Spatiotemporal dynamics of submerged macrophytes in a Mediterranean coastal lagoon

Biel Obrador & Joan Lluís Pretus

obrador@ub.edu

Departament d'Ecologia, Universitat de Barcelona, Av. Diagonal, 645, Barcelona 08028, Spain

POST-PRINT VERSION OF THE ARTICLE

Obrador, B. & Pretus, J.L. 2010. Spatiotemporal dynamics of submerged macrophytes in a Mediterranean coastal lagoon. Estuarine, Coastal and Shelf Science 87: 145-155. https://doi.org/10.1016/j.ecss.2010.01.004

ABSTRACT

The seasonal and interannual dynamics of the biomass and spatial distribution of a macrophyte meadow were explored in a Mediterranean coastal lagoon (Albufera des Grau, Balearic Islands) from 2002 to 2007. The dynamics in the main physicochemical variables were also analysed to assess the factors involved in the spatiotemporal variability of the submerged macrophytes. The meadows were dominated by Ruppia cirrhosa, which showed a marked seasonal cycle with winter quiescence and complete annual regrowth. The annual production of R. cirrhosa had high interannual variability and was amongst the highest described for this species in the literature, ranging 327–919 gDW m-2. The spatial distribution of macrophytes was determined by light availability and wave exposure, with the highest abundances found in shallow and gently sloped areas sheltered from the strong northerly winds. The interannual variations in macrophyte descriptors (area of occurrence, average depth of the meadows, and maximum biomass) were mainly related to water turbidity and salinity, but the effect of these variables was constrained to the spring and summer months, respectively. A significant negative correlation between the extent of coverage of R. cirrhosa and the water level at the end of the previous annual cycle was observed, suggesting a positive effect of desiccation on the extent of coverage of the macrophytes. After six years of apparent stability, the macrophytes abruptly disappeared from the lagoon. Although the mechanisms are not clear, this shift was likely attributable to a combination of several factors.

Introduction

In coastal ecosystems, submerged macrophytes are key species with important structuring, roles serving as habitat and food resources not only for aquatic organisms but also for many waterbird species (Yáñez-Arancibia et al., 1994; Levin et al., 2001). In these highly productive systems, the primary producers are either dominated by rooted macrophytes, macroalgae or phytoplanktonic communities, usually in relation to nutrient levels (Knoppers, 1994; Duarte, 1995; Taylor et al., 1999; Hauxwell and Valiela, 2004; Sand-Jensen and Nielsen, 2004). During the last century, increased nutrient inputs to coastal environments have favoured the spread of fast-growing macroalgae, replacing the original rooted macrophytes and leading to strong environmental alterations (Valiela et al., 1997; Raffaelli et al., 1998). The characterisation of the submerged aquatic vegetation in coastal ecosystems is thus of prime importance for assessing their ecological status (Dennison et al., 1993). Moreover, the shifts in the dominance of primary producers in eutrophic coastal lagoons have recently been interpreted as a sequence of alternative stable states (Trobajo et al., 2002; Viaroli et al., 2008) similar to those in freshwater shallow lakes that inspired the regime shifts theory in ecology (Scheffer et al., 1993).

Apart from this, the characterisation of the dynamics of submerged macrophytes in medium to low impacted systems will contribute to a better understanding of the factors controlling their distribution and abundance under natural conditions (Duarte, 2002). Despite the large number of factors that appear to be involved (Hemminga and Duarte, 2000), salinity and light availability have traditionally received most of the attention. However, the need to consider other factors (physical, geological and geochemical) has recently been highlighted (Koch, 2001; Viaroli et al., 2008).

In Mediterranean coastal lagoons in particular, the need for a comprehensive depiction of macrophyte dynamics based on long-term data sets is especially relevant given the inherently high temporal variability of these environments (Quintana et al., 1998; Comín et al., 2004; Viaroli et al., 2005). Nonetheless, long-term studies reporting the spatiotemporal dynamics of submerged macrophytes in low impacted systems are scarce in the literature. This study aims to characterise the spatiotemporal variability of submerged vegetation in a well-preserved Mediterranean coastal lagoon with dense and extensive macrophyte meadows (Albufera des Grau, Menorca, Western Mediterranean). Extremely high biomass of the euryhaline macrophyte *Ruppia cirrhosa* was recently observed in the lagoon (Obrador et al., 2007). This paper is part of a major research program dealing with the properties and stability of the macrophyte-dominated state in the Albufera des Grau. *R. cirrhosa* is an aquatic angiosperm which often forms dense and productive meadows in European transitional waters (Verhoeven, 1979). It is not considered to be a true seagrass species because it does not occur at

consistently high salinities (Den Hartog, 1970 in Borum et al., 2004). Previous studies have pointed to salinity, water turbidity or the redox status of surface sediments as factors controlling its distribution and abundance (Verhoeven, 1979, 1980; Menéndez and Comín, 1989; Azzoni et al., 2001; Menéndez et al., 2002).

The main objectives of this study were to characterise the spatial, seasonal and interannual dynamics of the macrophyte meadows and to determine the factors involved in the dynamics of submerged vegetation. We also aimed to quantify the variability in annual production of *Ruppia cirrhosa* to confirm the extremely productive character of the lagoon depicted by Obrador et al. (2007). This includes a brief comparison of four methods described in the literature to calculate macrophytic annual production.

Methods

Study site

The Albufera des Grau (surface area 78 ha, volume 1.0 hm³) is an enclosed brackish coastal lagoon located in the northeast coast of the island of Menorca (Balearic Islands, Western Mediterranean; Fig. 1). The lagoon was declared a Nature Park in 1995 and currently does not support recreational, commercial or intense fishing industries. Its average depth is 1.37 m with a maximum of 3 m (Pretus, 1989). The lagoon, which is subject to high seasonal and interannual hydrological variability, is irregularly connected to the sea (Obrador et al., 2008). The freshwater inputs are frequently torrential and are supplied by two streams that drain an area of 56 km². The main land covers in the watershed are comprised of natural vegetation and extensive dry farming land. Currently, the lagoon exhibits dense littoral meadows of *Ruppia cirrhosa*, which attain biomass values of up to 1760 gDW m⁻² (Obrador et al., 2007). Macroalgae (*Polysiphonia* spp ,Gracilaria sp. and *Chaetomorpha crassa*) are currently sparsely observed, but macroalgae-dominated states without macrophytes were also observed in previous decades (Margalef, 1952; Pretus, 1989).

