop

Introduction

Nowadays macroalgae constitute the dominant primary producers of most eutrophic temperate coastal systems (Geertz-Hansen *et al.*, 1993; Kolbe *et al.*, 1995; Sfriso, 1995; Peckol & Rivers, 1996; Hernández *et al.*, 1997; Valiela *et al.*, 1997; Flindt *et al.*, 1997a). Due to the complex and important links that macroalgae establish with other components within the system (e.g. seagrasses—Herman *et al.*, 1996; McClelland & Valiela, 1998; Lapointe *et al.*, 1994; Short *et al.*, 1995; Masini *et al.*, 1995; Koch & Beer, 1996; macrofauna—Raffaelli *et al.*, 1991; Lillebø *et al.*, 1999; Pardal *et al.*, 2000; wading birds—Múrias *et al.*, 1996, 1997; Lopes *et al.*, 2000;

sediment characteristics and composition—Neira & Rackemann, 1996; nutrient cycles—Viaroli *et al.*, 1992, 1993, 1996; Valiela *et al.*, 1997), it becomes essential to know which variables control macroalgal abundance and regulate their biomass. Although, these factors will differ from system to system, their identification at each coastal area will contribute to a deeper knowledge of coastal eutrophication and, possibly deal with this environmental problem by helping to find suitable mitigation measures.

The aim of this work was to identify the main factors controlling opportunistic macroalgal growth in the south arm of the Mondego Estuary and to understand how these factors regulate the yearly standing crop of macroalgal populations.

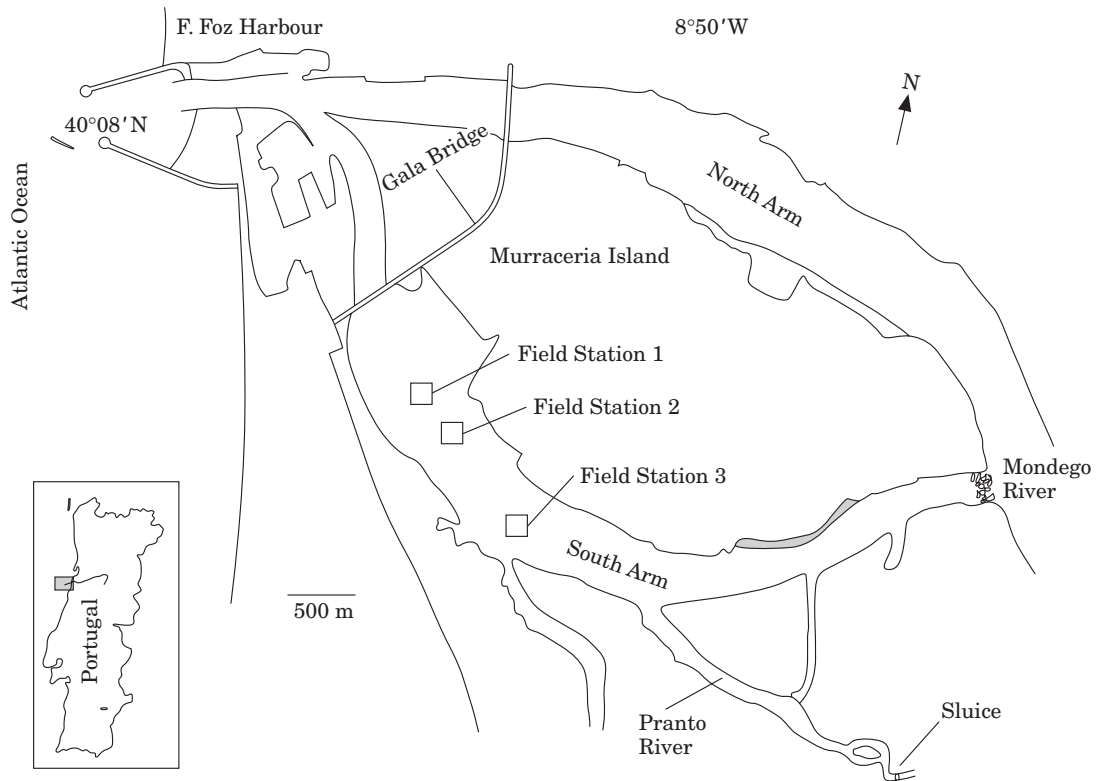


FIGURE 1. The Mondego Estuary with indication of the field stations along the south arm.

The Mondego Estuarine system and data available

Study site

The Mondego Estuary, located on the Atlantic coast of Portugal (40°08 N, 8°50 W), is about 7 km long, with an area of approximately 1072 ha of wetland habitats. The estuary consists of two different arms, north and south, separated by an alluvium-formed island (Murraceira Island) (Figure 1). The north arm is deeper (4–8 m during high tide, tidal range 1–3 m) and constitutes the main navigation channel and the location of the Figueira da Foz commercial harbour. Due to dredging activities in the north arm, related with harbour facilities, and to the fact that the south arm is almost silted up in its upper part, the river discharge flows predominantly through the north arm. As a consequence of the combined effects of fresh water discharge and tidal penetration, the north arm has higher daily salinity changes, and the bottom sediments consist mainly of medium to coarse sand (Marques *et al.*, 1993a). The south arm is shallower (2–4 m during high tide, tidal range 1–3 m), and due to siltation in its upstream section the water circulation is mostly dependent on the tides and the fresh water input from the Pranto River (Marques *et al.*,

1993b; Flindt *et al.*, 1997a). The discharge from the Pranto River is controlled by a sluice (Flindt *et al.*, 1997a; Pardal *et al.*, 2000), and is regulated according to the water needs in rice fields from the Pranto Valley. Due to fertilizers used in the rice crops (Anastácio *et al.*, 1999; Lillebø *et al.*, 1999; Pardal *et al.*, 2000; Martins, 2000), the freshwater discharge proceeding from the Pranto into the south arm also represents an important inorganic nutrient (mainly nitrogen) input to the system (Flindt *et al.*, 1997a). For a more detailed characterization of the system see also Pardal (1998), Marques *et al.* (1997, 1999).

Reference and monitoring studies

Previous work on the ecology of the Mondego Estuary was carried out throughout the 1980s (Marques & Nogueira, 1991; Marques *et al.*, 1993a, b). A major conclusion regarding structure and biodiversity of the macrobenthic communities was that the north arm constituted an impoverished sub-system in comparison with the south arm. This was attributed to a higher instability of the north arm sediments, mainly caused by dredging activities (Marques *et al.*, 1993b). The richest area in the system with regard to macrofaunal abundance and biodiversity was found to be the

Zostera noltii meadows located downstream of the south arm (Marques *et al.*, 1993a). As a whole, the south arm was considered less affected by human activities. It was nevertheless pointed out that, due to its natural features (shallowness, hydrodynamics) and to the discharge of inorganic nutrients from the Pranto River, it would also be more vulnerable to environmental stress (Marques *et al.*, 1993a, b). During the 1990s, eutrophication became a problem in the south arm and macroalgal blooms, especially of *Enteromorpha* spp., occurred repeatedly (Marques *et al.*, 1997; Flindt *et al.*, 1997a; Pardal, 1998; Lillebø *et al.*, 1999; Martins, 2000). The most abundant *Enteromorpha* species in the system are *E. intestinalis* (L.) Link and *E. compressa* (L.) Greville, which are found attached to small stones, empty shells, wood sticks or polychete tubes. Although *Enteromorpha* individuals are present throughout the year, macroalgal growing season starts in late winter and their maximal biomass usually occurs in spring. Summer is characterized by low macroalgal biomass and a second but smaller biomass peak may occur in early autumn (Pardal, 1998; Martins, 2000).

