Light regime and components of turbidity in a Mediterranean coastal lagoon

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ABSTRACT

The underwater light regime of a Mediterranean coastal lagoon (Albufera des Grau, Balearic Islands) was studied during four years in order to characterise the spatial and temporal variations in the light attenuation coefficient (K) and to assess the relative contribution of the different water components to total light attenuation.

During the studied period K averaged 1.42 m^{-1} and ranged from 0.63 m^{-1} to 3.80 m^{-1}. High temporal variability was observed in light attenuation coefficients, but the lagoon was spatially uniform.

Percentage bottom irradiance in relation to specific requirements for the dominant macrophyte species (*Ruppia cirrhosa*) was used as an indicator of benthic light limitation. Macrophyte light limitation was expected to occur in the deepest areas of the lagoon during winter, the most turbid period of the annual cycle. During the macrophyte growing season, higher bottom irradiances were observed but a significant percentage of the lagoon benthos (17% in spring and 7% in summer) was expected to be light limited.

In the deepest areas of the lagoon (>2 m) changes in bottom irradiance were related more to variations in the light attenuation coefficient than to variations in water level. However, water level appeared to play an important role in determining benthic light limitation at intermediate depths (1.5 m) for the range of K from 1.8 m^{-1} to 3.3 m^{-1}.

The partitioning of the light attenuation coefficient showed that phytoplankton was the main driver of the temporal dynamics of K, but only accounted for 44% of total light attenuation on average. The mean contributions of the other water components to K were: DOC (47%), tripton (6%), and water (3%). At low values of K, attenuation by DOC was responsible for up to 75% of total attenuation. An equation to predict K from the concentration of water components explained 93% of the variance.

Introduction

The underwater light environment is a fundamental factor in the ecology of aquatic ecosystems (Wetzel 2001). The quality and quantity of light in the wavelengths 400-700 nm (PAR, Photosynthetically Active Radiation), is crucial for the photosynthesis of benthic and pelagic primary producers (Kirk 1994). Underwater light availability depends on the properties of the incoming irradiance and on the behaviour of light in the aquatic medium (Kirk 1994). The attenuation of light with depth is quantified by the vertical attenuation coefficient, K, which is an Apparent Optical Property, AOP, in contraposition to the Inherent Optical Properties, IOP. The difference between AOPs and IOPs is that the latter depend only on the concentrations of the optically active components in water and not on the angular nature of the light field in the aquatic medium (Kirk 1994). The absorption coefficient, a, and the scattering coefficient, b, are both IOPs and have the same units as K (m^{-1}).

The attenuation of light with depth depends on the absorbance and scattering of photons, which in turn depend on the concentrations of the optically active constituents in the medium. Water components responsible for light attenuation are typically divided in three categories: the water itself, the particulate matter and the dissolved matter. The absorption by water typically contributes to a small fraction of the total absorption of light in natural aquatic systems, and its contribution to the scattering is negligible (Kirk 1994). Chromophoric Dissolved Organic Matter, CDOM (also known as gelbstoff, yellow substance or gilvin), is the coloured fraction of the total dissolved organic matter. Particulate materials (Total Suspended Solids, TSS, or seston) include both the organic (OSS) and inorganic (ISS) fractions. OSS can be divided into living (Phytoplankton) and non-living (Detritus) organic materials. The term Tripton refers to the sum of the non-living organic and inorganic particulate materials, and it is common to use the terms organic Tripton and inorganic Tripton to refer to detritus and inorganic suspended solids respectively.

In shallow aquatic ecosystems light availability plays an important role in the distribution and abundance of submersed aquatic vegetation. In shallow estuaries and coastal waters in particular light availability is a fundamental factor in the distribution of seagrasses and other benthic primary producers in relation to water depth (Dennison 1987).

Moreover, the underwater light regime is believed to be determinant in the alternative equilibria in shallow lakes, that is the existence of two stable states, one clear and one turbid, over different levels of nutrient concentrations (Scheffer et al. 1993). Although many stabilizing mechanisms appear to be involved (Weisner et al. 1997; Jeppesen et al. 1998; Scheffer 1998), one simple graphical illustration of the alternative stable states theory of shallow lakes is based upon water turbidity as the critical variable that describes the shift from one state to the other (Scheffer et al. 1993). Some of the reported stabilizing mechanisms are based on a limitation of macrophyte growth by light limitation due to attenuation of light by phytoplankton or by wind-induced sediment resuspension in the absence of

macrophytes (Scheffer 1998). Characterising the underwater light environment can thus contribute to the understanding of the factors involved in the competence and dynamics of benthic and pelagic primary producers in any particular system.