Spatial distribution of macrophytes

The spatial distribution of macrophytes was determined from systematic surveys of the lagoon conducted annually during the period of maximum biomass (summer) for the years 2002–2007. Macrophyte cover was determined by visual observation from a boat, and repeated dives were conducted in order to identify macrophyte species when necessary. The surface of the lagoon was divided into a 25 x 25 m grid and the abundance of each macrophyte species was determined for each unit. Macrophyte abundance was recorded using a percent cover scale with five classes (absent, <25%, 25–50%, 50–75%, >75%). The surface area of occurrence of each species

was calculated, together with the average depth of the meadows weighted by the area assigned to each level of the cover index. The spatial distribution of macrophytes was compared with the basic morphometrical descriptors of the lagoon. The depth (from 0 to 300 cm), slope (from 0 to 90^o) and slope direction (from 0 to 360^o) were calculated for each grid unit from the bathymetry of the lagoon. The effect of the environmental variables on macrophyte cover was evaluated with a factorial regression analysis where the cover index was treated as an ordinal multinomial variable (logit transformed). Complementary 3D graphs were used to better visualise the effects on macrophyte cover, applying a weighted least-squares smoothing method. All the statistics were performed using Statistica 8.0 software.

Biomass and production of Ruppia cirrhosa

The biomass of Ruppia cirrhosa was determined at approximately monthly intervals (weekly in the summer of 2002) from 2002 to 2007. Three littoral sites located within the macrophyte beds (sites A–C; Fig. 1) were sampled by triplicate (except in the years 2005–2007, when site C was not sampled). The biomass was determined with a cylindrical sampler measuring 37 cm in diameter and above-ground biomass was sorted by hand from the core. The biomass measurements were performed until the water level was too high to work with the sampling device. After sorting and cleaning with tap water, the biomass samples were dried (70 °C to constant weight) and weighed. The carbon content of the samples was determined in a CarloErba EA1108 elemental analyser with a mean error of 1%. The mean carbon content of the R. cirrhosa biomass was 36.7 \pm 2.4% DW (n= 70). Four methods to estimate the annual production of Ruppia cirrhosa were compared during three years (from 2002 to 2004) at the three littoral sampling sites. For the first method we followed a harvesting technique described in Menéndez (2002). This method, hereinafter referred to as B b M, is appropriate for thinleaved macrophytes with seasonal development such as R. cirrhosa and estimates changes in biomass correcting for the loss of biomass due to mortality between two sampling times (Menéndez, 2002). Mortality was determined by collecting the detached biomass (D_i) in permanent enclosures of known surface area (4 m²) made of 1 cm plastic mesh located close to the sampling sites. The values of the detached biomass were corrected for decomposition with the equation $M = D \cdot e^{-Kdt}$, where k_d is the decomposition rate (d⁻ ¹), and t is the time interval. We used a decomposition rate of 0.018 d⁻¹, previously estimated for *R. cirrhosa* in the Albufera des Grau with the litter bag method following Menéndez et al. (2004) ($R^2 = 0.85$; n = 54; p < 0.01, author's unpublished data).

The other methods to calculate annual production were: 1) by assuming that annual production equalled the maximum achieved biomass (Congdon and Mccomb, 1979); 2) by summing all of the positive biomass changes between sampling intervals

(Murthy et al., 1986); and 3) by summing the total mortality during a complete year cycle, assuming a turnover of 100%. The differences between the four methods were tested with a non-parametric Kruskall–Wallis test.

Water parameters

The main physicochemical descriptors of the lagoon were monitored in order to evaluate their role in macrophyte dynamics. Monthly water samples were taken at 50-cm depth intervals at a central deep site located in the macrophyte-free area of the lagoon (site P; Fig. 1). Vertical profiles of water salinity and temperature were obtained with field sensors (WTW Multiline-P3 and WTW Cond315i). Salinity is reported using the Practical Salinity Scale. Nutrient concentrations (nitrate, nitrite, ammonia, total phosphorus and SRP) were determined in pre-filtered water samples following standard methods (Hansen and Koroleff, 1999). Data on nitrate concentration were unavailable from January 2003 to May 2003. Water turbidity (K, in m⁻¹) was calculated from the chlorophyll- a concentration with a specific equation for the light attenuation coefficient in the Albufera des Grau, which is mostly associated with pigment concentration in water (Obrador and Pretus, 2008). Pigment concentrations were determined by the trichromatic method after extraction in 90% acetone (Jeffrey and Humphrey, 1975). The percentage of irradiance reaching the bottom of the lagoon was calculated from K and the depth of the water column.

An extensive survey from 2002 to 2004 was conducted to assess spatial variation in salinity by taking vertical profiles at the three littoral sites (A–C, Fig. 1) and at 5–7 sites distributed along the east–west axis of the lagoon. The EW coordinate was categorised in eight zones 200 m wide, and the differences in salinity were tested with a non-parametric Kruskall–Wallis test.

Daily values of water level in the lagoon (in cm above sea level, cm a.s.l.) were measured with a fixed scale near the outlet channel and were provided by the Albufera des Grau Nature Park, together with the time series of local precipitation. The mean, maximum and minimum monthly water temperature was obtained from a time series of daily water temperature, which was in turn calculated from an empirical relationship with air temperature ($R^2 = 0.93$; n = 100; p < 0.001, author's unpublished data). The daily values of air temperature and wind speed were obtained from the nearest (7 km) meteorological station (Spanish Meteorological Institute).

Overall changes in the macrophyte meadows

To evaluate the overall changes in the macrophyte meadows, data for the period 2000–2001 from Obrador et al. (2007) were appended to our data so that we could cover a larger time span. The macrophyte variables that we considered were the total

surface area of occurrence, grouped in shallow (<1 m) and deep (>1 m) areas, the average depth of occurrence (weighted by the surface area of each level of the cover index), the maximum biomass, and the date of the biomass peak (expressed in Julian days). The relationships between the macrophyte descriptors and the limnological and climatic variables were evaluated using a non-parametric Spearman's coefficient at a significance level of 0.01. The factors that we considered were water level (WL), salinity (Sal), turbidity (Turb), percent bottom irradiance (bottIrrad), total dissolved inorganic nitrogen (DIN), soluble phosphorus (SRP), water temperature (Temp), total precipitation (Prec) and mean wind speed (Wind); all factors were analysed using annual, seasonal and monthly averages. Hydrological years (from September to August) were used. Given the near-absence of macrophytes in 2007, an analysis of the whole data set was conducted to identify the variables with anomalous behaviour for that year. We selected those variables for which the 2007 value fell outside the range observed in the period 2000-2006. Relative anomaly for these variables was calculated as the departure from the 2000–2006 range relative to the mean. A multivariate approach was not used given the low number of data points (8 years) in comparison with the number of variables.

