

Spatial distribution and biomass of aquatic rooted macrophytes and their relevance in the metabolism of a Mediterranean coastal lagoon

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SUMMARY: This work aims to characterise the current autotrophic compartment of the Albufera des Grau coastal lagoon (Menorca, Balearic Islands) and to assess the relationship between the submerged macrophytes and the limnological parameters of the lagoon. During the study period the submerged vegetation was dominated by the macrophyte *Ruppia cirrhosa*, which formed dense extensive meadows covering 79% of the surface. Another macrophyte species, *Potamogeton pectinatus*, was also observed but only forming small stands near the rushing streams. Macroalgae were only occasionally observed. Macrophyte biomass showed a clear seasonal trend, with maximum values in July. The biomass of *R. cirrhosa* achieved 1760 g DW m⁻², the highest biomass ever reported for this species in the literature. The seasonal production-decomposition cycle of the macrophyte meadows appears to drive the nutrient dynamics and carbon fluxes in the lagoon. Despite the significant biomass accumulation and the absence of a washout of nutrients and organic matter to the sea, the lagoon did not experience a dystrophic collapse. These results indicate that internal metabolism is more important than exchange processes in the lagoon.

Keywords: coastal lagoons, macrophytes, *Ruppia cirrhosa*, Western Mediterranean.

RESUMEN: DISTRIBUCIÓN ESPACIAL Y BIOMASA DE LOS MACRÓFITOS SUMERGIDOS Y SU RELEVANCIA EN EL METABOLISMO DE UNA LAGUNA LITORAL MEDITERRÁNEA. – El presente estudio pretende caracterizar el componente autotrófico de la laguna litoral de s'Albufera des Grau (Menorca, Islas Baleares) y determinar la relación entre los macrófitos acuáticos y la dinámica de los principales parámetros limnológicos del sistema. Durante el periodo estudiado, la vegetación sumergida estuvo dominada por el macrófito *Ruppia cirrhosa*, que formaba extensas praderas en toda la laguna. También se observó otra especie de macrófito, *Potamogeton pectinatus*, pero sólo formando pequeñas formaciones cerca de la entrada de los torrentes a la laguna. La biomasa de macrófitos mostró un claro ciclo estacional, con los valores máximos centrados en verano. La biomasa de *R. cirrhosa* alcanzó 1760 g DW m⁻², que supone el valor más alto de biomasa descrito para esta especie en la literatura. El ciclo estacional de producción-descomposición de las praderas de macrófitos parece ser el responsable de la dinámica de nutrientes y de los flujos de carbono en la laguna. A pesar de las elevadas biomásas acumuladas y de la ausencia de un lavado de nutrientes y materia orgánica hacia el mar, la laguna no mostró un colapso distrófico, sugiriendo la importancia del metabolismo interno de la laguna por encima de los procesos de intercambio con el mar.

Palabras clave: lagunas litorales, macrófitos, *Ruppia cirrhosa*, Mediterráneo Occidental.

INTRODUCTION

Submerged aquatic macrophytes account for an important part of the primary production in shallow lakes (Margalef, 1983). In coastal lagoons, which are amongst the most productive ecosystems in the world (Barnes, 1980), the primary production is per-

formed by macrophytes, macroalgae or, to a lesser extent, periphyton or phytoplankton (Castel *et al.*, 1996; McGlathery *et al.*, 2001). The dominance of one of these groups of primary producers can be related to nutrient levels, but many factors appear to be involved (Duarte, 1995; Taylor *et al.*, 1995; Valiela *et al.*, 1997). Nonetheless, the accumulation

of significant biomass of either macroalgae or rooted macrophytes together with the highly dynamic character of coastal lagoons can periodically lead these systems to dystrophic crises (Castel *et al.*, 1996; Viaroli *et al.*, 1996; Duarte *et al.*, 2002).

The Albufera des Grau is a coastal lagoon located on the northeast coast of Menorca, Balearic Islands. The lagoon is the most important wetland of the island and one of the most well preserved coastal lagoons of the western Mediterranean. The few previous studies of the Albufera des Grau described different submerged vegetation in its recent history (Margalef, 1952; Pretus, 1989; Cardona, 2001). In the early 1950s the eminent ecologist Ramon Margalef described the flora of the lagoon as *Chaetomorpha-Polysiphonietum*, with no indication of the presence of aquatic submerged flowering plants (Margalef, 1952). During the 1980s the green macroalgae *Chateomorpha crassa* formed extensive beds covering 100% of the surface most of the time (Pretus, 1989). A dystrophic crisis was reported due to a massive mortality of macroalgal beds after the entrance of seawater to the lagoon and subsequent salinity changes (Pretus, 1989). The presence of rooted macrophytes in the lagoon was first reported in the 1990s in the seaward littoral areas, with an estimated cover of 40% (Cardona, 2001).