In this paper the underwater light regime of a Mediterranean coastal lagoon is studied. The Albufera des Grau is a coastal lagoon located in the northeast coast of Menorca, Balearic Islands. The lagoon is the most extensive wetland of the island and was declared Nature Park in 1995. Severe dystrophic collapses due to massive mortality of the extensive macroalgal beds were reported in the 1980s (Pretus 1989). In recent years, the lagoon was described as a macrophyte dominated system with dense and extensive meadows of the euryoic macrophyte *Ruppia cirrhosa* (Obrador et al. 2007). Intense phytoplankton peaks are observed each year, usually related to the entrance of nutrients form the watershed or from the decomposition of the macrophyte meadows (Obrador et al. 2007).

The objective of the present study is to characterise the light regime in the Albufera des Grau coastal lagoon by describing the spatial and temporal variability in the light attenuation coefficients to determine the light availability for pelagic and benthic primary producers. Furthermore, the partial contribution of the different optically active water constituents to total light attenuation is also assessed by means of empirical partitioning methods to better understand the interannual phytoplankton-macrophyte equilibria.

Methods

Study site

The Albufera des Grau has a surface area of 78 ha and a volume of 1 Hm^3 (Fig. 1). The average depth is 1.37 m and it reaches a maximum of 3 m (Pretus 1989). Climate is typically Mediterranean, with a mean air temperature of 17 ºC and 599 mm annual precipitation. Freshwater inputs are irregular and typically centred on autumn and winter. The lagoon is connected to the sea by a narrow channel 500 m long, where a small floodgate allows the regulation of the lagoon-sea connection when the sand-barrier is opened. Exchange with the sea is irregular and does not result in an important water renewal of the system. The water of the lagoon is oligo-mesohaline with a range of salinity between 5 and 20 during the last five years (salinity in practical salinity units). There is a marked seasonality in salinity and water level due to a naturally preserved Mediterranean evaporation/precipitation regime. Macrophyte meadows of *Ruppia cirrhosa* and *Potamogeton pectinatus* are found all along the lagoon except in the deepest areas (>2 m) and the dense littoral beds of *R. cirrhosa* in the Albufera des Grau have the highest biomass reported for this species (Obrador et al. 2007).
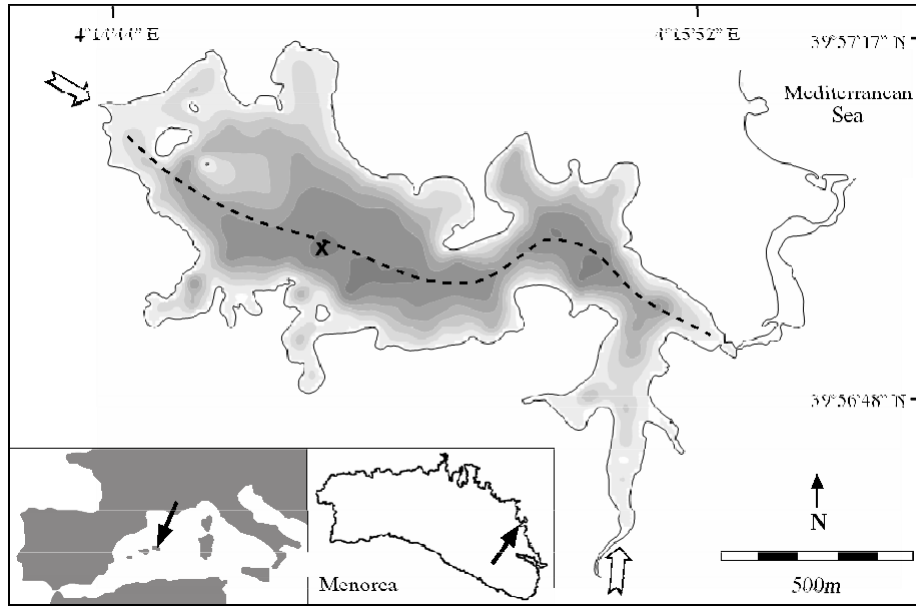
Figure 1. Location and bathymetric map (50 cm isobaths) of the Albufera des Grau coastal lagoon. The EW transect for the vertical profiles (dotted line) and the fixed sampling site (cross) are shown. Arrows correspond to the freshwater inputs.

