ECSA39

Spartina maritima influence on the dynamics of the phosphorus sedimentary cycle in a warm temperate estuary (Mondego estuary, Portugal)

Ana Isabel Lillebø · J. P. Coelho · M. R. Flindt · H. S. Jensen · J. C. Marques · C. B. Pedersen · M. A. Pardal

© Springer Science+Business Media B.V. 2007

Abstract During the last decades the Mondego estuary has been under severe ecological stress mainly caused by eutrophication. In this salt march system, *Spartina maritima* covers about 10.5 ha of the intertidal areas. The objective of the present study was to evaluate the effect of *Spartina maritima* marshes on the dynamics of phosphorus (P) binding in the surface sediment. We compare phosphate and oxygen fluxes,

Guest editors: M. J. Costa, H. Cabral & J. L. Costa Towards an integrated knowledge and management of estuarine systems

A. I. Lillebø (⊠) · J. P. Coelho · J. C. Marques · M. A. Pardal

IMAR – Institute of Marine Research, Department of Zoology, University of Coimbra, 3004-517 Coimbra, Portugal

e-mail: lillebo@dq.ua.pt

A. I. Lillebø · J. P. Coelho CESAM – CESAM-Centre for Environment and Marine Studies, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal

M. R. Flindt · H. S. Jensen Institute of Biology, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark

C. B. Pedersen

Freshwater Biological Laboratory, University of Copenhagen, Helsingørgade 51, DK-3400 Hillerød, Denmark

P-adsorption capacity, phosphate concentrations and total amount, and the extractable P forms in the upper 20 cm of sediment in vegetated sediment with adjacent mudflats without vegetation. Sediment pore-water profiles followed a clear trend, with lower P concentrations in more superficial layers, and increasing with depth. The vegetated mudflats presented lower concentrations of dissolved inorganic phosphorus than adjacent bare bottom mudflats, lower phosphate total amount, as well as higher P-adsorption capacity. Results from the extraction procedure show that the superficial layers are the most important for estuarine phosphorus dynamics, since maximum concentrations of labile P pools are present here. In contrast, higher proportions of refractory P pool are found in deeper layers. Spartina marsh sediments had less total P, less iron bound P, and less exchangeable P than adjacent bare bottom mudflats. Also the pool of loosely sorbed P is lower in the Spartina marsh. Phosphate regeneration from the sediment to the overlying water was only 11.8 kg ha⁻¹ year⁻¹ in vegetated sediment while 25.8 kg ha⁻¹ year⁻¹ in the bare mud flat. Plant uptake for growth combined with an enhanced P-adsorption capacity of the sediment, may explain these differences. Therefore, Spartina marshes are very important agents in the sedimentary P cycle worldwide, and can be considered a useful management tool in estuarine ecosystem recovery efforts.

Keywords Spartina maritime · Phosphate fluxes · Phosphorus speciation · Sediment–water interactions · Estuary

Introduction

Worldwide, the reduction of salt marsh areas, as a result of anthropogenic disturbance is of major concern, and several studies on the ecology of estuaries have emphasized the negative consequences of its disappearance. As well, eutrophication of shallow coastal areas has led to a decline in environmental quality, particularly through the replacement of perennial benthic macrophytes by fast-growing opportunistic algae (epiphytic green macroalgae and/ or phytoplankton).

The Mondego estuary is about 7 km long and is 2-3 km across at its widest part, and is comprised of two arms, a northern, and a southern, separated by the Murraceira Island. The northern arm is deeper (± 10 m during high tide, tidal range 0.5-3.5 m), and is the main navigation channel and the location of the Figueira da Foz harbor. The southern arm is shallower (2-4 m during high tide), and is characterised by large areas of intertidal flats exposed during low tide. During tidal ebbing, ephemeral tide pools may cover a considerable percentage of the intertidal area. These tidal pools may vary from some square centimetres to a few square metres. During emersion of the tidal flats important biogeochemical processes take place in these ephemeral pools as a result of anabolic/catabolic balances, and of a combination of shallow water and enhanced temperature (Flindt et al., 2002; Lillebø et al., 2002, 2004).