Results

Spatial distribution of macrophytes

The total surface covered by macrophytes showed considerable differences between years, but a common pattern in the spatial distribution was observed (Fig. 2). The meadows were dominated by *Ruppia cirrhosa*, but another species, *Potamogeton pectinatus*, was also present. The maximum density of *R. cirrhosa* was observed in the littoral areas, especially in the shallow extensive inlets (Fig. 2).

The depth distribution of the surface area covered by the meadows (Fig. 2b) showed that the lagoon moved from monospecific *Ruppia* meadows in the littoral areas (2002), to mixed beds with *Potamogeton pectinatus*, initially only in the littoral (2003–2005) and finally in the whole depth gradient (2006). In 2007 a drastic reduction of the macrophyte beds occurred at all depths, and only occasional patches with vegetation were observed.

The results of the factorial regression between the cover index and the morphometrical descriptors of the lagoon showed significant effects of depth, slope and slope direction (Table 1). Depth was the main factor for both *Ruppia cirrhosa* and *Potamogeton pectinatus*, as seen from the high likelihood scores in comparison with the other simple models (Table 1). An illustrative graphical visualization of the effects of depth, slope and slope direction on the cover index of *R*.

cirrhosa is shown for the year 2006 (Fig. 3). The highest abundances were found at shallow depths and low slopes, whereas the shallow steep areas on northern exposures showed a pronounced decrease in macrophyte abundance. At greater depths (>100 cm) abundance was lower, and while north-exposed areas were poorly vegetated, south-exposed areas showed high macrophyte abundance.

Temporal dynamics of Ruppia cirrhosa biomass and production estimates

The biomass of Ruppia cirrhosa showed a clear seasonal trend with total disappearance in winter and a growing period starting in spring and leading to the maximum values in summer (Fig. 4). All sites showed the same seasonal pattern and only differed in peak biomass. High interannual variability was observed, with a decrease in biomass from 2002 to 2004 (peak values ranging 718–919 gDW m⁻² in 2002, and 327–476 gDW m⁻² in 2004). After a recovery of the maximum biomass to values above 500 gDW m^{-2} in 2005–2006, the biomass of *R*. cirrhosa was undetectable in 2007. The temporal pattern of biomass loss by mortality of Ruppia cirrhosa showed high variability between sites and years. The detached biomass in the enclosures was on average less than 15% of the living biomass during the sampling interval (Fig. 4). Continuous biomass loss was observed during the study period every year, but some anomalous patterns were observed such as the massive mortality at the beginning of the sampling period at site C in 2002 and at the end of the annual cycle at site B in 2003 (in which cases biomass production was not estimated). In 2004, detached biomass values at sites A and B were much lower than in the previous years, and visual observations showed that those enclosures did not reflect the general macrophyte density of the site.

The comparison of the four methods to estimate annual production yielded no significant differences (Kruskall– Wallis = 0.71; N = 12; p = 0.87), with a relative s.d. of 6% between methods on average (Table 2). If the anomalous value of the estimate based on total mortality for 2004 is omitted, the production estimates ranged from 154 to 324 gC m⁻² y⁻¹.

Water parameters and pigment concentration in the water column

The chlorophyll-a concentration did not show a clear seasonal pattern, and erratic peaks were observed annually (Fig. 5a). A basal concentration of chlorophyll below 15–20 mg L⁻¹ was observed every year, but values above 100 mg L⁻¹ were reached during the peaks. Such extremes declined rapidly and pulses did not last more than one or two months, but every year showed a different pattern of recovery to the basal condition. The calculated water turbidity, expressed as the light attenuation coefficient, ranged 0.82– 3.32 m⁻¹ (Fig. 5a). The years 2002 and 2005 were characterised by continuous low turbidity, whereas long turbid periods were observed from March 2003 to August 2004 and from July 2006 to March 2007. The timing of the

phytoplankton peaks was roughly in accordance with peaks of nutrient concentration in the water, mainly nitrogen (Fig. 5b). The ammonia concentration was below 5 mM most of the time, with occasional peaks above 10 mM (maximum of 28 mM on July 2006). The peaks of nitrate were typically observed in spring and autumn, with maximum values of 26 mM, whereas during the rest of the year nitrate was below 1 mM. Despite the fact that the dynamics of both nutrients were highly erratic, the nitrate peaks were temporally coincident with torrential inputs from the watershed, identified by sharp increases in water level during rainy periods (Fig. 5c). Ammonia levels, by contrast, were unrelated to water inputs. Water salinity ranged from 2.7 to 18.9 and showed a clear seasonal pattern with maximum and minimum values in early autumn and late spring, respectively (Fig. 5c). During the transect salinity survey no significant differences in salinity were observed between the sampling sites (Kruskall–Wallis = 0.16; N = 148; p = 0.98), nor between the categorised EW coordinates (Kruskall–Wallis = 6.4; N = 339; p = 0.49). The standard deviation in salinity between sites was always below 1.4 units (mean s.d. 0.33 ± 0.31).

Overall changes in the macrophyte meadows

The overall pattern of variation in macrophyte cover for the period 2000–2007 is shown in Fig. 6 by grouping the different depths into shallow (0–1 m) and deep (above 1 m). The decrease in the distribution of *Ruppia cirrhosa* observed from 2001 to 2004 is associated with declines in the deep areas of the lagoon (total decrease of 86% from 2001 to 2004) rather than to declines in the littoral zone (decrease of 40%). The other macrophyte descriptors (i.e., the weighted average depth of the meadows and the maximum achieved biomass) showed a similar pattern of annual variation. The mean depth of *R. cirrhosa* beds was 0.87 ± 0.35 m (Fig. 6).