The lagoon is isolated in the sense that the communication with the sea does not imply an important water renewal of the system. This means that the export of organic matter and nutrients to the sea is not as important as it usually is in other lagoons (Duarte *et al.*, 2002). In such a situation, we would expect the internal metabolism of the lagoon to play

an important role in the trophic status of the system. Consequently, the knowledge of the trophic status including the relative importance of the different primary producers is essential for the understanding and further management of the lagoon.

This study aims to characterise the current autotrophic component of the lagoon and to assess the spatial and temporal variability of aquatic rooted macrophytes on a seasonal basis. A parallel description of the basic chemical parameters is also conducted to briefly discuss the relation of the production cycle with the metabolism of the lagoon.

MATERIAL AND METHODS

Study site

The Albufera des Grau has a surface area of 78 ha and a volume of 1 hm³ (Fig. 1). The average depth is 1.37 m and it reaches a maximum depth of 3 m (Pretus, 1989). The climate is typically Mediterranean, with a mean air temperature of 17°C and an annual precipitation of 599 mm during the last three decades. The lagoon receives freshwater inputs from two streams that drain an area of 56 km², the watershed being mainly composed of Palaeozoic siliciclastic sands and silts and Mesozoic dolomites. Freshwater inputs are irregular and centred on spring and autumn. The lagoon is connected to the sea by a narrow, 500 m long channel, Sa Gola, in which a small floodgate allows the lagoon-sea connection to be regulated when the sand-barrier is opened. The water of the lagoon is oligo-mesohaline with a salinity of between 5 and 20 during the last five years. There is a marked seasonality in the salinity and water level due to the Mediterranean evaporation/precipitation regime, which can potentially lead the system to critical situations such as hypersaline events (up to 60 in 1995, authors' unpublished data), haline stratification and dystrophic events (Pretus, 1989; Cardona, 2001).

Sampling methods

During the year 2000 the biomass of submerged macrophytes was determined at approximately monthly intervals at three littoral sites (~1 m depth) beneath dense meadows. Sites A and B were located near the rushing streams, while site C was located on the northern coast of the lagoon (Fig. 1). Three

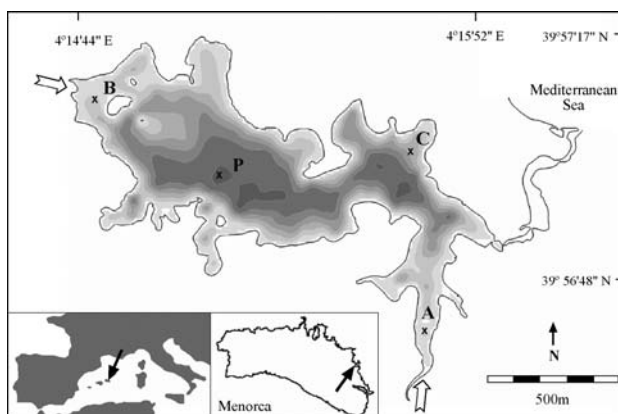


FIG. 1. – Location and bathymetric map of the Albufera des Grau in the island of Menorca, western Mediterranean. Isobaths are every 50 cm. Sampling sites (crosses) and freshwater inputs (arrows) are shown.

replicates were conducted at each sampling site. Biomass samples were collected with a cylindrical core sampler of 16 cm diameter (Menéndez, 2002) and above-ground biomass was sorted by hand from the core. The sediment was sieved through a 1 mm mesh to collect below-ground biomass (rhizomes and roots). After sorting and cleaning with tap water, samples were dried (70°C to constant weight) and weighed.

Macrophyte cover was determined in July 2000 by visual observation from a boat. Repeated diving immersions were performed in order to identify macrophyte species when necessary. The surface of the lagoon was divided into a 50 × 50 m grid, and the abundance of the macrophyte species was determined for each unit. The whole lagoon was surveyed. Macrophyte abundance was determined by a percent cover scale.

During the studied period the basic limnological parameters of the lagoon were determined monthly at a 3 m depth site in the central area of the lagoon. All samplings were conducted at the same time of the day. Five water samples were taken at different depths every 50 cm from surface to bottom. Water salinity, pH, temperature and oxygen concentration were determined in situ with field sensors (WTW Multiline P3 and WTW Cond315i). Water samples were filtered, stored frozen and analysed in the laboratory as soon as possible. Nutrient concentration (nitrate, nitrite, ammonia, total phosphorus and SRP) were determined following standard methods (Hansen and Koroleff, 1999). Alkalinity was determined by potentiometric titration with H₂SO₄ and Gran evaluation (Stumm and Morgan, 1981). The parameters of the carbonate system (total dissolved

inorganic carbon and partial pressure of CO₂) were calculated from the pH and alkalinity values using the dissociation constants for seawater (Millero, 1995). Phytoplankton biomass was evaluated from pigment concentrations in water, which were extracted in 90% acetone and determined by the trichromatic method (Jeffrey and Humphrey, 1975).