In this system, the anthropogenic activities coupled to favourable physical characteristics (high water residence time and shallowness) and climate conditions (low precipitation) have imposed a high environmental pressure resulting in a eutrophication process (e.g. Martins et al., 2001; Dolbeth et al., 2003; Marques et al., 2003; Cardoso et al., 2004; Pardal et al., 2004; Ferreira et al., 2005). Until 1998, the sedimentation of suspended particles increased the phosphorus content in the sediments, which served as a sink for a substantial phosphorus loading. After the implementation of management measures in 1998 the nutrient loading to the system was reduced and the hydrodynamics improved (Ferreira et al., 2005). Yet, after the sedimentation of particles, dissolved phosphate may be released from the sediment particulate organic matter by P-mineralization and P-desorption, and thereby supply the efflux of phosphate to the water column (Flindt et al., 1999; Coelho et al., 2004; Lillebø et al., 2004). Thus, ecological stress may still persist due to internal Ploading (Coelho et al., 2004) in a similar manner to that known for shallow lakes (e.g. Jensen and Andersen, 1992) and temperate estuaries (Holmboe et al., 1999).

Salt marsh plants are able to aggregate sediment by acting as sediment traps for macroalgae and detritus, and their interactions with the surrounding sediment may promote chemical changes at the rhizosphere level, such as increase in the oxidation level, enhancement of the accretion of metals, and lowering of the concentrations of dissolved nutrients (e.g. Vale et al., 1990; Warren and Niering, 1993; Christensen & Andersen, 1996; Sánchez et al., 2001; Flindt et al., 2002).

Spartina maritima (Curtis) Fernald, 1916 is a rhizomatous grass with a continuous but very slow growth (Adams and Bate, 1995) that is forming extensive monotypic stands in temperate systems (Sánchez et al., 1997). These flood-tolerant plants have the ability to transport oxygen to the belowground parts down to a depth of 20 cm, into otherwise impermeable sediments, through a welldeveloped aerenchyma. There it is used for root respiration and oxidation of the rhizosphere (Adams and Bate, 1995). This process may lead to the precipitation of iron hydroxides as coatings on the roots at the expense of iron sulphide forms that otherwise precipitate in the bulk sediment, enhancing the adsorption of phosphorus (Vale et al., 1990; Sundby et al., 1998; Caetano and Vale, 2002). In the Mondego estuary, S. maritima marshes cover about 10.5 ha of the higher intertidal downstream mudflat and sand-flat areas (Fig. 1), which represent 4% of the south arm area, while the mudflats without vegetation, represents 52%. S. maritima has a mean annual above/belowground biomass of 2.26 ± 0.82 kg



Dwt m^2 and 1.16 ± 0.28 kg Dwt m^2 , respectively (IMAR-Data base).

Due to the importance of this species in tidal temperate estuaries, the objective of the present study was to characterise the effect of *Spartina maritima* on P speciation and availability, focussing on several sediment water interaction processes involved in the possible retention and export of phosphorus.

Materials and methods

A selected marsh area of the Mondego system (Fig. 1) was studied through comparison, in *Spartina* rhizosphere and adjacent bare bottom mudflats, for: (a) the sediment P-adsorption capacity; (b) daily O_2 and PO_4 -P fluxes in low water pools; c) P seasonal/annual net internal loading; (d) sediment profiles for interstitial dissolved inorganic P (PO_4 -P) in the upper

20 cm; (e) the total amount of PO_4 -P in the upper 10 cm of sediment; (f) the extractable Pforms in the upper 35 cm of sediment; (g) the amounts and proportions of possibly exchangeable P in the upper 20 cm of sediment. Phosphate adsorption measurements ($\mu g PO_4 - P g^{-1} Dwt$ sediment) were performed as saturation kinetic experiments and run on triplicate sub-samples of the upper 10 cm surface sediment taken in summer 1997. Three sediment cores were gently harvested from each field location. In the laboratory the sediment cores were pooled and mixed to improve the homogeneity among the sub-samples. From each location, eight sub-samples, each about 2.5 g Wwt, were introduced into 250 ml medical bottles where the sediment was suspended with 200 ml pre-filtered estuarine water. The sub-samples were then exposed to increasing concentrations of phosphate, ranging from 0.0 mg PO₄–P l^{-1} to 5.0 mg PO₄–P l^{-1} . Afterward the bottles were placed in a shaking bath for 36 h

and the adsorption of phosphate was measured, following the method used by (Jensen et al., 1992). The average adsorption values from each location were fitted to the Langmuir adsorption isotherm:

SP = (PSC * Ce)/(Ce + K) - NAP

where SP is the adsorption of phosphate, Ce is the equilibrium concentration of phosphate, K is the phosphate equilibrium concentration where half of the maximal adsorption is obtained, PSC is the phosphate sorption capacity (maximal adsorption capacity) and NAP is the native adsorbed phosphate. The SAS non-linear statistic regression model PROC NLIN (Marquarth methods) was used to find PSC, K and NAP. The P-values for the muddy and Spartina covered stations were predicted by the produced PROC NLIN which calculate the statistical explanation by the model and by residuals, as sum of squares. The P-values for the Spartina and muddy areas were then calculated as: (1-(model score/summed score)). At the same location and on the same day, two intertidal pools (one covered by Spartina and the other without vegetation) were followed during low tide, of two consecutive tidal cycles for comparison of the day and night situation. Each pool was measured for surface area and depth, and monitored hourly for O2 and P-flux measurements. Analysis of dissolved reactive phosphate was carried out using a rapid flow autoanalyser (RFA 300 Alpkem) and performed according to Alpkem methodologies (Alpkem, 1990).

Phosphate and oxygen fluxes were calculated taking into account the initial concentrations in the pool, which corresponded to the very first measurement just after the formation of the pool (t_0) . So, for each consecutive sample $(t_1, t_2...t_n)$, the calculated rates were given by the difference between the phosphate amount (mg m⁻²) at time t_n and the initial amount, and then divided by the number of hours between the two samples (data were previously standardised to avoid bias caused by differences in pool size).

To estimate the phosphorus seasonal/annual net internal loading of the Mondego system, flux measurements were performed in *Spartina* marshes and in mudflats without vegetation, during 24 h cycles, in order to cover a complete tidal cycle under day and night situation (Lillebø et al., 2004). Two methodologies were applied to asses for P-flux measurements at each tidal cycle: (a) the low tide pools during ebb (between 1999 and 2000), and (b) flux chambers during high tide (between 2000 and 2001). Calculations of the mean seasonal phosphate efflux rates were performed taking into account mean daily efflux rates (mg $m^{-2} d^{-1}$) at each site (day and night) and considering high and low tide, and the correspondent estuarine mudflat area covered by Spartina maritima and without vegetation (Lillebø et al., 2004). It was assumed that the mean efflux rates in May and July/August represented an average value for spring and summer respectively, and that the mean efflux rates in November and January represented an average value for autumn and winter, respectively (Lillebø et al., 2004).

Sediment dissolved inorganic P (PO₄-P) profiles were studied seasonally, in the year 2002, by placing vertical dialysis chambers in the selected Spartina marsh and in the adjacent barebottom mudflat (Fig. 1). This method discriminates the nutrient profiles with maximum resolution of 5 mm in the first top 7 cm, and 10 mm resolution from 7 cm to 20 cm depth. The in situ dialyses were made, based on the description by Kamp-Nielsen and Flindt (1993). Water samples were collected with a syringe (2.5 ml, corresponding to each chamber volume). To evaluate the effect of plants, samples were taken after 12 h of dark conditions (night period) and after 12 h of light conditions (day). Water samples were analysed for dissolved inorganic phosphate in a rapid flow autoanalyser (RFA 300 Alpkem) and performed according to Alpkem methodologies (1990). At the same time triplicate sediment cores (10 cm depth) were sliced into 1 cm layers and analysed for water content (Wwt - Dwt, 105°C for 24 h), and loss on ignition (LOI) (Dwt - AFDW, 550°C for 6 h), in winter, spring, summer and autumn. The estimation of the total amount of PO₄-P was done by taking into account the amount of PO₄-P in the interstitial water at each depth, the sediment sample specific mass, and the water volume fraction. The total amount of phosphorus in the top 10 cm of the sediment was obtained by