During the last decade the south arm of the Mondego Estuary has been almost continuously monitored with respect to: (a) environmental factors, namely inorganic nutrient concentrations in the water column (Marques *et al.*, 1997; Flindt *et al.*, 1997a; Lillebø *et al.*, 1999; Martins, 2000; Pardal *et al.*, 2000); (b) biomass variation and productivity of benthic primary producers (Martins, 2000; Pardal *et al.*, 2000); (c) population dynamics and production of macrofaunal key species (Marques *et al.*, 1994; Lillebø *et al.*, 1999; Pardal *et al.*, 2000); (d) seasonal and inter-annual variation of wading birds (Múrias *et al.*, 1996, 1997); (e) impacts of macroalgae blooms on macrofaunal communities and waders (Múrias *et al.*, 1996; Martins *et al.*, 1997; Lillebø *et al.*, 1999; Lopes *et al.*, 2000; Pardal *et al.*, 2000). This paper deals with the relationships between external abiotic variables and the growth and biomass of *Enteromorpha* spp. in the south arm of the estuary.

From January 1993 to December 1994, samples of macrophytes, macroalgae and associated macro-invertebrates were taken every 2 weeks and then monthly until September 1995 (except January 1995) at three places (stations 1, 2 and 3) (Figure 1) during low water tide (Pardal *et al.*, 2000). The choice of these places was related with the observation of a macroalgal coverage gradient in the south arm, increasing from downstream to upstream. Each time at each site, 6 to 10 cores (with a 143 cm² section) were taken from a depth of 15 cm. Each core was placed in a separate plastic bag and sieved within an

hour of sampling by washing it in estuarine water through a 500 µm mesh sieve. The residue (sediment, macrophytes, algae and animals) was placed into plastic bottles and preserved with 4% formalin in estuarine water. In the laboratory, all material was separated and processed (Pardal, 1998; Lillebø *et al.*, 1999; Pardal *et al.*, 2000). In the case of green macroalgae, individuals were separated by genus, dried (for 48 h at 60 °C) and ash free dry weight (AFDW) was assessed after combustion of samples for 8 h at 450 °C. Simultaneously, temperature (°C), salinity, dissolved oxygen (mg l⁻¹ and %) and pH data were measured *in situ* and water samples (approximately 250 ml) were collected for estimating dissolved inorganic nutrients (PO₄-P, NO₃-N, NO₂-N and NH₄-N). In the laboratory, water samples were filtered and analysed following Greenberg *et al.* (1992) procedures for orthophosphate and N-compounds.

From January 1996 to January 1997, monthly growth experiments with *Enteromorpha* spp. were conducted in the estuary at station 3 where, in favourable years macroalgal accumulation tends to be higher. Macroalgae were kept inside semi-cylindrical plexiglass devices surrounded laterally and on the bottom by 500 µm calibrated net. This type of device allowed light penetration and water circulation inside and prevented, at the same time, grazers from entering (Martins, 2000). In each experiment, 20 healthy *Enteromorpha* individuals were collected in the field, washed carefully with estuarine water and weighed (initial wet weight) after the excess of water had been removed. Then, macroalgae were taken to the field inside the plexiglass devices, which were fixed by ropes to wooden sticks buried in the sediment. Groups of five replicates were removed from the field after 5, 10, 15 and 20 days and weighed to final wet weight. Monthly growth rates were estimated as the slopes of fitted regressions, after ln transformation of data considering an exponential growth model (Sokal & Rohlf, 1996). At the same time in stations 1 and 3, physicochemical parameters were measured and water samples collected, following the procedure previously described.

From June 1993 to May 1994, information on the daily number of hours during which sluice gates were opened was provided by the rice farmers. In the same period, during some of the days when the sluice gates were opened, current velocities were measured at the inlet (immediately after the sluice) and the outlet of the south arm (immediately after the Gala Bridge) (Figure 1) at different depths. Additionally, River Pranto discharge were calculated taking in consideration current velocities and the

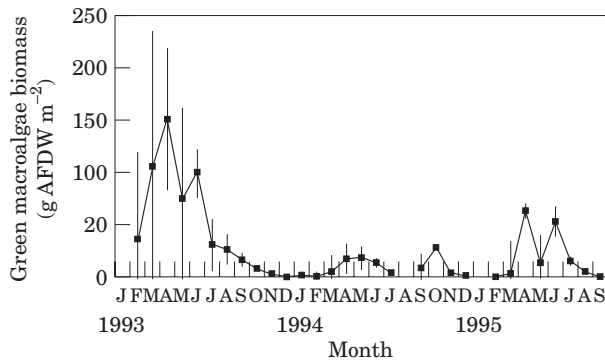


FIGURE 2. Average green macroalgal biomass (g AFDW m^{-2}) \pm standard error (SE) at the three field stations from 1993 to 1995. *Enteromorpha* spp. constituted 85% of total green macroalgal biomass.

section of the river. Data on tidal amplitude were collected from a tide table provided by the Portuguese Harbour Institute.

During 1997, four seasonal 24 h cycles (one per season) were carried out at station 3 and hourly measurements of physicochemical parameters were performed, including PFD (photon flux density, μ moles photons $m^{-2} s^{-1}$) which was measured at the surface and at the maximum depth. Using these data the light extinction coefficient was calculated through Beer's law:

$$I_z = I_0 \times e^{-kz}$$

where I_z is light intensity (light units) at depth z (depth units), I_0 is light intensity at the surface (light units) and k is the light extinction coefficient (depth units $^{-1}$), solved to the form:

$$k = \frac{\ln I_0 - \ln I_z}{z}$$

Data on precipitation were obtained from the Geophysics Institute of the University of Coimbra and concern precipitation values at the City of Coimbra (located about 40 km east of the Mondego Estuary).