RESULTS

Spatial distribution and biomass of submerged vegetation

Two vascular submerged macrophytes were found during the survey of aquatic vegetation in the lagoon, *Ruppia cirrhosa* (Petagna, Grande) and *Potamogeton pectinatus* L., which formed dense extensive meadows all along the lagoon. Occasional occurrence of red algae (*Polysiphonia* spp., *Gracilaria* sp.) and filamentous green algae (*Chaetomorpha crassa*) was observed. In the study site emerged macrophytes (*Scirpus maritimus* and *Phragmites australis*) were also observed in narrow vegetated belts in some areas along the shoreline.

The spatial extent of macrophytes was dominated by *R. cirrhosa*, which was widely distributed throughout the lagoon, forming the denser beds in the littoral parts (Fig. 2). Individual stands were also found at intermediate depths (1-2 m), with shoots reaching the surface. *R. cirrhosa* was only absent in the deepest part of the lagoon (>2 m), and its total area of appearance was estimated to be 59 ha. On the other hand, *P. pectinatus* only appeared forming small stands among *R. cirrhosa* meadows and its distribu-

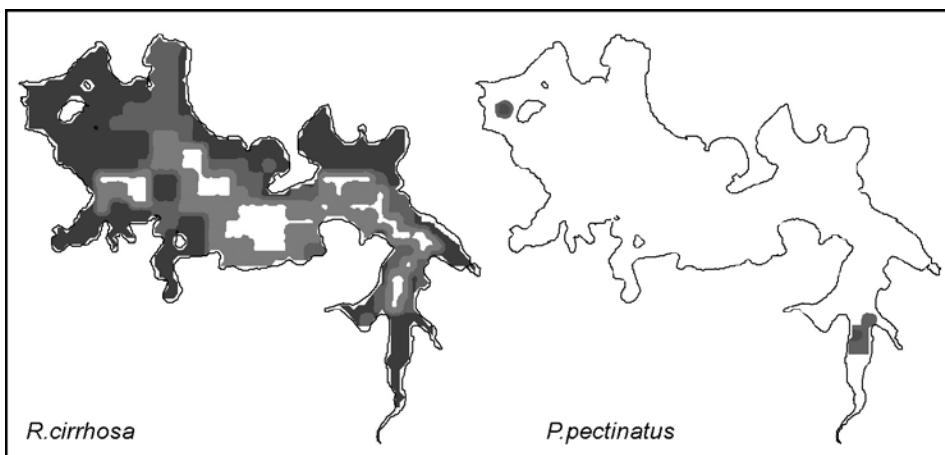


FIG. 2. – Spatial distribution of *R. cirrhosa* (left) and *P. pectinatus* (right) in summer 2000, including both living and recently desiccated littoral stands. Cover scale from dark grey to white: 100%, >50%, <50%, and absence or scarce individuals.