The significant relationships between the macrophyte descriptors and the water and climatic variables for the period with macrophytes (2000–2006) are shown in Table 3. Given the lower number of data points for *Potamogeton pectinatus* (4 years) the analysis was only performed for *Ruppia cirrhosa*. The total area of occurrence and the area of deep meadows were both positively correlated with salinity and this influence was restricted to the summer months (June–August), with no effect of salinity in spring. The total area of occurrence and the average depth of the meadows were both positively correlated with light availability (as seen by the water turbidity itself and by the percent bottom irradiance). In both cases the relationships were restricted to spring months (from March to May). A negative correlation between the area of the meadows and the water level of the previous September and October was observed. The date of the maximum biomass was highly negatively correlated with the maximum temperature in April.

The anomalies in the environmental variables for the year 2007 are shown in Fig. 7.

The variables in 2007 that fell outside the range of variation during the period 2000–2006 were related to water level, temperature, turbidity, nutrient concentrations, rainfall and wind speed. The largest anomalies were observed in the precipitation in April, with a value 180% higher than the mean in 2000–2006, and in the turbidity during autumn and winter months (between 40% and 115% higher). The year 2007 was also characterised by low water levels in winter, high phosphorus and nitrate concentrations in September and March, respectively, and low ammonia and total DIN in autumn and summer, despite the fact that these variables showed large variability during the reference period, as seen by the high relative standard deviations (Fig. 7).

Discussion

Spatial distribution

Horizontal salinity gradients are a common feature of many coastal ecosystems and often determine the spatial distribution of macrophytes (Menéndez et al., 2002; Agostini et al., 2003; Lirman et al., 2008). Nonetheless, in the Albufera des Grau, the spatial distribution of macrophytes cannot be explained by salinity variations because no significant horizontal gradients were observed. The lack of horizontal gradients has also been described for water turbidity in this system (Obrador and Pretus, 2008).

The results of the factorial regressions showed that depth was the main factor that explained the spatial distribution of macrophytes, thus suggesting that light limitation has a major effect on their distribution. This finding is in accordance with previous observations that macrophyte light limitation potentially occurs across considerable areas of the lagoon throughout the annual cycle (Obrador and Pretus, 2008). Nonetheless, the best models to explain macrophyte cover where those that included the combined effect of depth, slope and slope direction (Table 1). The areas exposed to the north showed a marked reduction of macrophyte abundance, especially in shallow areas with steep slopes. These results likely reflect an avoidance of wave stress generated by the strong northerly winds, which are dominant in frequency and strength on the island (Jansa`, 1979). The importance of physical factors such as slope and wave exposure on the spatial distribution of submerged macrophytes has been observed previously in other systems (Berglund et al., 2003; Charpentier et al., 2005; Feldmann and Noges, 2007). The effect of slope may be related not only to the associated wave stress but also to other factors such as sediment stability (Duarte and Kalff, 1986). Given the combined effect of depth, slope and slope direction observed in this study, and given the low fit or even non-significance of the models based only on slope (Table 1), the direct effect of wave stress on macrophyte meadows is the most plausible explanation. Such an effect may include several mechanisms such as

changes in plant morphology, edge erosion, direct breakage or seed accumulation (Koch, 2001; Steinhardt and Selig, 2007). Interestingly, the significance of the geospatial models was maintained in the different years, thus highlighting the robustness of the depth and depth–slope direction models in explaining macrophyte occurrence.

Biomass dynamics and production estimates

In permanent waters, *Ruppia cirrhosa* typically shows an annual life cycle with winter quiescence and vegetative growth from stolons (Verhoeven, 1979), although perennial stands have also been observed elsewhere (Gesti et al., 2005). In this study, the stands of *R. cirrhosa* showed a clear seasonal development with winter disappearance and complete annual regrowth.

With regard to the production estimates, all four methods used to estimate the annual production of *Ruppia cirrhosa* gave similar results. It is often assumed that macrophyte mortality is on the same order of magnitude as variations in biomass (Menéndez, 2002; Bartoli et al., 2008). However, in this study, the detached biomass was always a minor fraction of the living biomass. The permanent enclosures used to estimate macrophyte mortality occasionally exhibited a different pattern than the adjacent meadows. Higher sampling effort would be necessary to accurately estimate mortality, with replicate enclosures at each site, higher frequency samplings, and continuous evaluation of the state of the enclosures. Given the required sampling effort, the associated uncertainty of the B \wp M method, and the complete annual regrowth observed during the study period, the annual production of *R. cirrhosa* appears to be adequately estimated simply from the maximum achieved biomass (Casagranda and Boudouresque, 2007).

The maximum biomass observed during the study period ranged from 120 to 337 gC m⁻². These values are lower than the extreme peak biomass observed in 2000 (up to 646 gC m⁻²; Obrador et al., 2007), but are still among the highest values reported for *Ruppia cirrhosa* in the literature (Verhoeven, 1980; Calado and Duarte, 2000; Azzoni et al., 2001; Menéndez, 2002; Pasqualini et al., 2006; Pergent et al., 2006; Casagranda and Bou- douresque, 2007; Bartoli et al., 2008). Moreover, our results place the macrophyte meadows in the Albufera des Grau in the upper range of production for macrophyte-dominated ecosystems, which are typically in the range of 150–400 gC m⁻² y⁻¹ (Knoppers, 1994; Gattuso et al., 1998; Duarte and Chiscano, 1999). Such high production contrasts with the role of light limitation in the spatial distribution of macrophytes. This may be explained by the fact that the production estimates were performed in littoral areas where light limitation is not expected to affect macrophytes, in accordance with previous observations (Obrador and Pretus, 2008). Nonetheless, further research is needed to determine the factors responsible

for the high macrophytic production measured in this system.

With regard to the phenology of the meadows, Verhoeven (1979) observed that the growth and flowering of *Ruppia cirrhosa* were related to water temperature and that the decay of the vegetation took place after four months of exponential growth. With the methodology used in this study, we could not determine the beginning of the exponential growth period. Instead, we worked with the date of the maximum biomass. The marked negative relationship between the maximum temperature in April and the date of maximum biomass may be related to the shift from winter quiescence to exponential growth, in accordance with Verhoeven (1979). In cold years with lower spring water temperatures, exponential growth starts later in spring and the maximum biomass is achieved later. On the contrary, in years with warmer springs, the winter quiescence ends earlier and the maximum biomass is achieved early in the summer.