Results

Green macroalgal biomass and growth

Throughout the entire period of macroalgal sampling (1993–1995), *Enteromorpha* spp. represented more than 85% of the total biomass of green macroalgae and important inter-annual variations were detected (Figure 2). In 1993, the average green macroalgal biomass in the south arm was about

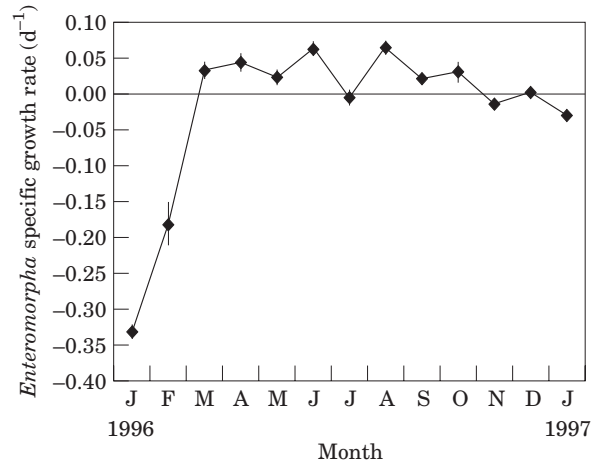


FIGURE 3. Monthly *Enteromorpha* spp. growth rates (d^{-1}) \pm standard error (SE) ($N=25$) estimated from January 1996 to January 1997 at station 3.

149 g AFDW m^{-2} , while in 1994, it attained only 26 g AFDW m^{-2} . In spring 1993, the maximum biomass of macroalgae (409 g AFDW m^{-2}) was detected in station 3, while in 1994, the maximum value (49 g AFDW m^{-2}) was registered in station 2. In the spring of 1995 (March–June), the average macroalgal biomass (33 g AFDW m^{-2}) was intermediate between spring (March–June) average biomass in 1993 and in 1994 (Figure 2) and similar values were detected in station 2 and 3.

During 1996, no significant spring *Enteromorpha* bloom was observed in the south arm of the Mondego Estuary (personal observation) and *Enteromorpha* growth rates ranged from negative values, during winter and autumn, to a maximum of 6% day $^{-1}$ in June and August (Figure 3).

NO₂-N, NO₃-N, NH₄-N, PO₄-P and N:P variation

Dissolved inorganic nutrients are monthly averages from station 1 and 3, the two places where water samples were almost continuously collected from January 1993 to January 1997.

Throughout the study period, the variation of NO₂-N, NO₃-N in the water column followed a similar yearly pattern, usually with higher concentrations in autumn and winter, and lower concentrations in spring and summer (Figure 4). However, the relationship between NO₂-N+NO₃-N and precipitation is not always direct, as could be seen in spring 1993 (Figure 4). In spite of the significant precipitation in April and May, the amount of nitrite and nitrate did not increase in the system. On the contrary, the Pranto River discharge, which expresses

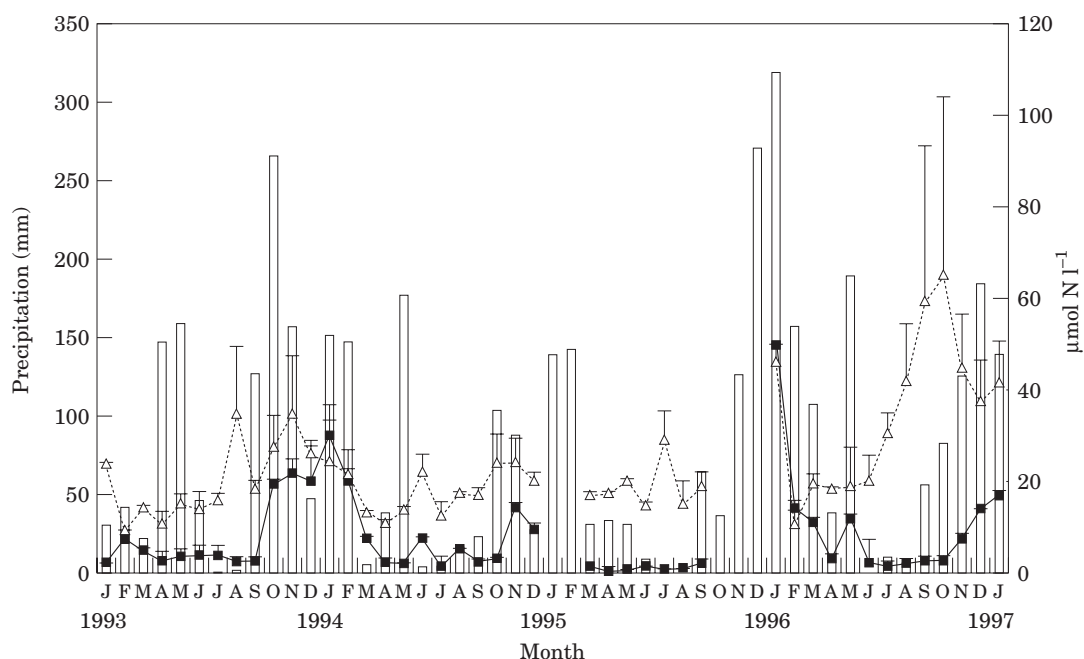


FIGURE 4. Variation of precipitation (mm), nitrite+nitrate and ammonium ($\mu\text{mol N l}^{-1}$) + 1 SE in stations 1 and 3 between January 1993 and January 1997. Bars: precipitation; squares: $\text{NO}_2\text{-N} + \text{NO}_3\text{-N}$; triangles: $\text{NH}_4\text{-N}$.

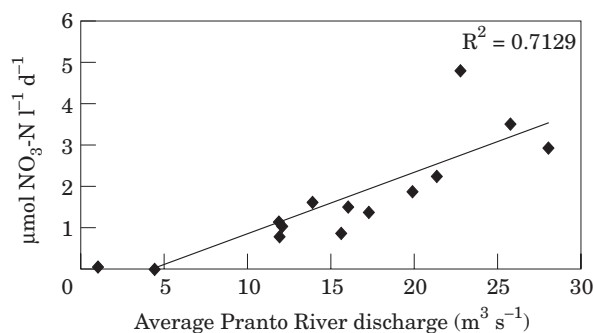


FIGURE 5. Relationship between Pranto River discharge ($\text{m}^3 \text{s}^{-1}$) and nitrate concentration of the water ($\mu\text{mol NO}_3\text{-N l}^{-1} \text{d}^{-1}$) at the inlet, immediately after sluice gates ($N=14$, $R^2=0.71$).

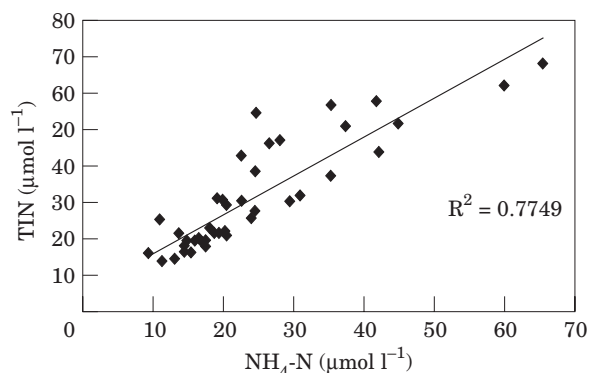


FIGURE 6. Relationship between ammonium and total inorganic nitrogen concentrations ($\mu\text{mol N l}^{-1}$) in the south arm of Mondego Estuary ($N=43$, $R^2=0.77$).

directly the amount of fresh water entering the system, is highly correlated with $\text{NO}_3\text{-N}$ concentration at the inlet (immediately after the sluice) (Figure 5).