Light attenuation coefficients

Monthly samplings of the lagoon were conducted from February 2001 to December 2004 to determine the spatial and temporal variability in the underwater light environment. The sampling design is part of a general research program to study phytoplankton-macrophyte dynamics. The vertical light attenuation coefficient was determined at five to seven sites distributed along the major axis of the lagoon (east-west), and their UTM coordinates were recorded with a GPS device (Fig. 1). The sampling sites were always in open water to avoid shading by macrophytes and covered the entire range of depths of the lagoon. At each site, Photosynthetically Active Radiation, PAR, was measured at different depths with a spherical quantum sensor (LI-193SA) for the measurement of diffuse light irradiance (in µmol m^{-2} s^{-1}). Measurements were done every 50 cm from surface to bottom, and two vertical profiles were conducted at each site. The vertical profiles of PAR were assumed to follow an exponential attenuation of irradiance with depth:

$$E_z = E_0 \cdot e^{-k \cdot z}$$ Eq. (1)

where E_z and E_0 are the scalar PAR irradiances at depth z (m) and below the water surface respectively, and K is the attenuation coefficient (m^{-1}). The values of K for each profile were determined by linear regression between depth and $\ln(E_z/E_0)$. Only those significant regressions (p<0.05) with R^2>0.90 were considered.

To test the statistical differences between sampling sites and dates, a nonparametric Kruskall-Wallis

test was carried out with the factors EW coordinate and Date. The EW coordinate was categorised in four zones 200 m wide.

Light availability for primary producers

For each sampling site the euphotic depth, the depth at which irradiance reaches 1% of E_0, was calculated from the measured light attenuation coefficient. The euphotic depth refers to the depth below which phytoplankton photosynthesis is expected to be light limited (Kirk 1994), but macrophytes are expected to have higher light compensation points in order to compensate for higher respiratory demands (Dennison 1987). Light availability for macrophyte growth was expressed as the percentage of surface irradiance reaching the bottom of the water column (Phlips et al. 1995b). It was calculated for each PAR profile from the light attenuation coefficient and the maximum depth of the site. Two values of bottom irradiance were taken from the literature as indicative of light limitation for macrophytes. A general value of 11% was selected from worldwide depth distribution of seagrasses (Duarte 1991) and a more specific value was selected for the dominant macrophyte species in the Albufera des Grau. The physiological light requirements described for *Ruppia cirrhosa* to maintain net production at the average water temperature of the lagoon is on the order of 3% (Menéndez and Peñuelas 1993). The depths of the 3% and 11% critical light levels were determined for each date. The surface area of the lagoon in which *R. cirrhosa* was expected to be light-limited was calculated for each sampling date from the critical depths and the bathymetry of the lagoon (authors' unpublished data).

The bottom irradiance values were plotted on a plane defined by the water level and the light attenuation coefficient in order to examine the relative contribution of these factors to benthic light availability. Critical isolines of expected light limitation were calculated for different depths from a rearrangement of Eq. (1). The relationship between effective depth (*Z*, the measured water depth), relative depth, (Z_{rel}, the distance between the bottom of the lagoon and sea level) and the water level of the lagoon at each sampling date, *WL*, was used ($Z_{rel} = Z - WL$). Eq. (1) was rearranged to express the water level as a function of *K*, Z_{rel} and the critical bottom irradiance (3% or 11%): $WL = -\left(1/K\right)\left(\ln\left(E_Z/E_0\right)\right) - Z_{rel}$. The water level of the lagoon was measured with a fixed scale near the outlet channel and expressed in cm above sea level (cm a.s.l.).

Components of light attenuation

The contribution of the different optically active constituents to light attenuation was evaluated from January 2003 to December 2004. Together with PAR profiles, water samples for the physicochemical analyses were taken at a 3 m depth site in the central area of the lagoon (Fig. 1).