Overall trends in the macrophyte meadows

The meadows of Ruppia cirrhosa in the Albufera des Grau showed considerable interannual variability. While we cannot rule out an interaction with *Potamogeton pectinatus* (Kautsky, 1991), our results show that the main factors involved in the interannual dynamics of R. cirrhosa were water level, water salinity and light availability. The hydrological variables of the lagoon showed a marked seasonal trend which is mainly driven by the precipitation-evaporation regime of the Mediterranean climate (Obrador et al., 2008). The other water variables, namely nutrients and water turbidity, showed the highly variable dynamics with erratic peaks characterizing coastal lagoons (Quintana et al., 1998; Comín et al., 2004). The positive effect of summer salinity on the area of occurrence of macrophytes must be understood in the context of the current range of salinity (oligo-mesohaline; Fig. 5) because this relationship could change in magnitude or direction if different ranges of salinity were to be considered. Nonetheless, our results are in accordance with the salinity tolerance described for Ruppia cirrhosa (Verhoeven, 1979; Menéndez and Comín, 1989). On the other hand, the effect of light availability was constrained to the growing period during the spring months. The absence of a correlation after the initial growing period is not surprising given the relatively rapid velocity at which the canopy of *R. cirrhosa* reaches the water surface and the importance of self-shading rather than water turbidity in the attenuation of light beneath the meadows (Calado and Duarte, 2000).

The negative correlation between the area of meadows and the water level of the previous autumn might be related to higher bottom irradiance due to low water levels, but this is not very likely because no significant relationship with bottom irradiance during autumn months was observed (Table 3). Moreover, the water level in September and October was in the lowest range of variation (from -65 to 7 cm a.s.l.

in September; Table 3) which implies considerable littoral desiccation. For *Ruppia cirrhosa*, one might expect a positive relationship between water level and the macrophyte descriptors, as a result of the lethal effect of desiccation

on this species (Verhoeven, 1979) which only tolerates desiccations shorter than 5 h (Adams and Bate, 1994). Our results, however, suggest that desiccation is not only not lethal nor sub-lethal for *R. cirrhosa*, but rather favours its coverage extent in the following year. One hypothesis to explain this may be related to a high plasticity of reproductive effort in this species in relation to water permanency. Gesti et al. (2005) described higher seed production in temporarily flooded environments than in permanently submerged ones, where vegetative growth from stolons dominates and plant fructification is minimal. Similar resource allocation into seed production under desiccation stress was reported for *Ruppia maritima* by Costa and Seeliger (1989). Thus, we hypothesise that the lagged negative relationship between the area of the meadows and the water level at the end of the previous annual cycle observed in this study may be related to increased seed production and a further expansion of the meadows.

With regard to the disappearance of the meadows in 2007, the mechanisms involved in such a drastic reduction in coverage are far from evident. It could be hypothesised that the disappearance was related to the runoff of herbicides from farmlands in the watershed. This is not likely given the rather non-intensive agricultural practises in the watershed (M. Truyol, 2008 pers. comm.), and because healthy stands of Ruppia cirrhosa are easily found in systems with polluted agriculture-derived water inputs, such as those found in the Ebro Delta (Menéndez et al., 2002). Alternatively, despite we did not evaluate the redox potential of surface sediments, it is unlikely that sulphide release is responsible for the macrophyte collapse (Azzoni et al., 2001). Bottom oxygen concentration in the lagoon was not especially low in 2007 in comparison with other years (data not shown), and previous studies have demonstrated that summer bottom hypoxia is of minor importance in the lagoon, even beneath the dense macrophyte meadows (Obrador, 2009). At this level of empirical approach, it is more plausible that the macrophyte disappearance is related to a combination of several naturally driven factors. Firstly, the correlation analysis showed that those variables that were markedly correlated with the macrophyte descriptors, namely summer salinity and spring light availability, also maintained the significance of the correlation when the year 2007 was included in the analysis (Table 3). Low levels of bottom irradiance in May and low salinity in summer (Fig. 5) could have triggered macrophyte decline. Secondly, the search for anomalies in 2007 showed that this year was characterised by extremely high precipitation in April. This may be related to the increased turbidity in May from nutrients entering into the lagoon, but, as stated above, neither the nutrient concentration nor the turbidity in May was out of range (Fig. 7). Apart from this, the anomalously high turbidity, mainly in autumn, could accelerate macrophyte decline in the following year, preventing them from performing possible phenological functions later in the life cycle such as resource reallocation in belowground tissues. Assuming this argument is plausible, both lagged (fall) and current (spring) light limitations would have combined to prevent macrophytic emergence in 2007.

Temporal changes in the sensitivity of macrophytes to the different environmental factors were strongly relevant. In an applied context, an understanding of the temporal sequence of this sensitivity appears to be fundamental to design adequate targets in the management of coastal lagoons. Moreover, it highlights that approaches to coastal lagoon ecology based on annual averages are misleading. Changing sensitivity together with the large interannual variability of coastal ecosystems necessitates that any approach to ascertain the factors that drive the dynamics of submerged vegetation in these environments requires a temporally extended and seasonally explicit analysis of the system.

Conclusions

The macrophyte meadows in the Albufera des Grau were characterised by high peak biomass values for *Ruppia cirrhosa*, indicating that the Albufera des Grau is among the most productivesystems for this species. The spatial distribution of macrophytes was determined by light availability and wave stress. Considerable interannual variability was observed in annual production and in the basic descriptors of the status of the meadows, whose dynamics were mainly related to water salinity and light availability in summer and spring, respectively. Despite the apparent stability of the meadows observed during the early years of the study, the system sharply shifted to a nonvegetated state. Meadow disappearance may be related to a combination of several factors with lagged influences along the life cycle of the macrophytes.

Acknowledgements

This study was funded by the Govern de les Illes Balears, the Consell Insular de Menorca and the Spanish Ministry of Education and Science (project CGL2008-05095/BOS). BO was supported by a BRD grant from the University of Barcelona. We acknowledge Margarita Menéndez for her help in the design of the production enclosures, and Sam Pons, Melisa Gañán, and the staff of the Albufera des Grau Nature Park for their assistance in the field work. Valuable comments from Miquel Truyol and Margarita Menéndez are also highly appreciated. Three anonymous reviewers contributed a great deal to the improvement of the original manuscript.