$\text{NH}_4\text{-N}$ variation did not show any clear relationship with precipitation and values tend to increase from summer until autumn and early winter (Figure 4). $\text{NH}_4\text{-N}$ variation was highly and positively correlated with total inorganic nitrogen (Figure 6), which reflects the important contribution of ammonium to the total inorganic nitrogen concentration in the south arm of the estuary.

Throughout the study period, the highest concentrations of $\text{PO}_4\text{-P}$ occurred mostly during summer

(Figure 7). As suggested by Figure 8, in the system the efflux of phosphorus from sediments to the water column is related with temperature.

Although N:P ratios usually increased with precipitation (Figure 9), reflecting the increase in $\text{NO}_2\text{-N}$ and $\text{NO}_3\text{-N}$ in the system, the relationship between the two parameters is not direct (Figure 10). This is in agreement with the fact that, sometimes the occurrence of precipitation is not translated in fresh water input to the system (as in spring 1993) and the increase in $\text{NH}_4\text{-N}$, the major contributor to TIN in the system, is not dependent on precipitation. Additionally, the inverse relationship between N:P

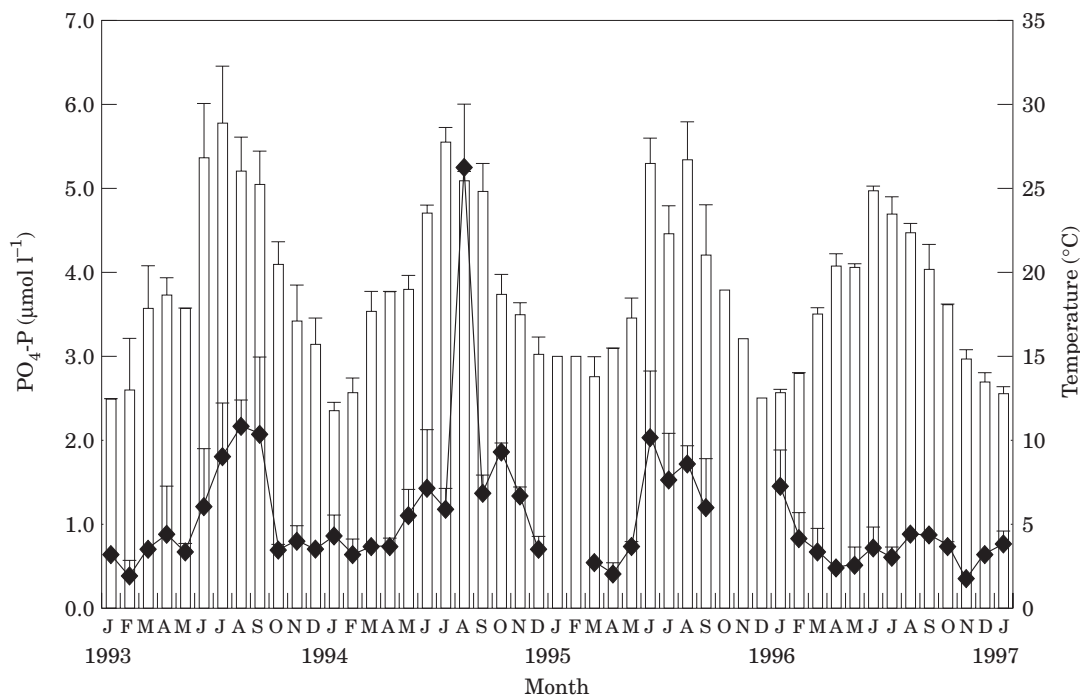


FIGURE 7. Variation of temperature ($^{\circ}\text{C}$) and orthophosphate ($\mu\text{mol PO}_4\text{-P l}^{-1}$) + 1 SE in stations 1 and 3 between January 1993 and January 1997. Bars: temperature; diamonds: $\text{PO}_4\text{-P}$.

ratios and salinity (Figure 11) suggests that whenever salinity decreases, N:P ratios increase. The decrease of salinity depends on the amount of fresh water input from the river as explained next.

Salinity variation

During periods with significant precipitation like October–December 1993, January–February 1994, January–February 1995 and the end of 1995 and the beginning of 1996, salinity dropped to less than 20, reaching sometimes values equal or lower than 5

(Figure 12). However, the dependency of salinity on precipitation is not direct, for instance, in April–May 1993 and in October–November 1994, the increased precipitation was not followed by a decrease of salinity (Figure 12). This is related with river management practices. If the upstream rice fields have a water-deficit, the sluice gates are kept closed even if it is raining. Thus, considering data from the whole period of study, the variation of salinity is not clearly related with precipitation [Figure 13(a)]. On the contrary, in a wet year such as 1996, the correlation between salinity and precipitation is high and inverse [Figure 13(b)] because in this situation, sluice gates are often opened to avoid rice fields being flooded.

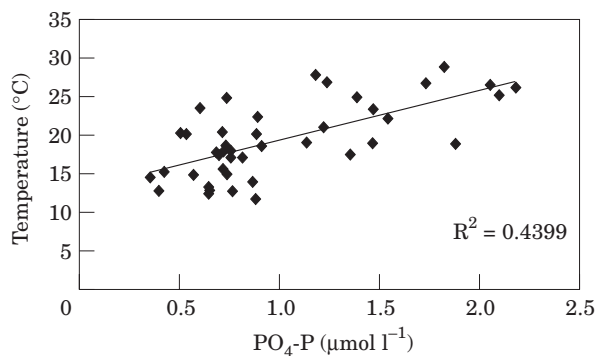


FIGURE 8. Relationship between orthophosphate ($\mu\text{mol PO}_4\text{-P l}^{-1}$) and temperature ($^{\circ}\text{C}$) in the south arm of the Mondego estuary ($N=43$, $R^2=0.44$).