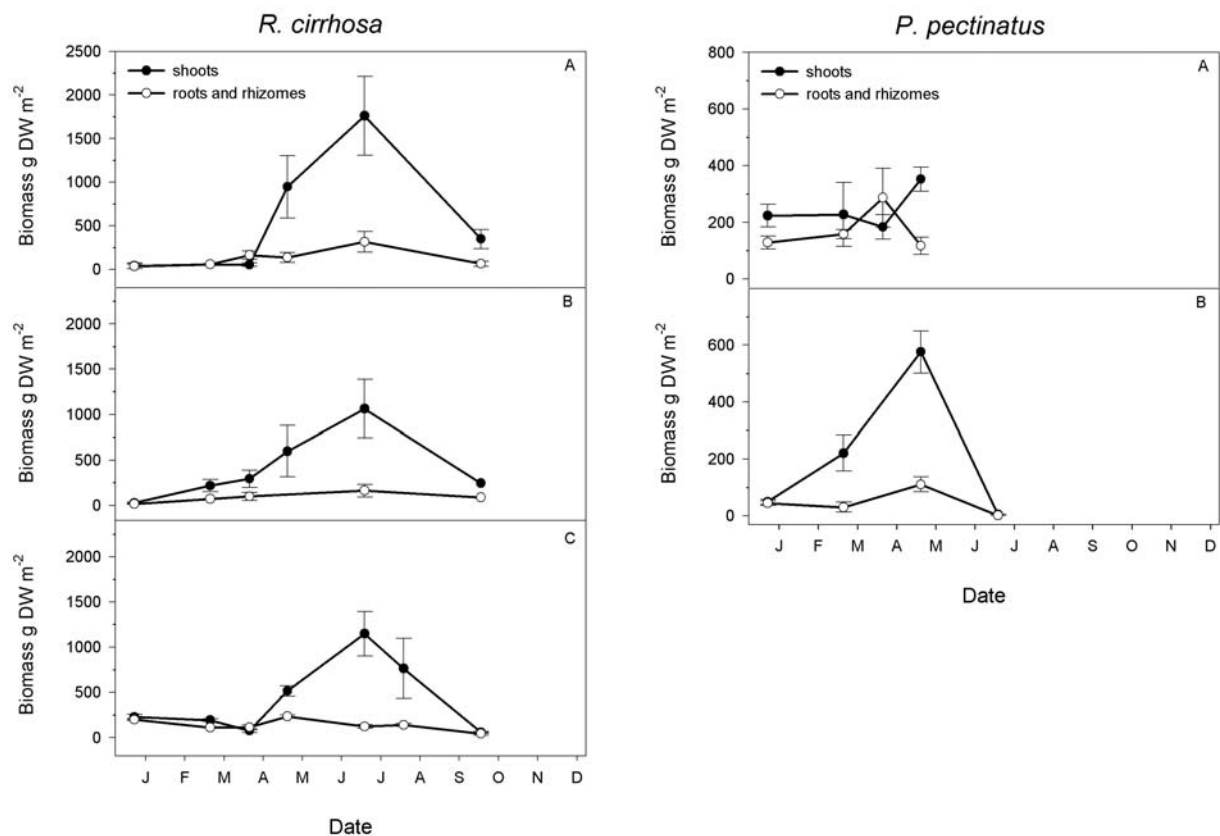


Fig. 3. – Temporal dynamics of *R. cirrhosa* (left) and *P. pectinatus* (right) biomass at the three sampling sites. Aboveground (filled circles) and belowground (open circles) biomass is shown.

tion was limited to the areas near the entrance of freshwater streams to the lagoon (Fig. 2).

Ruppia cirrhosa was present at the three sampling sites throughout the study period and showed a clear seasonal trend in terms of biomass at the three sampling sites (Fig. 3). Similar trends in aboveground (shoots and leaves) and belowground (roots and rhizomes) biomass were observed. Aboveground biomass was below 300 g DW m⁻² from January to April. In spring increasing values of biomass were observed until July, when it peaked with more than 1000 g DW m⁻² at the three sites. Maximum achieved biomass was 1760 g DW m⁻² at site A. The maximum belowground biomass was also observed in July at sites A and B, but was never above 300 g DW m⁻². During the summer the contribution of belowground biomass to total biomass was very small, and aboveground biomass accounted for more than 85% of total plant biomass on average. Beyond the biomass maximum, *R. cirrhosa* progressively declined and both above and belowground biomass decreased, quickly reaching the low values of the previous winter (below 300 g DW m⁻²) and then absolutely disappearing from the lagoon.

Potamogeton pectinatus only appeared at sites A and B (Fig. 3). The maximum observed aboveground biomass of *P. pectinatus* was 576 g DW m⁻² at site B, representing 80% of total plant biomass. From the few data available, no clear seasonal trends can be inferred, but it disappeared completely from the lagoon after July.

Water parameters

During the study period, water level was always below sea level (s.l.) and showed clear seasonal fluctuations with extremely low values in summer (Fig. 4). The minimum level was reached in September, with -85 cm below s.l., leading to major littoral desiccation. From the bathymetry of the lagoon (Pretus, 1989 and unpublished data) we were able to estimate the desiccated area at approximately 31 ha. This value accounts for 40% of the total lagoon surface and 90% of the surface corresponding to littoral areas (<1 m depth). Average salinity was 17, but great seasonal variation was observed (Fig. 4). The winter values of 12 progressively increased until October, when maximum salinity

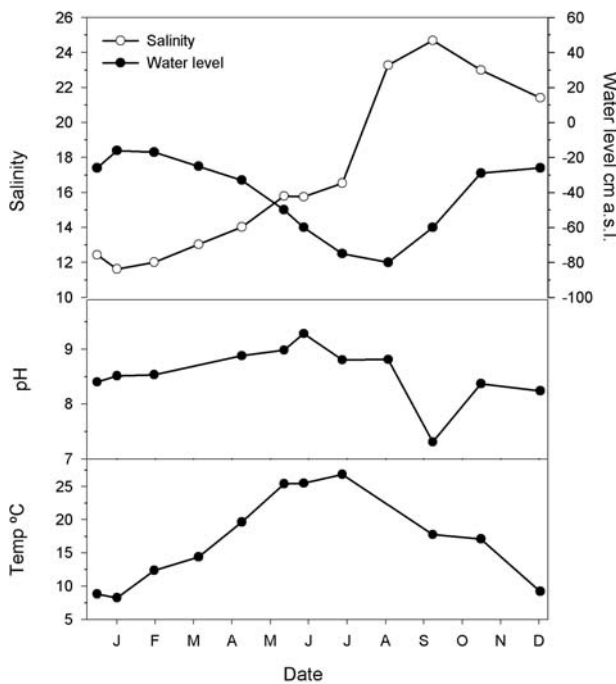


FIG. 4. – Temporal evolution of salinity, water level, pH and temperature during the study period.

was observed (25). This increase was related to the evaporation balance and to the sporadic entrance of small amounts of seawater into the lagoon due to low water levels. During the study period the water column was always mixed and only smooth vertical gradients in salinity were observed. A clear seasonal trend in pH was observed, with a slight progressive increase reaching the maximum of 9.3 in June (Fig. 4). A rapid decrease below seawater pH values was observed at the end of the summer. This variation in pH (range 7.3-9.3) occurred despite the high alkalinity of the water (Table 1).