References

Adams, J., Bate, G., 1994. The tolerance to desiccation of the submerged macrophytes Ruppia cirrhosa (Petagna) Grande and Zostera capensis Setchell. Journal of Experimental Marine Biology and Ecology 183, 53–62.

Agostini, S., Capiomont, A., Marchand, B., Pergent, G., 2003. Distribution and estimation of basal area coverage of subtidal seagrass meadows in a Mediterranean coastal lagoon. Estuarine, Coastal and Shelf Science 56, 1021–1028.

Azzoni, R., Giordani, G., Bartoli, M., Welsh, D.T., Viaroli, P., 2001. Iron, sulphur and phosphorus cycling in the rhizosphere sediments of a eutrophic Ruppia cirrhosa meadow (Valle Smarlacca, Italy). Journal of Sea Research 45, 15–26.

Bartoli, M., Nizzoli, D., Castaldelli, G., Viaroli, P., 2008. Community metabolism and buffering capacity of nitrogen in a Ruppia cirrhosa meadow. Journal of Experimental Marine Biology and Ecology 360, 21–30.

Berglund, J., Mattila, J., Ronnberg, O., Heikkila, J., Bonsdorff, E., 2003. Seasonal and interannual variation in occurrence and biomass of rooted macrophytes and drift algae in shallow bays. Estuarine, Coastal and Shelf Science 56, 1167–1175.

Borum, J., Duarte, C.M., Krause-Jensen, D., Greve, T. (Eds.), 2004. European Seagrasses: An Introduction to Monitoring and Management. The Monitoring and Management of European Seagrasses. European Union, Copenhagen, p. 95.

Calado, G., Duarte, P., 2000. Modelling growth of Ruppia cirrhosa. Aquatic Botany 68, 29–44.

Casagranda, C., Boudouresque, C.F., 2007. Biomass of Ruppia cirrhosa and Potamogeton pectinatus in a Mediterranean brackish lagoon, Lake Ichkeul, Tunisia. Fundamental and Applied Limnology 168, 243–255.

Charpentier, A., Grillas, P., Lescuyer, F., Coulet, E., Auby, I., 2005. Spatio-temporal dynamics of a Zostera noltii dominated community over a period of fluctuating salinity in a shallow lagoon, Southern France. Estuarine, Coastal and Shelf Science 64, 307–315.

Comín, F.A., Menéndez, M., Herrera, J., 2004. Spatial and temporal scales for monitoring coastal aquatic ecosystems. Aquatic Conservation: Marine and Freshwater Ecosystems 14, S5–S17.

Congdon, R.A., Mccomb, A.J., 1979. Productivity of Ruppia: seasonal changes and dependence on light in an Australian estuary. Aquatic Botany 6, 121–132.

Costa, C.S., Seeliger, U., 1989. Vertical distribution and resource allocation of Ruppia maritima L. in a southern Brazilian estuary. Aquatic Botany 33, 123–129.

Den Hartog, C., 1970. The Seagrasses of the World. North Holland Publishing Company, Amsterdam, 275 pp.

Dennison, W., Orth, R., Moore, K., Stevenson, J., Carter, V., Kollar, S., Bergstrom, P., Batiuk, R., 1993. Assessing water quality with submersed aquatic vegetation. BioScience 43, 86–94.

Duarte, C.M., Kalff, J., 1986. Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. Limnology and Oceanography 31, 1072–1080.

Duarte, C.M., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41, 87–112.

Duarte, C.M., Chiscano, C.L., 1999. Seagrass biomass and production: a reassessment.

Aquatic Botany 65, 159–174.

Duarte, C.M., 2002. The future of seagrass meadows. Environmental Conservation 29, 192–206.

Feldmann, T., Noges, P., 2007. Factors controlling macrophyte distribution in large shallow Lake Vo[~]rtsja[~] rv. Aquatic Botany 87, 15–21.

Gattuso, J.P., Frankignoulle, M., Wollast, R., 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. Annual Review of Ecology and Systematics 29, 405–434.

Gesti, J., Badosa, A., Quintana, X.D., 2005. Reproductive potential in Ruppia cirrhosa (Petagna) Grande in response to water permanence. Aquatic Botany 81, 191–198. Hansen, H., Koroleff, F., 1999. Determination of nutrients. In: Grasshoff, K., Kremling, K., Ehrhardt, M. (Eds.), Methods of Seawater Analysis. Wiley-VCH,

Wenheim, pp. 159–228.

Hauxwell, J., Valiela, I., 2004. Effects of nutrient loading on shallow seagrass- dominated coastal systems: patterns and processes. In: Nielsen, S., Banta, G., Pedersen, M.F. (Eds.), Estuarine Nutrient Cycling: The Influence Of Primary Producers. Kluwer, Dordrecht, pp. 59–92. Hemminga, M.A., Duarte, C.M. (Eds.), 2000. Seagrass Ecology. Cambridge University Press,

Cambridge, p. 298.

Jansa`, A., 1979. Climatologia de Menorca. In: Vidal, J.M. (Ed.), Enciclope`dia de Menorca. Obra Cultural de Menorca, Mao´, pp. 85–160.

Jeffrey, S., Humphrey, G., 1975. New spectrophotometric equations for determining chlorophyll a, b, c1, and c2 in higher plants, algae and phytoplankton. Biochemie und Physiologie der Pflanzen 167, 191–194.

Kautsky, L., 1991. In situ experiments on interrelationships between six brackish macrophyte species. Aquatic Botany 39, 159–172.

Koch, E.W., 2001. Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. Estuaries 24, 1–17. Knoppers, B., 1994. Aquatic primary production in coastal lagoons. In: Kjerfve, B.

(Ed.), Coastal Lagoon Processes. Elsevier Science, Amsterdam, pp. 243–286.

Levin, L.A., Boesch, D.F., Covich, A., Dahm, C., Erse´us, C., Ewel, K.C., Kneib, R.T., Moldenke, A., Palmer, M.A., Snelgrove, P., Strayer, D., Weslawski, J.M., 2001. The function of marine critical transition zones and the importance of sediment biodiversity. Ecosystems 4, 430–451.