Sluice management, Pranto River discharge and current velocities

The variation of the number of hours per day during which the sluice gates remained opened from October 1993 to May 1994, and the daily precipitation variation in the same period, suggest that sometimes there is a time lag between the occurrence of precipitation and the opening of the sluice gates and that, when precipitation stops, sluice gates remains open for a longer period (Figure 14). From October to December 1993, the average number of hours during which the sluice gates remained opened was

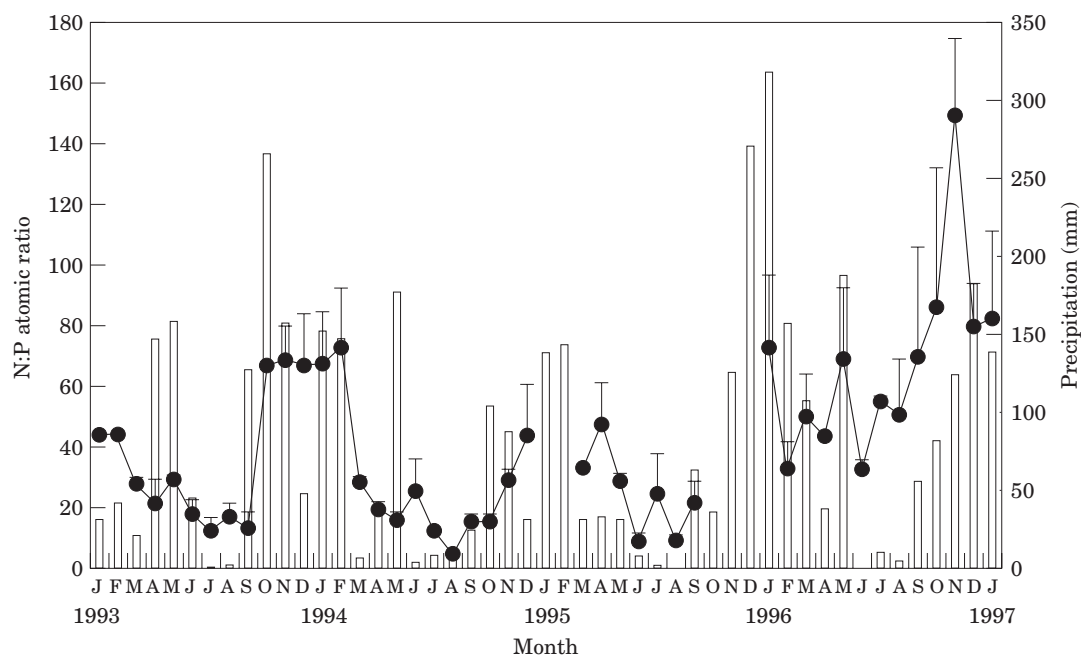


FIGURE 9. Variation of precipitation (mm) and N:P atomic ratio of the water +1 SE in stations 1 and 3 between January 1993 and January 1997. Bars: precipitation; circles: N:P.

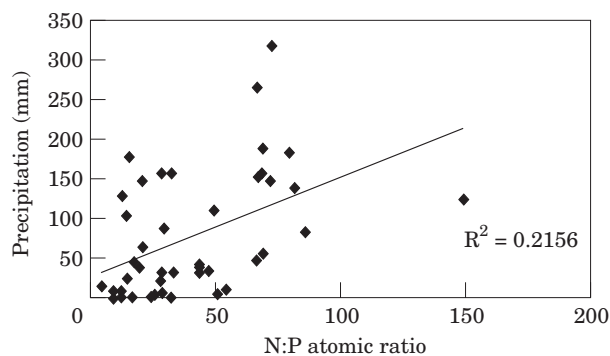


FIGURE 10. Relationship between N:P atomic ratio and precipitation (mm) in the south arm of Mondego Estuary ($N=44$, $R^2=0.22$).

correlated with average daily precipitation, but that situation changed during 1994. In March 1994, the amount of precipitation was very low and yet the sluice gates opened almost every day, with an average of 6 h per day. In April 1994, a dry month, the sluice was almost always closed, even during the precipitation in late April. The significant precipitation during middle and late May 1994 was, however, followed by intensive sluice gate opening. The average number of hours per day during which the sluice gates remained opened was negatively correlated with salinity (Figure 15). Additionally, although sluice gates might be kept open in periods of low precipitation (like March 1994), the Pranto River discharge differs

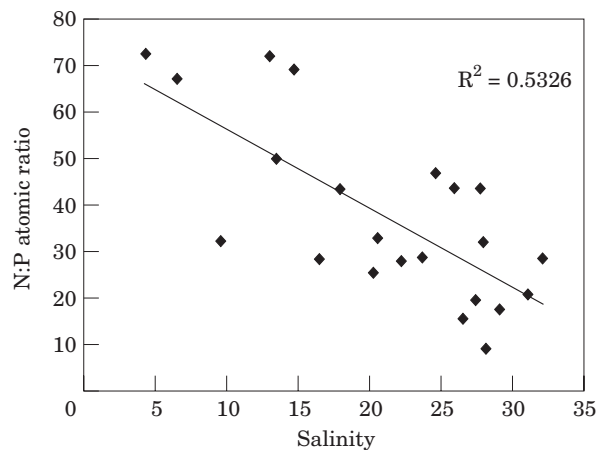


FIGURE 11. Relationship between salinity and N:P atomic ratio in the south arm of Mondego Estuary between January and June (winter/spring) 1993–1996 ($N=22$, $R^2=0.53$).

between periods of low and periods of high precipitation (Figure 16). According to our results, there is a direct relationship between maximal current velocities and tidal amplitude, and for the same tidal amplitude, current velocities are higher when sluice gates are opened (Figure 17).

Light extinction coefficient variation

Average values of light extinction coefficient were estimated during the seasonal 24 h cycles, which did