Six water samples were taken at different depths every 50 cm from surface to bottom. Water samples were filtered in pre-combusted GF/F fibre filters, stored frozen and analysed in the laboratory as soon as possible. Pigments were extracted in 90% acetone and the concentration determined by the trichromatic method (Jeffrey and Humphrey 1975). The presence of phaeopigments was monitored with the ratio of the optical density at 430 nm to that at 410 nm (Moss 1967). The concentration of Dissolved Organic Carbon, [DOC], was determined in a TOC-500 Shimadzu as an approximation to CDOM. The concentration of Total Suspended Solids, [TSS], was determined gravimetrically on pre- combusted fibre filters after the filtration of a known volume of water (APHA 1985). The concentration of Inorganic Suspended Solids, [ISS], was determined by weight loss on the same filters before and after ignition (APHA 1985), and the concentration of Organic Suspended Solids, OSS, was determined from the difference between [TSS] and [ISS].

The concentration of Detritus or organic Tripton, [Det], was calculated from the difference between [OSS] and the concentration in dry weight of phytoplankton, [Phyt], which was determined from the Chlorophyll-a concentration assuming the relationship $[Phyt]/[Chl] = 100$, where [Chl] is the concentration of Chlorophyll-a in mg m^{-3} (Reynolds 1984; Phlips et al. 1995b). Individual correlations between K and the water parameters and between the water components were evaluated with the Pearson r coefficient.

To examine the contribution of each water component to the total light attenuation coefficient (K) it was assumed that the relative contributions of the components are additive. Although this is not strictly true for the Apparent Optical Properties such as K, this assumption has proved to be very useful leading to minimal errors (Gordon 1989; Gallegos 2001). Under this assumption the light attenuation coefficient can be partitioned into:

$$K_t = K_w + K_{doc} + K_{chl} + K_{det} + K_{iss}$$ Eq. (2)

where K_t refers to the total attenuation coefficient and K_w, K_{doc}, K_{chl}, K_{det} and K_{iss} are the partial attenuation coefficients (in m^{-1}) of water, DOC, Chlorophyll-a, Detritus and ISS respectively (McPherson and Miller 1987; Gallegos 2001; Christian and Sheng 2003; Kelble et al. 2005). Each partial attenuation coefficient was expressed as a function of the concentration of each component multiplied by the specific attenuation coefficient of the component, yielding the equation:

$$K_t = K_w + K'_{doc}[DOC] + K'_{chl}[Chl] + K'_{det}[Det] + K'_{iss}[ISS]$$ Eq. (3)

where K'_{doc}, K'_{chl}, K'_{det} and K'_{iss} are the specific attenuation coefficients of DOC, Chlorophyll-a,

Detritus, and ISS respectively, and the terms in brackets refer to the concentrations of the components (all in g m^{-3} except Chl, in mg m^{-3}). The units of the specific attenuation coefficients are m^2 g^{-1} except for Chl, in m^2 mg^{-1}. The attenuation coefficient of water, K_w was taken to be 0.0384 m^{-1} (Lorenzen 1972).

In a first approach, a Stepwise Multiple Linear Regression of the water components concentrations (DOC, Chl, Det and ISS) on K was performed to determine the specific attenuation coefficients K'_{doc}, K'_{chl}, K'_{det} and K'_{iss}.

A least squares linear regression method based on a sequential evaluation of the constant of the fitted models (Reynolds 1984; described in detail in Armengol et al. 2003) was also used to estimate the relative contributions of the components. The method is based on simple linear regressions between K and each component, considering in this case DOC, Tripton (Trip) and Chlorophyll-a (Chl). Note that Trip includes both the organic (Detritus) and inorganic (ISS) fraction of Tripton, and that the contribution of particulate matter is represented by $K_{chl} + K_{tripton}$. The partition of light attenuation is:

$$K_t = K_w + K_{doc} + K_{chl} + K_{tripton} \qquad \text{Eq. (4)}$$

which substituting $K_{chl} + K_{tripton}$ by K_{TSS}, can be written as:

$$K_t = K_w + K_{doc} + K_{TSS} \qquad \text{Eq. (5)}$$

In a first step, a regression of TSS on K_t of the form $K_t = a_1 + b_1[TSS]$ was performed and the values of a_1 and b_1 determined. The constant of the function, a_1 must correspond to the contribution of the non-particulate components (in m^{-1}). In this case a_1 equals $K_w + K_{doc}$ (Eq. (5)), thus yielding the determination of K_{doc} by subtracting K_w from a_1.