integration of the amounts through the depth in each area. During the same year and at the same selected area (Fig. 1), three replicate sediment cores (plexiglas tubes, $3.5 \text{ cm} \times 50 \text{ cm} \text{ deep}$) were collected for sediment profile characterisation in July 2002, at the Spartina marsh and in the adjacent barebottom mudflat. The sediment cores were capped, placed on ice in an upright position and rapidly transported to the laboratory to be processed. In the laboratory the cores were sectioned under N₂-atmosphere (0.5 cm sections in the top cm, 1 cm sections from 1 cm to 3 cm depth, 2 cm sections from 3 cm to 7 cm, a 3 cm section from 7 cm to 10 cm depth and 5 cm sections from 10 cm downward). Sediments from the three replicate cores were pooled together to account for within site variability (Jensen and Thamdrup, 1993; Paludan and Morris, 1999). Sediment samples were homogenised, and large plant material and macrofauna removed before freezing in sealed bags until analysis. The sequential P extraction was conducted after a modification of the Jensen and Thamdrup (1993) method (Coelho et al., 2004). The P fractions considered were: loosely sorbed P (MgCl₂ extract), Fe/Mn bound P (BD extract), Al/clay mineral bound P (NaOH extract), humic acid associated P (humic acid fraction, removed from NaOH extract by acidification and filtration), Ca bound P (HCl extract), NRP (non reactive P from the MgCl₂ and NaOH extracts) and refractory organic P (residual fraction).

P concentrations were integrated with depth and density to obtain the total P mass in the top 20 cm of the sediment layer per m². To calculate the possibly exchangeable P mass in the sediment, fractions MgCl₂~P, BD~P, NRP and NaOH~P were plotted together (Coelho et al., 2004), as the more refractory fractions are considered immobile and unavailable for organisms (Jensen and Thamdrup, 1993).

Results

The *Spartina maritima* covered sediment had an adsorption capacity of 140 μ g PO₄-P cm⁻³ sediment, and a *K*-value of about 400 μ g PO₄-P l⁻¹, while the muddy sediment without vegetation



Fig. 2 Sediment P-adsorption capacity at *Spartina maritima* marsh (\blacksquare) and at the adjacent bare bottom mudflat (\blacktriangle)

reached 80 μ g PO₄–P cm⁻³ sediment, with a Kvalue of 2000 μ g PO₄–P l⁻¹ (Fig. 2, Table 1A). The NAP value was similar for both areas. The Pvalue for the Langmuir model explanation for the Spartina and muddy stations were significant (P < 0.005, Table 1B). Phosphate and oxygen fluxes in intertidal low water pools, quantified during summer, showed that, during the day, the release rates of PO₄-P were lower in the pools covered with Spartina (mean efflux of 13.3 µmol - PO_4 -P m⁻² h⁻¹), while the release rates of O_2 efflux were higher (mean efflux of 2619 μ mo- $1 O_2 m^{-2} h^{-1}$). During the night period, the release rates of PO₄-P increased in the pools covered with Spartina (mean efflux of 40.7 µmol PO₄- $P m^{-2} h^{-1}$), while the O₂ uptake rates increased (mean uptake of $-1804 \ \mu mol O_2 \ m^{-2} \ h^{-1}$). In the

Table 1 (A) The phosphate adsorption characteristics at the mudflat without vegetation and covered by *Spartina maritima*. NAP is the "Native Adsorbed P" and PSC is the "Phosphate Sorption Capacity", both values in μ g P cm⁻³. K is the "half-saturation" concentration in μ g P l⁻¹; (B) The P-values for the muddy and *Spartina* covered stations predicted by the produced PROC NLIN which calculate the statistical explanation by the model and by residuals, as sum of squares.

A	Spartina maritima		Mudflat	
NAP PSC K	$0 \\ 140 \\ 400$		5 80 2000	
B Model Residuals	Score 375,927 1,603 377,530	Р 0.0043	Score 391,846 1,207 393,053	Р 0.0031



Fig. 3 P-release rates *vs.* oxygen uptake rates at *Spartina* marsh (**a**) and bare bottom mudflats (**b**) low water pools: calculated rates for the period between 11:30 a.m. and 05:30 p.m. \blacklozenge ; for the period between 12:30 a.m. and 08:30 p.m. \triangle , and for the period between 10:30 p.m. and 08:30 a.m.

bare bottom sediment pools the release rates of PO₄–P were higher, especially during the day (mean efflux of 47.8 μ mol PO₄–P m⁻² h⁻¹ during the day and of 25.8 μ mol PO₄–P m⁻² h⁻¹ during the night period), and the uptake rates of O₂ were higher during the night period (mean efflux of 5341 μ mol O₂ m⁻² h⁻¹ during the day and uptake of -3101 μ mol O₂ m⁻² h⁻¹ during the night) (Fig. 3).