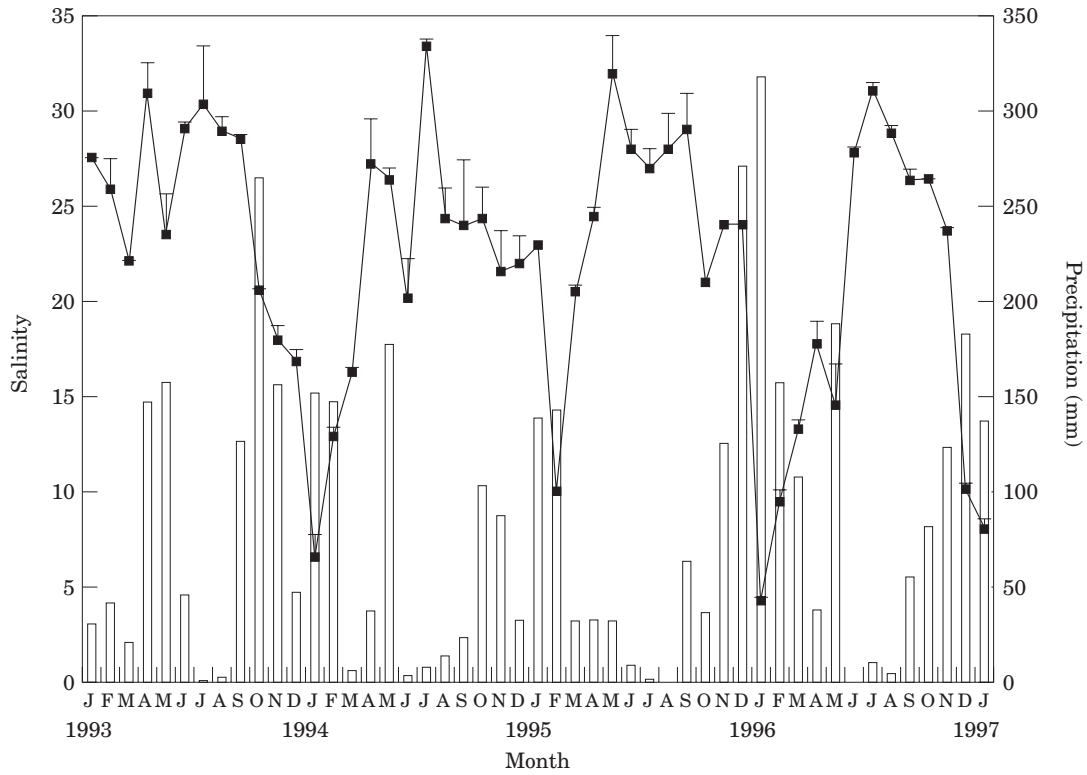


FIGURE 12. Variation of precipitation (mm) and salinity+1 SE in stations 1 and 3 between January 1993 and January 1997. Bars: precipitation; squares: salinity.

not correspond to typical season days. For example, the winter cycle was carried out in a dry day preceded by a dry period (0 mm=cumulative precipitation for the period of 1-week before sampling) with high PFD (Martins, 2000). The importance of these results remains in the fact that, the average light extinction coefficient estimated in autumn (cumulative precipitation=75.8 mm) was about 5.59 m^{-1} , while winter, spring and summer averages (cumulative precipitation=0, 40.8 and 0 mm, respectively) were 1.55, 1.99 and 1.92 m^{-1} , respectively (Figure 18).

Green macroalgal biomass and salinity

The relationship between green macroalgal biomass and salinity is not direct. In summer when salinity is higher (>25), macroalgal biomass is usually very low (Figure 19). However, in winter–spring (February–June) with higher salinity, green macroalgal biomass is also higher, as suggested by the exponential increase of macroalgal biomass with salinity (Figure 20).

Discussion

The results suggest that, in the south arm of the Mondego Estuary, the growth and production of

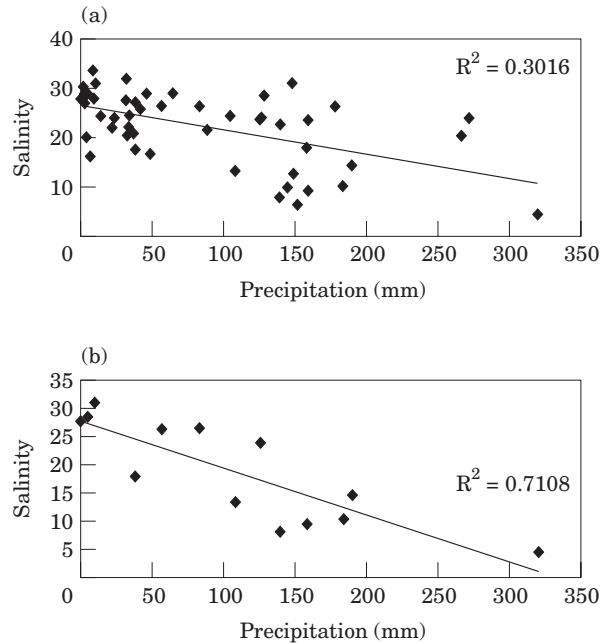


FIGURE 13. Relationship between precipitation (mm) and salinity in the south arm of the Mondego Estuary, (a) throughout the entire study period ($N=49$, $R^2=0.30$), (b) only in 1996, the most rainy year of the study period ($N=13$, $R^2=0.71$).

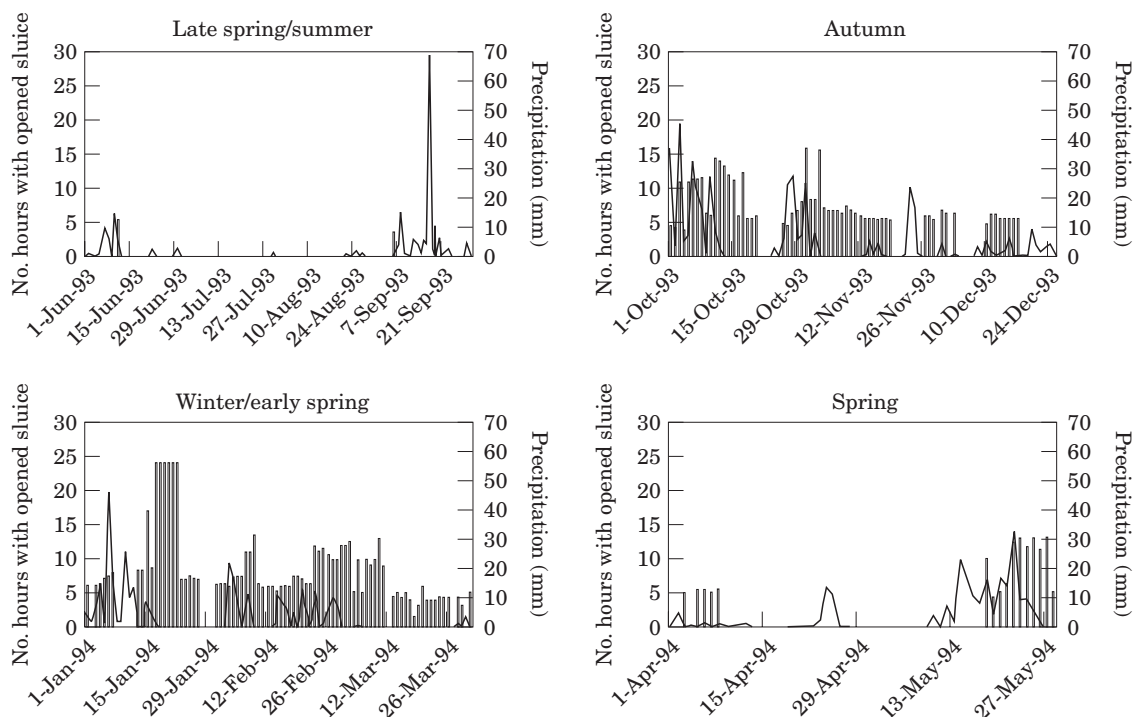


FIGURE 14. Number of hours during which sluice gates were opened (column) and precipitation (line) during late spring/summer (June–September 1993), autumn (October–December 1993), winter/early spring (January–March 1994) and spring (April–May 1994).