TABLE 1. – Summary of water characteristics in s'Albufera des Grau

	range
Water level (cm a.s.l)	-85 - 16
Volume ($\times 1000 \text{ m}^3$)	921 - 1026
Salinity	11.6 - 24.7
Temperature ($^{\circ}\text{C}$)	8.2 - 26.8
pH	7.3 - 9.3
Oxygen (% saturation)	70 - 133
Oxygen ($\text{mg}\cdot\text{L}^{-1}$)	6.7 - 12.2
Phosphorus SRP ($\mu\text{mol}\cdot\text{L}^{-1}$)	0.02 - 2.0
TP ($\mu\text{mol}\cdot\text{L}^{-1}$)	0.26 - 5.34
NH_4^+ ($\mu\text{mol}\cdot\text{L}^{-1}$)	0 - 9.18
NO_3^- ($\mu\text{mol}\cdot\text{L}^{-1}$)	0.30 - 4.62
Alkalinity ($\text{meq}\cdot\text{L}^{-1}$)	1.93 - 3.64
$p\text{CO}_2$ (μatm)	10 - 3870
HCO_3^- ($\text{mmol}\cdot\text{L}^{-1}$)	1.39 - 3.16
CO_2 ($\text{mmol}\cdot\text{L}^{-1}$)	0.0004 - 0.1431

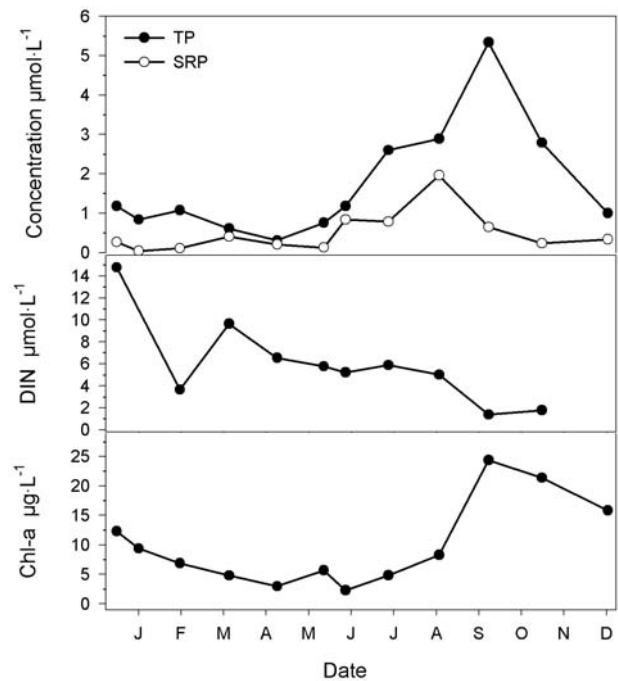


FIG. 5. – Temporal evolution of nutrient (total phosphorus, TP, SRP-phosphorus and dissolved inorganic nitrogen, DIN) and chlorophyll *a* concentrations during the study period.

Nutrient concentrations were low during the study period (Table 1). Dissolved inorganic nitrogen, DIN, ranged from 1 to $15 \mu\text{mol L}^{-1}$ and a progressive reduction was observed during the year (Fig. 5). Soluble reactive phosphorus, SRP, showed a clear seasonal trend, peaking in summer ($2 \mu\text{mol L}^{-1}$; Fig. 5). The total phosphorus, TP, including both dissolved and particulate forms of phosphorus, showed a similar trend (Fig. 5). The lowest values ($<1.5 \mu\text{mol L}^{-1}$) were found during winter and spring months, and the concentration started a progressive increase from June. The maximum TP was achieved in October, with $5.3 \mu\text{mol L}^{-1}$. Chlorophyll *a* concentration was at intermediate levels during the winter months ($5\text{-}12 \mu\text{g L}^{-1}$) and decreased during spring (Fig. 5). In July the concentration began to increase progressively and achieved the maximum value of $25 \mu\text{g L}^{-1}$ in October, when the eutrophic situation started to revert.

Interestingly, the dissolved inorganic carbon, DIC, showed a clear seasonal trend. During the growing period of *R. cirrhosa*, the DIC concentration showed a progressive decrease and $p\text{CO}_2$ was below atmospheric equilibrium (Fig. 6). After the summer minimum DIC concentration, a huge increase was observed, presumably due to the release of carbon from macrophyte biomass decomposition. A fast and dramatic supersaturation of CO_2