The estimated seasonal internal P-loading in the Mondego estuary (Table 2) shows generally lower P effluxes from the *S. maritima* marsh into

Table 2 Seasonal and annual P-effluxes into the overlying water during a complete tidal cycle (kg PO_4 – $P ha^{-1}$) from mudflats and *Spartina maritima* marshes

Seasonal kg (PO ₄ –P) ha $_{\frac{1}{2}}$ year ⁻¹	Spartina maritima	Mudflat
Spring	-3.4	5.5
Autumn	4.2 8.7	4.6
Winter Annual kg(PO ₄ -P) ha year ⁻¹	2.3 11.8	3.4 25.8

the overlying water column, and even the uptake of phosphorus during spring. The exception was recorded in autumn, when the vegetated sediment released more P than the bare mudflats. Moreover, there is always efflux of phosphorus from the intertidal mudflats without vegetation, with a clear seasonal variation, in which the higher fluxes take place during the warmer season.

Sediment pore-water profiles followed a clear trend, with lower P concentrations in more superficial layers, and increasing concentrations with depth, especially in the mudflat area without vegetation, where barebottom sediment had higher concentrations of dissolved inorganic P (Fig. 4). In the first 6–8 cm of depth, the maximum mean concentration of phosphorus at the Spartina porewater was 0.452 mg PO₄–P l^{-1} (summer) and the mean concentration minimum was 0.134 mg PO₄–P l^{-1} (winter), while in the sediment without vegetation, the maximum mean concentration was 0.513 mg PO₄–P l^{-1} (spring) and the minimum mean concentration was 0.150 mg PO₄-P l^{-1} (autumn). Between 8 and 20 cm depth, the maximum mean concentration at the Spartina pore-water increased to 1.196 mg PO₄-P l⁻¹ (winter and autumn) and the minimum mean concentration was 0.319 mg PO₄–P l^{-1} (summer), while in the sediment without vegetation, the maximum mean concentration increased to 1.941 mg PO₄–P l^{-1} (spring) and the minimum mean concentration was 0.713 mg PO_4 -P l⁻¹ (autumn).

The mean organic mater content (% loi in Wwt of sediment) found in the upper 10 cm for bare bottom sediment and sediment with Spartina was 2.3 and 2.6, respectively in winter; 3.5 and 4.9 in spring; 3.3 and 4.2 in summer; and 5.5 and 6.1 in autumn. The total amount of dissolved inorganic P in the upper 10 cm, calculated for each of the seasonal profiles, shows that the mudflats without vegetation contained higher phosphate masses than Spartina rhizosphere (Fig. 5). In addition the pool-sizes measured at day were very similar in winter, summer and autumn, (respectively 40, 41 and 41 mg PO₄–P m⁻²) although, slightly larger during the night periods. In spring, the phosphate pools increase proportionately during day and night, reaching a maximum of 61 mg PO_4 – $P m^{-2}$. At the Spartina rhizosphere, phosphate pools



Fig. 4 Seasonal phosphate sediment profiles during day and night conditions and in all four seasons in *Spartina* marsh sediments (\Box day; \blacksquare night) and bare bottom mudflats (\bigcirc day; \blacksquare night)

were always comparatively lower than at bare bottom for all seasons (23, 34, 30 mg PO₄–P m⁻², respectively for winter, summer and autumn). As for the bare bottom, values were also higher during the night periods, except in autumn, and the phosphate pool also increased in spring reaching 45 mg PO₄–P m⁻².

Results from the extraction procedure showed that the superficial layers of both types of sediment had the maximum concentrations of labile P pools. Higher proportions of refractory P forms



Fig. 5 Total amount of dissolved inorganic phosphorus in the upper 10 cm of sediment in mudflats with *Spartina* rhizosphere and in bare bottom mudflats in all four seasons

were found in deeper layers (Fig. 6A). Calculated on area basis, *Spartina* marsh sediments contained less total P while iron bound P and exchangeable P were probably not significantly different from the adjacent mud flat without vegetation (Fig. 6B). Organic P pools were larger in sediment with plant cover, which can also account for the higher proportion of exchangeable P relative to total P.