Lirman, D., Deangelo, G., Serafy, J., Hazra, A., Smith-Hazra, D., Herlan, J., Luo, J., Bellmund, S., Wang, J., Clausing, R., 2008. Seasonal changes in the abundance and distribution of submerged aquatic vegetation in a highly managed coastal lagoon. Hydrobiologia 596, 105–120.

Margalef, R., 1952. Materiales para la hidrobiología de la isla de Menorca.

Publicaciones del Instituto de Biologí a Aplicada XI, 5–112.

Menéndez, M., Comín, F.A., 1989. Seasonal patterns of biomass variation of Ruppia cirrhosa

(Petagna) Grande and Potamogeton pectinatus L. in a coastal lagoon. Scientia Marina 53, 633–638.

Menéndez, M., 2002. Net production of Ruppia cirrhosa in the Ebro Delta. Aquatic Botany 73, 107–113.

Menéndez, M., Herna' ndez, O., Comín, F.A., 2002. Spatial distribution and ecophysiological characteristics of macrophytes in a Mediterranean coastal lagoon. Estuarine, Coastal and Shelf Science 55, 403–413.

Menéndez, M., Herna' ndez, O., Sanmartı', N., Comín, F.A., 2004. Variability of organic matter processing in a Mediterranean coastal lagoon. International Review of Hydrobiology 89, 476–483.

Murthy, M.S., Ramakrishna, T., Sarat-Babu, G.V., Rao, Y.N., 1986. Estimation of net primary productivity of intertidal seaweeds – limitations and latent problems. Aquatic Botany 23, 383–387.

Obrador, B., Pretus, J.L., Menéndez, M., 2007. Spatial distribution and biomass of aquatic rooted macrophytes and their relevance in the metabolism of a Mediterranean coastal lagoon. Scientia Marina 71, 57–64.

Obrador, B., Pretus, J.L., 2008. Light regime and components of turbidity in a Mediterranean coastal lagoon. Estuarine, Coastal and Shelf Science 77, 123–133.

Obrador, B., Moreno-Ostos, E., Pretus, J.L., 2008. A dynamic model to simulate water level and salinity in a Mediterranean coastal lagoon. Estuaries and Coasts 31, 1117–1129.

Obrador, B., 2009. Environmental Shaping and Carbon Cycling in a Macrophyte- dominated Coastal Lagoon. Ph.D. thesis. University of Barcelona, Barcelona, 215 pp.

Pasqualini, V., Pergent-Martini, C., Fernandez, C., Ferrat, L., Tomaszewski, J.E., Pergent, G., 2006. Wetland monitoring: aquatic plant changes in two Corsican coastal lagoons (Western Mediterranean Sea). Aquatic Conservation: Marine and Freshwater Ecosystems 16, 43–60.

Pergent, G.R., Pasqualini, V., Pergent-Martini, C., Ferrat, L., Fernandez, C., 2006. Variability of Ruppia cirrhosa in two coastal lagoons with differing anthropogenic stresses. Botanica Marina 49, 103–110.

Pretus, J.L., 1989. Limnologı´a de la Albufera de Menorca (Menorca, Espan˜a).

Limnetica 5, 69–81.

Quintana, X., Moreno-Amich, R., Comín, F.A., 1998. Nutrient and plankton dynamics in a Mediterranean salt marsh dominated by incidents of flooding. Part 1: differential confinement of nutrients. Journal of Plankton Research 20, 2089–2107.

Raffaelli, D., Raven, J., Poole, L., 1998. Ecological impact of green macroalgal blooms. In: Ansell, A., Gibson, R., Barnes, M. (Eds.), Oceanography and Marine Biology: An Annual Review. Routledge, pp. 97–125.

Sand-Jensen, K., Nielsen, S., 2004. Estuarine primary producers. In: Nielsen, S., Banta, G., Pedersen, M. (Eds.), Estuarine Nutrient Cycling: The Influence of Primary Producers. Kluwer, Dordrecht, pp. 17–57.

Scheffer, M., Hosper, H., Meijer, M.-L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in

shallow lakes. Trends in Ecology and Evolution 8, 275–279.

Steinhardt, T., Selig, U., 2007. Spatial distribution patterns and relationship between recent vegetation and diaspore bank of a brackish coastal lagoon on the southern Baltic Sea. Estuarine, Coastal and Shelf Science 74, 205–214.

Taylor, D., Nixon, S., Granger, S., Buckley, B., 1999. Responses of coastal lagoon plant communities to levels of nutrient enrichment: a mesocosm study. Estuaries 22, 1041–1056.

Trobajo, R., Quintana, X., Moreno-Amich, R., 2002. Model of alternative predominance of phytoplankton–periphyton–macrophytes in lentic waters of Mediterranean coastal wetlands. Archiv Fur Hydrobiologie 154, 19–40.

Valiela, I., Mcclelland, J., Hauxwell, J., Behr, P.J., Hersh, D., Foreman, K., 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnology and Oceanography 42, 1105–1118.

Verhoeven, J.T.A., 1979. The ecology of Ruppia-dominated communities in Western Europe. I. Distribution of Ruppia representatives in relation to their autecology. Aquatic Botany 6, 197–267.

Verhoeven, J.T.A., 1980. The ecology of Ruppia-dominated communities in Western Europe. III. Aspects of production, consumption and decomposition. Aquatic Botany 8, 209–253.

Viaroli, P., Mistri, M., Troussellier, M., Guerzoni, S., Cardoso, A., 2005. Preface: structure, functions and ecosystem alterations in Southern European coastal lagoons. Hydrobiologia 550, 7–9.

Viaroli, P., Bartoli, M., Giordani, G., Naldi, M., Orfanidis, S., Zaldı´var, J.M., 2008. Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: a brief overview. Aquatic Conservation: Marine and Freshwater Ecosystems 18, S105–S117.

Yáñez-Arancibia, A., Lara Domi´nguez, A., Pauly, D.,1994. Coastal lagoons as fish habitats. In: Kjerfve, B. (Ed.), Coastal Lagoon Processes. Elsevier, Amsterdam, pp. 363–376.

Figures and tables



Fig. 1. Location and bathymetric map (50 cm isobaths) of the Albufera des Grau coastal lagoon on the Island of Menorca (western Mediterranean). The sampling sites (crosses) and the freshwater inputs (grey arrows) are shown.



Fig. 2. Spatial distribution of the macrophyte meadows during the period 2002–2007, with the percent cover (colour scale) of *R. cirrhosa* (a). The depth distribution of the monospecific and mixed meadows (from black to light grey) is shown in (b).