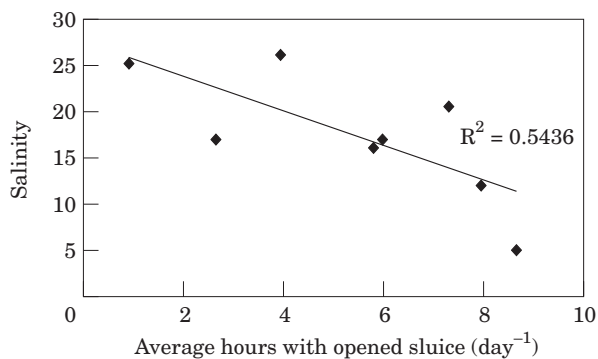


FIGURE 15. Relationship between the average number of hours during which sluice gates were opened (day⁻¹) and salinity in the south arm of the Mondego Estuary.

green macroalgae (especially *Enteromorpha*) depends on the amount of fresh water entering the system in late winter and spring. In turn, the amount of fresh water entering the system varies according with both precipitation and river management practices. In years with dry winters and springs, the upstream rice fields get water deficient and rice farmers keep the sluice gates closed. The same situation occurs in a rainy spring preceded by a dry winter, such as 1993. In spite of the spring rain, sluice gates were mostly closed, in

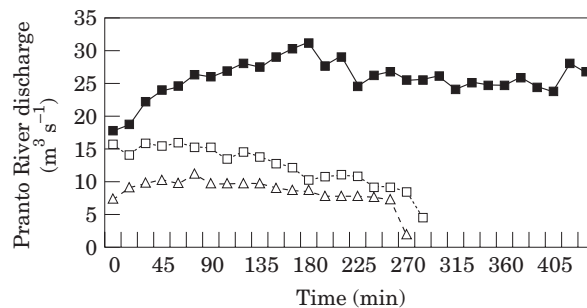


FIGURE 16. Pranto River discharge (m³ s⁻¹) in three different days in 1994: 18 January—high precipitation, 11 March—no precipitation, 26 May—high precipitation after a dry period. Closed squares: winter—high precipitation; open squares: spring—precipitation after a dry period; open triangles: spring—no precipitation.

order to re-establish the necessary water level in rice fields. From March to September, the Pranto valley rice fields must keep a constant level of water to optimize the annual rice crop (Anastácio *et al.*, 1999). Thus, in rainy winters and springs, the sluice gates remain open for long periods and several hours per day, allowing the excess of fresh water to flow from the valley into the south arm.

The quantity of fresh water flowing in the south arm will then determine the variation of other abiotic

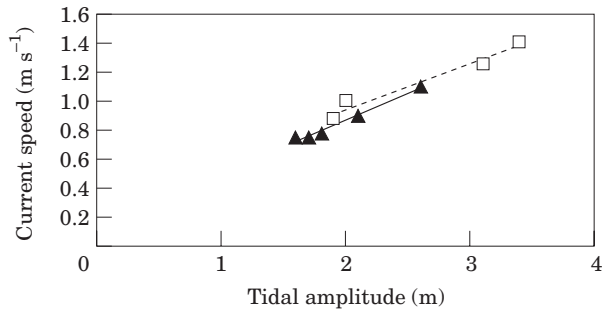


FIGURE 17. Variation of current velocity (m s^{-1}) with tidal amplitude (m) with opened sluice gates ($N=4$, $R^2=0.96$) and with the closed sluice gates ($N=5$, $R^2=0.98$). Squares: opened sluice; triangles: closed sluice.

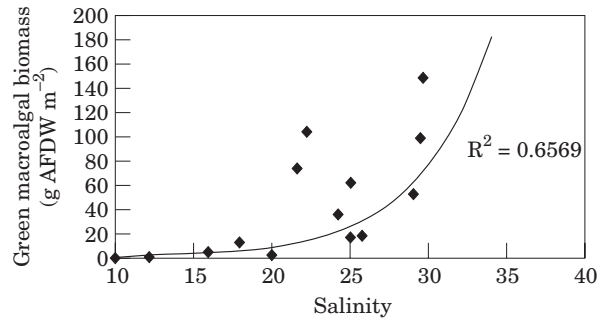


FIGURE 20. Relationship between salinity and green macroalgal biomass (g AFDW m^{-2}) in the Mondego Estuary between January and June (winter/spring) of 1993–1995 ($N=16$, $R^2=0.66$).

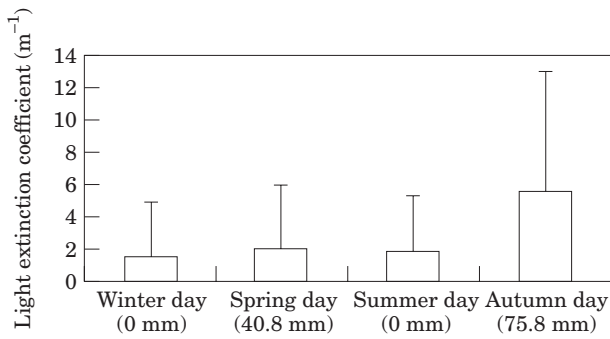


FIGURE 18. Average light extinction coefficients (m^{-1}) of the water column estimated in the days when seasonal cycles were carried out. Bars are 95% confidence interval for means and N (winter)=6, N (spring)=5, N (summer)=9 and N (autumn)=6. The numbers in brackets represent the cumulative precipitation of 1-week before measurements.

variables. Salinity is negatively correlated with the number of hours during which sluice gates remains open, thus salinity remains high (≥ 20) when the river flow is low such as in winter/spring of 1993 and 1995 (except January 1995) and falls to less than 15, whenever river flow increases significantly. Sometimes, average salinity may reach extremely low values (≤ 5), such as in January 1994 and January 1996. The input of fresh water to the system also contributes to N-enrichment of the water column, as suggested by the relationship between Pranto River discharge and $\text{NO}_3\text{-N}$ concentration. The increase in $\text{NO}_3\text{-N}$ and $\text{NO}_2\text{-N}$ together $\text{NH}_4\text{-N}$ concentration, which constitutes the main contributor to TIN in the system, contributes to the occurrence of very high N:P ratios