Discussion

Spartina maritima has a high sediment aeration capacity, where a fraction of the oxygen produced through photosynthesis is transported to the rhizosphere by diffusion (Azzoni et al., 2001). Commonly, this process may lead to the precipitation of iron oxides around the roots (Vale et al., 1990), and ultimately increase the phosphate adsorption capacity of the sediment (Coelho et al., 2004). Actually, results of the adsorption experiment show that intertidal mudflats colonised by *S. maritima* had a much higher P adsorption capacity (140 g PO₄–P cm³ sediment), when compared with adjacent mudflats without vegetation (80 μ g PO₄–P cm³ sediment). The difference



Fig. 6 Sediment depth profiles for extractable P pools (a) and amounts and proportions of possibly exchangeable P (b) in *Spartina* marsh sediments and bare bottom mudflats

between the two locations is even more pronounced when the pore-water concentrations are lower and more natural as in the upper part of the rhizosphere (as shown in Fig. 4). In this uppermost part of the sediment the pore-water concentration of phosphate is in general lower than 500 μ g PO₄–P l⁻¹. Inside this concentration range the Spartina covered sediment is able to adsorb about 70 μ g PO₄–P cm³ sediment while the bare mud only is able to adsorb about 18 μ g PO₄–P cm³ sediment. This means that the potential adsorption capacity inside natural concentrations is about four times higher in the Spartina maritima rhizosphere compared with the unvegetated area. The summer fluxes from the low water pools also suggest, on a daily scale, that Spartina is able to control the phosphate efflux from the sediment. However, during the night, high summer temperatures and oxygen depletion conditions may promote phosphate efflux into the overlying water column. Moreover, at the system level, the specific seasonal variation of the Pfluxes forming the two types of sediment probably reflects the dynamics of plant uptake for growth purposes, enhanced P-adsorption capacity at the rhizosphere during active growth, and release of phosphate from plant tissue during withering in autumn. In the mudflat without vegetation, the

higher phosphate concentrations during the night may reflect the oxygen depletion due to respiration, which during the day may be compensated by autotrophic oxygen production from associated micro-algae.

Most often the enhanced adsorption capacity of Spartina maritima rhizosphere, compared with the bare bottom mudflat, causes a relatively high concentration of inorganic P and iron around the roots (Vale et al., 1990; Sundby et al., 1998; Caetano and Vale, 2002). We could not verify this from our results, since the pool of iron-bound P was lower in vegetated sediment than in the mudflat without vegetation. One possible reason for this is that some iron-bound P is assimilated for growth purposes. The total amount of dissolved inorganic phosphate in the sediment also reflects this mechanism, with lower concentrations of pore-water phosphate and of the exchangeable P bulk in Spartina marsh. Coelho et al. (2004) found a higher ratio of BD-Fe to BD-P in the upper 2 cm of vegetated salt marsh sediment. This may explain the greater ability of the vegetated sediment to retain phosphate as observed both in the adsorption experiment and in the flux study. Iron oxides in this highly oxidized surface sediment act as an iron barrier and bind dissolved phosphate migrating from

deeper sediment layers, thus preventing release into the water column (Chambers and Odum, 1990; Sundby et al., 1992; De Groot and Fabre, 1993). Also, as a result of the high amounts of oxidized iron, the highest concentration of potentially mobile P-forms is found in the surface sediments. Release from this pool may be caused by lowered redox condition during night when no benthic photosynthesis occurs, or by high temperatures, stimulating the mineralization. Thus, shading provided by plant cover may also reduce sediment temperature, and therefore sediment phosphate efflux.

The mineralization of fresh organic matter represents an important phosphate contribution for the overall nutrient cycle (Sundby et al., 1992), and may explain the higher exchangeable P proportion of sediments covered by Spartina, although the difference to the bare flat sediment may not be significant. Spartina marshes are a very important driving force in the sedimentary P cycle and can be considered a useful management tool in estuarine ecosystem recovery efforts. Plant uptake for growth purposes combined with an enhanced P-adsorption capacity of the rhizosphere has an effective buffer effect on P-efflux from the sediment. In fact, the results suggest that in the Mondego estuary, the replacement of 1 ha of mud flat without vegetation, by 1 ha of Spartina maritima marsh may reduce the P-efflux in 14 kg PO_4 –P ha year⁻¹. However, Spartina marshes may not always function as a sink for phosphorus. At a certain stage of development, the marsh enters into a steady state situation (an established system) where it functions more as phosphorus transformers, converting inorganic phosphorus to detritus. In high energy marshes, this excess amount of detritus, produced by marsh-estuarine ecosystems, becomes eroded and can be transported within the system or exported to the near shore environment, as suggested in the "outwelling hypothesis" (Odum, 1980). Therefore, a better understanding of P transport and transformation in the estuarine system requires that future research aim on clarifying the paths of both sediment-bound P and detritus-bound P within the system.