Fig. 3. 3D plots of the effects of the morphometric descriptors on the abundance of *R*. *cirrhosa* for the year 2006. The equal abundance isolines in the plane defined by the slope and the slope direction are shown for the shallow (0–100 cm, left panel) and deep (>100 cm, right panel) areas of the lagoon.



Fig. 4. Temporal dynamics of *R. cirrhosa* biomass (mean \pm s.e.) at each sampling site (filled symbols). The open symbols refer to the detached biomass (*D*) between two sampling intervals in the permanent enclosures used for the production estimates in the period 2002–2004. Site C was not sampled after the year 2005.



Fig. 5. Temporal dynamics of the water variables during the study period. The concentration of chlorophyll-a and the resulting calculated water turbidity are shown in (a); the nutrient concentrations are shown in (b) and the hydrological variables (water salinity, daily water level (WL) and daily precipitation) are shown in (c). The asterisk indicates the absence of data of nitrate concentration (see text for details).



Fig. 6. Annual changes in the macrophyte descriptors and in the main environmental variables for the period 2000–2007. The surface area covered by *R. cirrhosa* is shown in (a). The colours in the bars refer to the surface area corresponding to the shallow (0–100 cm) and deep (>100 cm) areas of the lagoon. The lines are the average depth of occurrence (dark symbols) and the peak biomass of *R. cirrhosa* (open symbols). The mean \pm s.d. of the summer salinity (b), water level (WL) in autumn (c), and percent bottom irradiance in spring (d) are also shown.



Fig. 7. Relative anomaly of the year 2007 in relation to the period 2000–2006 for the selected climatic and limnological variables. The relative anomaly is defined as the departure from the 2000–2006 range relative to the mean (see text for details). The relative standard deviation (r.s.d.) in the period 2000–2006 is also shown for comparison (line). The legend below the bars indicates if the variable refers to the annual (AN), seasonal (uppercase) or monthly (lowercase) values (codes for season: AUT: autumn, WIN: winter, SPR: spring, SUM: summer).

Table 1. Results of the factorial regression to assess the relationship between the morpho- metric descriptors and the cover index of *R. cirrhosa* and *P. pectinatus*. The likelihood scores of the significant models (p < 0.01) for each year are shown. (n.s.: not significant).

		Likelihood sc	_			
Model	d.f.	2002	2003	2004	2005	2006
R. cirrhosa						
Depth	1	361.2	463.4	308.1	462.6	302.3
Slope	1	52.6	61.2	12.5	n.s.	54.2
Direction	1	12.7	16.3	21.9	35.4	43.4
Depth + slope	2	367.6	494.8	313.0	464.8	338.9
Depth + direction	2	374.9	483.2	334.9	511.2	352.0
Slope + direction	2	65.4	73.8	32.3	38.1	91.6
Depth + direction + slope	3	381.4	511.5	338.3	512.2	383.2
P. pectinatus						
Depth	1	_	109.4	303.3	295.9	423.6
Slope	1	_	46.5	62.8	11.5	33.2
Direction	1	_	n.s.	13.7	48.2	43.4
Depth + slope	2	_	142.5	347.1	304.6	441.2
Depth + direction	2	_	111.9	320.9	356.2	474.6
Slope + direction	2	_	47.4	73.0	56.6	71.9
Depth + direction + slope	3	-	144.0	361.1	361.8	488.5

	B + M	Maximum biomass	Biomass increment	Total s
			mortality	
2002	324 ± 8	312 ± 42	291 ± 70	304 ± 57
2003	270 ± 82	233 ± 71	233 ± 71	236 ± 185
2004	180 ± 40	154 ± 31	154 ± 30	85 ± 82

Table 2. Annual production estimates of *R. cirrhosa* (gC m⁻² y⁻¹). The mean and s.d. of the three sampling sites are shown for each method.

Table 3. Spearman's rank correlations between the macrophyte descriptors for *R. cirrhosa* and the limnological and climatic variables. Only the significant relationships are shown (p < 0.01). Codes as in Fig. 7 (see text for details on the codes of the variables). The (b) in brackets indicate those correlations that were also significant when the year 2007 was included in the analysis. The range observed in the period 2000–2006 is shown for reference.

Macrophyte descriptor	Predictor	Spearman's R		Range 2000–2006	
Total area of occurrence	WL (Sep)	-0.96		(-65; 7) cm a.s.l.	
(22; 61) ha	WL (Oct)	-1.00		(-53; 22) cm a.s.l.	
	Sal (Jul)	0.89	(þ)	(6; 18)	
	Sal (Aug)	0.89	(þ)	(10; 22)	
	Turb (May)	-0.94		(0.8; 1.4) m⁻¹	
	bottIrrad (May)	0.94	(þ)	(1.2; 11.1)%	
	bottIrrad (AN)	0.89	(þ)	(1.2; 10.8)%	
Area of occurrence	WL (Sep)	-0.96		(-65; 7) cm a.s.l.	
(shallow) (18; 31) ha	WL (Oct)	-0.93		(-53; 22) cm a.s.l.	
Area of occurrence	WL (Sep)	-0.93		(-65; 7) cm a.s.l.	
(deep) (4; 31) ha	WL (Oct)	-0.96		(-53; 22) cm a.s.l.	
	Sal (Jun)	0.89	(þ)	(4; 16)	
Average depth (56; 104) cm	WL maximum (AN)	-0.96		(-16; 96) cm a.s.l.	
	Turb (Mar)	-0.89	(þ)	(0.8; 3.3) m ⁻¹	
	Turb (Apr)	-0.96	(þ)	(0.8; 2.3) m ⁻¹	
	Wind (Jun)	0.96	(þ)	(3.6; 4.6) m s ⁻¹	
	bottIrrad (Mar)	0.89	(þ)	(0.1; 10.5)%	
	bottIrrad (Apr)	0.93	(þ)	(0.1; 10.3)%	
Maximum biomass	Turb (Aug)	-0.94		(0.9; 2.6) m⁻¹	
(476; 1760) gDW m ⁻²	SRP (Jul)	-0.94		(0.7; 14.2) mM	
Date of the peak	Temp maximum	-1.00		(18.2; 21.8) ^o C	
(130; 249) Julian d	(Apr)				