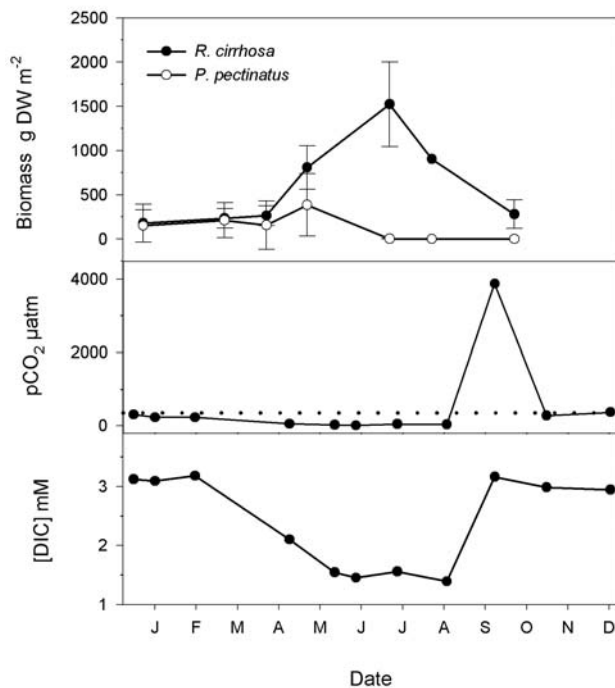


FIG. 6. – Temporal evolution of average total biomass of *R. cirrhosa* and *P. pectinatus* in relation with the partial pressure of CO₂ and the concentration of dissolved inorganic carbon in water. Dotted line is the partial pressure of CO₂ at atmospheric equilibrium.

in the lagoon occurred in October (up to 3870 µatm, ten times the atmospheric partial pressure), but two months later the 370 µatm range of atmospheric equilibrium was recovered.

DISCUSSION

The Albufera des Grau is a macrophyte-dominated system in which *R. cirrhosa* is the most important species. The low diversity of macrophytes is typical of brackish-water systems (Remane and Schlieper, 1971). The *Ruppia* meadow is densely distributed throughout the lagoon, especially in the littoral areas. The total estimated macrophyte cover was 80% of the lagoon surface, of which only 2% corresponded to mixed *Ruppia-Potamogeton* meadows (Table 3). The dominance of *R. cirrhosa* over *P. pectinatus* is probably due to the salinity range observed in the lagoon, which is in accordance with the salinity tolerance of these species (Verhoeven, 1980a). Indeed, *P. pectinatus* disappears in July when salinity increases sharply from 16 to 23.

The biomass of *R. cirrhosa* observed in this study is clearly the highest value ever reported for this species in the literature (Table 2) and indicates the importance of benthic production in the lagoon.

TABLE 2. – Range of biomass values reported in the literature for *R. cirrhosa*.

Biomass g AFDW·m ⁻²	Locality	Source
8-90 ^a	Murcia, Spain	Ballester (1985)
20-106 ^a	Certes fishponds, France	Viaroli <i>et al.</i> (1996)
90-140	Tvärminne, Finland	Verhoeven (1980b)
50-160	Camargue, France	Verhoeven (1980b)
55-190	Coastal ponds, Netherlands	Verhoeven (1980b)
128-282	Badia del Fangar, Spain	Pérez and Camp (1986)
226-365 ^a	Buda lagoon, Spain	Menéndez <i>et al.</i> (2002)
72 ^a -438	St. André lagoon, Portugal	Duarte <i>et al.</i> (2002)
473-642 ^a	Fra Ramon, Spain	Gesti <i>et al.</i> (2005)
75-672	Tancada Lagoon, Spain	Menéndez (2002)
380-1408 ^a	Albufera des Grau, Spain	This study

^a calculated from original data in g DW·m⁻², assuming 20% ash content.

Such high biomass may be related to the high irradiance and warm temperatures typical of the Mediterranean climate. Moreover, in a situation without light limitation, the greater depth of the littoral areas of the Albufera des Grau in comparison with other reported Mediterranean coastal lagoons could presumably be involved in the achievement of such high biomass values.

A clear seasonal trend in the production and decomposition of the *Ruppia* meadows was observed at the three sampling sites, which only differed in the maximum values of *Ruppia* biomass. The lower biomass at site B may be related to the high biomass of *P. pectinatus* at the sampling site (Fig. 3) but further work is required to confirm this assumption (Verhoeven, 1980a; Menéndez *et al.*, 2002). Similarly, the lower biomass at site C may be related to differences in sediment composition and to the presence of macroalgae at the sampling site (346 g DW m⁻² of *Polysiphonia* sp., authors' unpublished data).

The macrophyte production-decomposition cycle seems to drive most of the limnological parameters of the lagoon. During the macrophyte growing period nutrient concentrations are low, presumably limiting phytoplankton growth. From mid-summer the macrophyte beds decline and decomposition of macrophyte

TABLE 3. – Comparison of macrophyte cover and percentage of cover of each species in years 2000 and 2001

	2000	2001
Macrophyte cover (ha)	59	64
Percentage of total surface (%)		
absence of macrophytes	21	15
monospecific meadows of <i>R. cirrhosa</i>	77	85
<i>R. cirrhosa</i> - <i>P. pectinatus</i>	2	0
monospecific meadows of <i>P. pectinatus</i>	0	0

biomass takes place (Menéndez *et al.*, 2003), as suggested by the increase in SRP and DIC in the water column. The increase in DIC is actually delayed in relation to SRP and could also be related to carbonate dissolution due to low pH. On the other hand, a fast release of nutrients is expected due to the high decomposition rate of *R. cirrhosa* biomass (Menéndez *et al.*, 2003; Menéndez *et al.*, 2004). The average expected time to decompose 50% of *R. cirrhosa* biomass in the Albufera des Grau is 2 months (calculated from measured decomposition rates in the Albufera des Grau, authors' unpublished data), and the whole macrophyte community is mineralised after a year cycle (230 days to decompose the 95% of biomass).