Acknowledgements This study was carried out in the scope of the research project DYNAMOD (POCTI/ M6S137431/2001) funded by the Portuguese FCT and supported by the POCTI – Formar e Qualificar – Medida 1.1 program (Portuguese FCT) through a Post-Doc grant (SFRH/BPD/5650/2001) (A.I. Lillebø), and by The Danish National Science Foundation through a grant number 21020463 (J.P. Coelho, M. Flindt, and H.S. Jensen).

References

- Adams, J. B. & G. C. Bate, 1995. Ecological implications of tolerance of salinity and inundation by *Spartina maritima*. Aquatic Botany 52: 183–191.
- Alpkem, 1990. Rapid Flow Analyser—Methodology A303–S202, A303–S170, A303–S020. ALPKEM Corporation, Clackamas, Oregon.
- Azzoni, R., G. Giordani, M. Bartoli, D. T. Welsh & P. Viaroli, 2001. Iron, sulphur and phosphorus cycling in the rhizosphere sediments of an euthrophic *Ruppia cirrhosa* meadow (Valle Smarlacca, Italy). Journal of Sea Research 45: 15–26.
- Caetano, M. & C. Vale, 2002. Retention of arsenic and phosphorus in iron-rich concretions of Tagus salt marshes. Marine Chemistry 79: 261–271.
- Cardoso, P., M. A. Pardal, A. I. Lillebø, S. M. Ferreira, D. Raffaelli & J. C. Marques, 2004. Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. Journal of Experimental Marine Biology and Ecology 302: 233–248.
- Chambers, R. M. & W. E. Odum, 1990. Pore-water oxidation, dissolved phosphate and the iron curtain. Iron-phosphate relations in tidal freshwater marshes. Biogeochemistry 10: 37–52.
- Christensen, K. K. & F. Ø. Andersen, 1996. Influence of *Littorella uniflora* on phosphorus retention in sediment supplied with artificial porewater. Aquatic Botany 55: 183–197.
- Coelho, J. P., M. R. Flindt, H. S. Jensen, A. I. Lillebø & M. A. Pardal, 2004. Phosphorus speciation and availability in intertidal sediments of a temperate estuary: relation to eutrophication and annual P-fluxes. Estuarine, Coastal and Shelf Science 61: 583–590.
- De Groot, C. & A. Fabre, 1993. The impact of desiccation of a freshwater marsh (Garcines Nord, Camargue, France) on sediment-water-vegetation interactions. Hydrobiologia 252: 105–116.
- Dolbeth, M., M. A. Pardal, A. I. Lillebø, U. Azeiteiro & J. C. Marques, 2003. Short term and long term effects of eutrophication on the secondary production of an intertidal macrobenthic community. Marine Biology 143: 1229–1238.
- Ferreira, S. M., M. A. Pardal, A. I. Lillebø, P. Cardoso & J. C. Marques, 2005. Population dynamics of *Cyathura carinata* (Isopoda) in a eutrophic temperate estuary. Estuarine, Coastal and Shelf Science 61: 669–677.