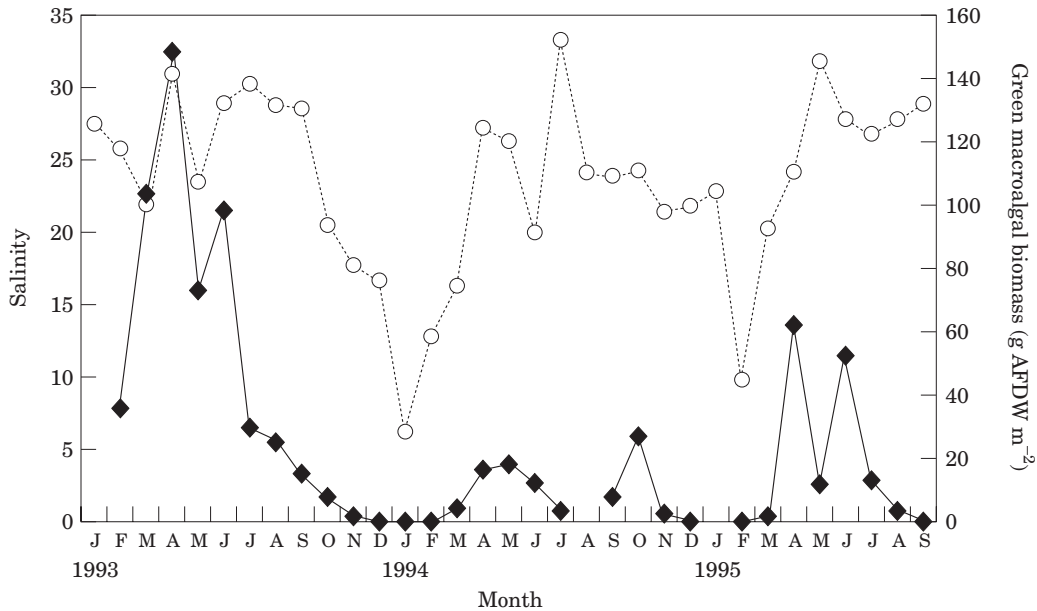


FIGURE 19. Variation of green macroalgal biomass (g AFDW m^{-2}) and salinity from January 1993 to September 1995 in the south arm of the Mondego Estuary. Circles: salinity; diamonds: biomass.

in the water column during periods of significant river flow. This is also suggested by the tendency to increased N:P ratios with decreased salinity (Figure 11). In a shallow and mesotidal environment, such as the south arm of the Mondego Estuary, water-flow velocity depend both on tidal amplitude and on the input of fresh water and, naturally that for the same tidal amplitude, water-flow velocity is higher whenever more fresh water is entering the system, as suggested by Figure 17. Additionally, light extinction coefficients will be higher whenever water flow rises due to significant re-suspension of sediments.

It is the variation of these abiotic factors that controls opportunistic macroalgal growth and biomass in the south arm of the estuary. The present results suggest an exponential increase of green macroalgal biomass with salinity until 30. The increase of macroalgal biomass with salinity agrees with a previous work (Martins *et al.*, 1999), which tested *Enteromorpha intestinalis* growth response along salinity gradients. Although *E. intestinalis* growth increased with salinity, the optimum range was 17–22 and then growth decreased with the rise of salinity. Nevertheless, *E. intestinalis* growth was lower at low salinity than at high salinity. This may also explain the low spring growth rates of *Enteromorpha* spp. (6% day⁻¹) obtained in 1996, when salinity was kept quite low (average salinity between January–June 1996=14). There is some evidence that green macroalgae accumulate detrimental polyamines (such as putrescine and spermidine) when submitted to hyposaline stress (Lee, 1998), which might explain their lower growth rates.

The occurrence of high N:P ratios in the water column might suggest that primary production is P-limited (Valiela, 1995). In the case of green macroalgae, such as *Enteromorpha* and *Ulva*, they can store both N and P (Fujita, 1985; Björnsäter & Wheeler, 1990; Poole & Raven, 1997) and their growth rate is considered to be dependent on internal nutrient concentrations (Björnsäter & Wheeler, 1990; Bendoricchio *et al.*, 1994; Solidoro *et al.*, 1997), while their uptake rates depend on the difference between internal nutrient concentration in macroalgal cells and external nutrient concentration in the water. Due to these mechanisms, there are time lags between low water column nutrient concentrations and the onset of nutrient-limited growth (Björnsäter & Wheeler, 1990; Poole & Raven, 1997), therefore, instantaneous water column concentrations are not suitable for establishing nutrient availability of macroalgae (Fujita, 1985). However, since in the south arm of the estuary, N:P ratios can remain high for significant periods of time (e.g. October–December 1993, throughout 1996) and

show a tendency to increase whenever river flow increases, it is possible that there is a potential for phosphorus limitation of primary producers in certain periods of the year.

Increased current velocities enhance the export of free-floating materials from the system to the ocean. In the case of macroalgae, it has been argued that advective transport is a significant mechanism in controlling their biomass, especially of the free-floating species like *Ulva* sp. (Salomonsen *et al.*, 1999). The transport of free-floating macroalgae (*Ulva* sp. and *Chaetomorpha* sp.) was linearly correlated with current velocity (Flindt *et al.*, 1997b) and, apparently significant amounts of macroalgal biomass can be lost due to export mechanisms (Hernández *et al.*, 1997; Flindt *et al.*, pers. comm.). In the case of *Enteromorpha*, in spite of their ability to fix to substrata on the sediment, it can not completely resist the water-flow. Strong tidal currents erode the attachment of *Enteromorpha* or tear away their fronds once they reach a critical length (Lowthion *et al.*, 1985). Such evidence was found in Langstone Harbour (U.K.), where maximum current velocity is about 1.22 m s⁻¹ (Lowthion *et al.*, 1985). In the south arm of the Mondego Estuary, where current velocity can reach 1.4 m s⁻¹, the loss of *Enteromorpha* biomass by export may thus constitute an important mechanism.

Increased light extinction coefficients caused by high turbidity of the water column contribute to decrease the amount of light available for photosynthesis. Because the south arm of the estuary is a shallow area and most of the flats where macroalgae proliferate are intertidal, light-limitation may not be an issue during low-tide hours, when intertidal flats are immersed. However, the amount of suspended matter in the water column will influence photosynthetic rates during high-tide hours and, as a result, macroalgal growth will certainly be lower whenever water-flow velocity is higher.

The processes described here seem to explain the significant inter-annual variation of macroalgal standing crop in the eutrophic system constituted by the south arm of the Mondego Estuary. Furthermore, the present results show that the annual productivity of *Enteromorpha* spp. is strongly dependent on the weather conditions and the river management practices during winter and spring. These mechanisms are summarized in Table 1.

This work shows how the onset of opportunistic macroalgal blooms in an estuarine system is dependent on precipitation and on water-management practices in upstream agricultural lands.

The dependency of macroalgal production on hydrodynamics also determines that during periods of

TABLE 1. Summarized description of the variation of the main factors controlling green macroalgal growth and production during spring in the south arm of the Mondego Estuary. The variation of these factors depends both on precipitation and on river management practices according with the water needs of the upstream rice fields

	Dry winter and/or spring	Rainy winter and spring
Sluice gates (river management)	Closed	Opened
Salinity	High	Low
TIN	Low	High
N:P	Near 16	High
Light extinction coefficients	Normal for shallow estuaries	
Water-flow velocity	Low	High
Green macroalgal growth	High	Low

high river-flow, important amounts of nutrients, especially $\text{NO}_3\text{-N}$, are rapidly exported to the ocean. When river-flow decreases, nutrients can remain for longer periods in the system and become incorporated in macroalgal tissues, which act as seasonally important nutrient sinks of the ecosystem.

Acknowledgements

We thank the Portuguese Foundation for Science and Technology (FCT) which supported this work through a Ph.D. grant to I. Martins, and EU projects 'MUST—Marine Universal Structural Model' and 'WET—Wetland Ecology and Technology'.

The authors are indebted to all colleagues that assisted in field and laboratory work and, especially, to P. Maranhão for allowing us to use his salinity data from 1995.

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