The nutrient release is presumably responsible for the autumn proliferation of phytoplankton, as suggested by the synchronous peak in chlorophyll *a* and TP concentrations. The increase in TP could be explained by a release of SRP from the sediments due to low pH, but such an increase in SRP was not observed and SRP actually decreased. This observation, together with the increase in chlorophyll *a*, strongly suggests that SRP is incorporated into phytoplankton and that the peak in TP is thus reflecting phytoplankton growth. The constant or even decreasing DIN, which is synchronous with the increase in SRP, may be due to a fast incorporation of nitrogen into phytoplankton or due to denitrification beneath the dense littoral meadows. Thus, anoxic conditions near the bottom are expected to be common in the littoral areas with large amounts of biomass (Calado and Duarte, 2000). However, the system did not fall into dystrophy as no hypoxia was observed in the open water (the oxygen saturation concentration in the open waters never decreased below 70%; Table 1).

The great reduction of DIC during the macrophyte growing period may cause both phytoplankton and macrophytes to be limited by carbon. Indeed, the minimum CO₂ concentration was below the compensation point described for *R. cirrhosa* (Table 1, Peñuelas and Menéndez, 1990). *R. cirrhosa*, however, is highly adapted to low CO₂ values because of its ability to use HCO₃⁻ (Peñuelas and Menéndez, 1990; Hellblom and Axelsson, 2003). Nonetheless, a HCO₃⁻ concentration below *R. cirrhosa*'s compensation point have been observed in the littoral waters of the Albufera des Grau on a typical summer daily cycle, suggesting growth limitation by inorganic carbon during extremely productive periods (authors' unpublished data).

With regard to the important role that macrophyte meadows play in the lagoon carbon cycle, the question of the stability of such a productive system in relation to the fluctuating physical factors (salinity and water level) emerges. In summer 2001 a new macrophyte mapping was conducted in order to evaluate the recovery of the meadows after the littoral desiccation of the previous summer. In 2001 only monospecific meadows of *R. cirrhosa* were observed, with no presence of *P. pectinatus*. This may be due to the higher salinities observed during the growing period (up to 14-20, unpublished data). As in 2000, dense stands of *R. cirrhosa* occupied littoral areas and sparse individuals were found in the central part of the lagoon. The total meadow area was estimated at 64 ha (Table 3), slightly higher than that observed in 2000. This expansion of *R. cirrhosa*, despite the very low water levels of the previous year, is consistent with the high tolerance to desiccation described for this species (Adams and Bate, 1994; Gesti *et al.*, 2005).

In conclusion, despite the magnitude of carbon fluxes in the lagoon, as exemplified by the huge pCO₂ increase in autumn, the system did not collapse into a dystrophic crisis, as would probably have been the case in a macroalgae-dominated situation in which a faster return of nutrients is expected (Viaroli *et al.*, 1996, Viaroli and Christian, 2003). The phytoplankton proliferation due to nutrient release did not achieve extreme chlorophyll *a* concentrations. Because the water level was below s.l. throughout the year, no outputs to the sea occurred. Consequently, the fast recovery of spring conditions (low phytoplankton and nutrient levels and pCO₂ near atmospheric equilibrium) occurred without the washout of nutrients or organic matter to the sea, and was more related to the internal metabolism of the lagoon. This is in discordance with other similar systems where an export of organic matter and nutrients to the sea or even a harvesting of macrophyte biomass help prevent eutrophication (Calado and Duarte, 2000; Duarte *et al.*, 2002).