- Flindt, M. R., M. A. Pardal, A. I. Lillebø, I. Martins & J. C. Marques, 1999. Nutrient cycling and plant dynamics in estuaries. Acta Oecologica 20: 237–248.
- Flindt, M. R., M. A. Pardal, A. I. Lillebø, I. Martins & J. M. Oliveira, 2002. Nutrient dynamics in the intertidal pools of the Mondego estuary. I- Nutrient sources, sediment profiles, mineralization and adsorption dynamics. In Pardal, M. A., J. C. Marques & M. A. Graça (eds), Aquatic Ecology of the Mondego River Basin. Global Importance of Local Experience. Imprensa da Universidade de Coimbra, Coimbra, 7– 13.
- Holmboe, N., H. S. Jensen & F. Ø. Andersen, 1999. Nutrient addition bioassays as indicators of nutrient limitation of phytoplankton in an eutrophic estuary. Marine Ecology Progress Series 186: 95–104.
- Jensen, H. S. & F. Ø. Andersen, 1992. Importance of temperature, nitrate and pH for phosphate release from aerobic sediments of four shallow, eutrophic lakes. Limnology and Oceanography 37: 577–589.
- Jensen, H. S., P. Kristensen, E. Jeppesen & A. Skytthe, 1992. Iron/phosphorus ratio in surface sediment as an indicator of phosphate release from aerobic sediments in shallow lakes. Hydrobiologia 235–236: 731–743.
- Jensen, H. S. & B. Thamdrup, 1993. Iron-bound phosphorus in marine sediments as measured by bicarbonatedithionite extraction. Hydrobiologia 253: 47–59.
- Kamp-Nielsen, L. & M. R. Flindt, 1993 On-line recording of pore-water profiles from in situ dialysis. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 25: 151–156.
- Lillebø, A. I., M. R. Flindt, M. A. Pardal, I. Martins, J. M. Neto & J. C. Marques, 2002. Nutrient dynamics in the intertidal pools of the Mondego estuary. II Seasonal efflux of PO₄–P and NH₄–N in bare bottom and vegetated pools. In Pardal, M. A., J. C. Marques & M. A. Graça (eds), Aquatic Ecology of the Mondego River Basin. Global Importance of Local Experience. Imprensa da Universidade de Coimbra, Coimbra, 257–272.
- Lillebø, A. I., J. M. Neto, M. R. Flindt, J. C. Marques & M. A. Pardal, 2004. Phosphorous dynamics in a temperate intertidal estuary. Estuarine, Coastal and Shelf Science 61: 101–109.
- Marques, J. C., S. N. Nielsen, M. A. Pardal & S. E. Jørgensen, 2003. Impact of eutrophication and river

management within a framework of ecosystem theories. Ecological Modelling 166: 147–168.

- Martins, I., M. A. Pardal, A. I. Lillebø, M. R. Flindt & J. C. Marques, 2001. Hydrodynamics as a major factor controlling the occurrence of green macroalgae blooms in an eutrophic estuary: a case study. Estuarine, Coastal and Shelf Science 52: 165–177.
- Odum, E. P., 1980. The status of three ecosystem level hypotheses regarding salt marshes: tidal subsidy, outwelling and the detritus based food chain. In Kennedy, V. S. (ed.), Estuarine Perspectives. Academic Press, New York, 485-496.
- Paludan, C. & J. T. Morris, 1999. Distribution and speciation of phosphorus along a salinity gradient in intertidal marsh sediments. Biogeochemistry 45: 197– 221.
- Pardal, M. A., P. G. Cardoso, J. P. Sousa, J. C. Marques & D. Raffaelli, 2004. Assessing environmental quality: a novel approach. Marine Ecology Progress Series 267: 1–8.
- Sánchez, J. M., X. L. Otero, J. Izco & F. Marcías, 1997. Growth form and population density of *Spartina maritima* (Curtis) Fernald in Northwest Spain. Wetlands 17: 368–374.
- Sánchez, J. M., D. G. SanLeon & J. Izco, 2001. Primary colonization of mudflat estuaries by *Spartina maritima* (Curtis) Fernald in Northwest Spain: vegetation structure and sediment accretion. Aquatic Botany 69: 15–25.
- Sundby, B., C. Gobeil, N. Silverberg & A. Mucci, 1992. The phosphorus cycle in coastal marine sediments. Limnology and Oceanography 37: 1129–1145.
- Sundby, B., C. Vale, I. Caçador, F. Catarino, M. J. Madureira & M. Caetano, 1998. Metal rich concretions on the roots of salt marsh plants: mechanism and rate of formation. Limnology and Oceanography 43: 245–252.
- Vale, C., F. M. Catarino, C. Cortesão & M. I. Caçador, 1990. Presence of metal-rich rhizoconcretions on the roots of *Spartina maritima* from the salt marshes of the Tagus estuary, Portugal. Science of the Total Environment 97–98: 617–626.
- Warren, R. S. & W. A. Niering, 1993. Vegetation change on a Northeast tidal marsh: interaction of sea-level rise and marsh accretion. Ecology 74: 96–103.