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REFERENCES

- Adams, J. and G. Bate. – 1994. The tolerance to desiccation of the submerged macrophytes *Ruppia cirrhosa* (Petagna) Grande and *Zostera capensis* Setchell. *J. Exp. Mar. Biol. Ecol.*, 183: 53-62.
- Ballester, R. – 1985. Biomasa, estacionalidad y distribución de tres macrófitos: *Ruppia cirrhosa*, *Cymodocea nodosa* y *Caulerpa prolifera* en el Mar Menor (Murcia, SE Spain). *Anal. Biol.*, 4, 31-36.
- Barnes, R.S.K. – 1980. *Coastal lagoons*. Cambridge University Press, Cambridge.
- Calado, G. and P. Duarte. – 2000. Modelling growth of *Ruppia cirrhosa*. *Aquat. Bot.*, 68: 29-44.
- Cardona, L. – 2001. Non-competitive coexistence between Mediterranean grey mullet: evidence from seasonal changes in food availability, niche breadth and trophic overlap. *J. Fish Biol.*, 59: 729-744.
- Castel, J., P. Caumette and R. Herbert. – 1996. Eutrophication gradients in coastal lagoons as exemplified by the Bassin d'Arcachon and the Étang du Prévost. *Hydrobiologia*, 329: ix-xxviii.
- Duarte, C. – 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia*, 41: 87-112.
- Duarte, P., J.M. Bernardo, A.M. Costa, F. Macedo, G. Calado and L. Cancela da Fonseca. – 2002. Analysis of coastal lagoon metabolism as a basis for management. *Aquat. Ecol.*, 36: 3-19.
- Gesti, J., A. Badosa and X. Quintana. – 2005. Reproductive potential in *Ruppia cirrhosa* (Petagna) Grande in response to water permanence. *Aquat. Bot.*, 81: 191-198.
- Hansen, H. and F. Koroleff. – 1999. Determination of nutrients. In: K. Grasshoff, K. Kremling and M. Ehrhardt (eds.), *Methods of seawater analysis*, pp. 159-228. Wiley-VCH, Weinheim.
- Hellblom, F. and L. Axelsson. – 2003. External HCO₃⁻ dehydrogenation maintained by acid zones in the plasma membrane is an important component of the photosynthetic carbon uptake in *Ruppia cirrhosa*. *Photosynth. Res.*, 77: 173-181.
- Jeffrey, S. and G. Humphrey. – 1975. New spectrophotometric equations for determining chlorophyll a, b, c1, and c2 in higher plants, algae and phytoplankton. *Biochem. Physiol. Pflanzen*, 167: 191-194.
- Margalef, R. – 1952. Materiales para la hidrobiología de la isla de Menorca. *Pub. Inst. Biol. Apl.*, XI: 5-112.
- Margalef, R. – 1983. *Limnología*. Omega, Barcelona.
- McGlathery, K.J., I.C. Anderson and A.C. Tyler. – 2001. Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. *Mar. Ecol. Prog. Ser.*, 216: 1-15.
- Menéndez, M. – 2002. Net production of *Ruppia cirrhosa* in the Ebro Delta. *Aquat. Bot.*, 73: 107-113.
- Menéndez, M., O. Hernández and F.A. Comín. – 2002. Spatial distribution and ecophysiological characteristics of macrophytes in a Mediterranean coastal lagoon. *Estuar. Coast. Shelf Sci.*, 55: 403-413.
- Menéndez, M., D. Carlucci, M. Pinna, F.A. Comín and A. Basset. – 2003. Effect of nutrients on decomposition of *Ruppia cirrhosa* in a shallow coastal lagoon. *Hydrobiologia*, 506-509: 729-735.
- Menéndez, M., O. Hernández, N. Sanmartí and F.A. Comín. – 2004. Variability of organic matter processing in a Mediterranean coastal lagoon. *Int. Rev. Hydrobiol.*, 89: 476-483.
- Millero, F.J. – 1995. Thermodynamics of the carbon dioxide system in the oceans. *Geochim. Cosmochim. Acta*, 59: 661-677.
- Peñuelas, J. and M. Menéndez. – 1990. HCO₃⁻ as an exogenous carbon source for *Ruppia cirrhosa* (Petagna) Grande. *Arch. Hydrobiol.*, 120(1): 89-96.
- Pérez, M.J. and J. Camp. – 1986. Distribución espacial y biomasa de las fanerógamas marinas de las bahías del Delta del Ebro. *Inv. Pesq.*, 50: 519-530.
- Pretus, J.L. – 1989. Limnología de la Albufera de Menorca (Menorca, España). *Limnetica* 5: 69-81.
- Remane, A. and C. Schlieper. – 1971. *Biology of brackish water*. John Wiley and Sons, New York.
- Stumm, W. and J. Morgan. – 1981. *Aquatic chemistry*. John Wiley and Sons, New York.
- Taylor, D.I., S.W. Nixon, S.L. Granger, B.A. Buckley, J.P. McMahon and H.J. Lin. – 1995. Responses of coastal lagoon plant communities to different forms of nutrient enrichment – a mesocosm experiment. *Aquat. Bot.*, 52: 19-34.
- Valiela, I., J. McClelland, J. Hauxwell, P.J. Behr, D. Hersh and K. Foreman. – 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnol. Oceanogr.*, 42: 1105-1118.
- Verhoeven, J. – 1980a. The ecology of *Ruppia*-dominated communities in western Europe. II. Synecological classification, structure and dynamics of the macroflora and macrofauna communities. *Aquat. Bot.*, 8: 1-85.
- Verhoeven, J. – 1980b. The ecology of *Ruppia*-dominated communities in western Europe. III. Aspects of production, consumption and decomposition. *Aquat. Bot.*, 8: 209-253.
- Viaroli, P., M. Bartoli, C. Bondavalli, R. Christian, G. Giordani and M. Naldi. – 1996. Macrophyte communities and their impact on benthic fluxes of oxygen, sulphide and nutrients in shallow eutrophic environments. *Hydrobiologia*, 329: 105-119.
- Viaroli, P. and R. Christian. – 2003. Description of trophic status, hyperautotrophy and dystrophy of a coastal lagoon through a potential oxygen production and consumption index—TOSI: Trophic Oxygen Status Index. *Ecol. Indic.*, 3: 237-250.

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