In the next step, the same procedure was applied on Chl. A simple regression between K_t and Chl was performed, with the form $K_t = a_2 + b_2[Chl]$. In this case the constant a_2 corresponds to the non-phytoplankton components, that is $K_w + K_{doc} + K_{Tripton}$ (Eq. (4)), thus allowing the determination of $K_{Tripton}$ by difference with a_1. The slope of the function, b_2 corresponds to the specific attenuation coefficient of Chlorophyll-a (K'_{chl} in m^2 mg^{-1}). All the statistics were performed in STATISTICA software.

Results

Spatial and temporal variation in light attenuation

From the 229 available profiles of PAR, 221 linear regressions to determine light attenuation coefficients were significant and had R^2 higher than 0.90 (the mean R^2 was 0.98). Measured K averaged 1.42 m^{-1} and ranged from 0.63 m^{-1} (in May 2002) to 3.80 m^{-1} (in March 2004). The values of K were skewed towards high values and centred on a median value of 1.21 m^{-1} (Fig. 2).
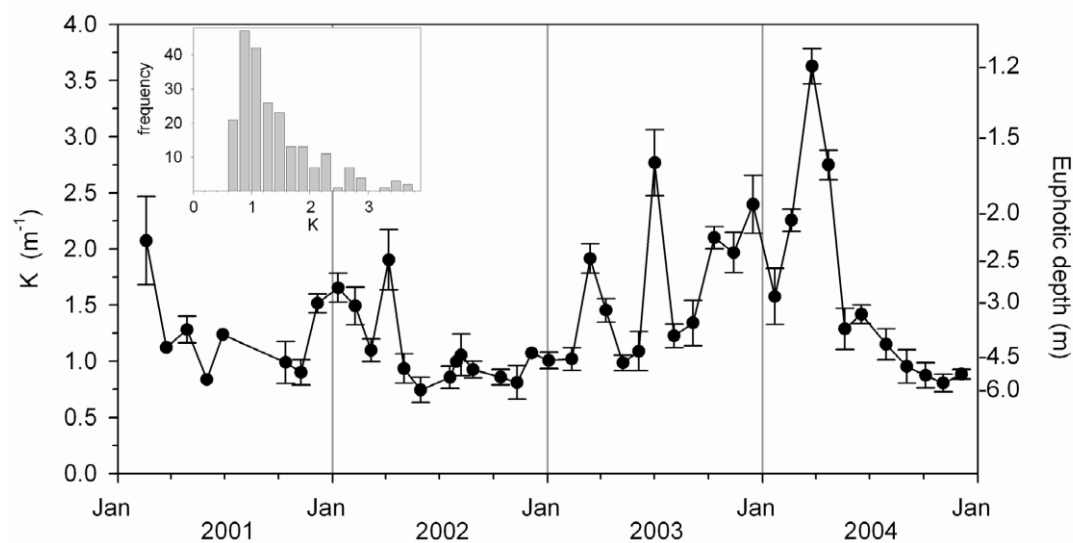
Figure 2. Temporal dynamics (mean ± s.d.) of light attenuation coefficient (m^{-1}) during the studied period. The equivalent scale of euphotic depth (m) is shown on the right axis. The inset shows the frequency distribution of the light attenuation coefficients.

During the studied period, there were no significant differences in K between the categorised EW coordinates of the sites (Kruskall Wallis=5.18; d.f.=7; p=0.61). On the contrary, K showed important temporal variations (Fig. 2), and significant differences between sampling dates were observed (K.W.=181.8; d.f.=43; p<0.001). A clear seasonal trend was not observed, but a very general pattern could be inferred with a turbid period in winter or early spring (Fig. 2). The trend for 2003 broke this general pattern with a peak in summer. The maximum values were found in March 2004 (3.63 m^{-1} on average) and July 2003 (2.77 m^{-1} on average). The existence of a basal value of K about 0.70 m^{-1} was observed during the studied period.

Estimates of light availability for phytoplankton and macrophytes

The values of euphotic depths calculated from the light attenuation coefficients are shown in Fig. 2. The mean euphotic depth was 3.8 m, a value slightly deeper than the maximum depth of the lagoon (3 m). However, minimum euphotic depth was 1.2 m (in March 2004) which is slightly shallower than the average depth of the lagoon (1.37 m). Fig. 3 shows percentage irradiance at the bottom of the water column for each sampling site and date. Benthic light availability averaged 13% of surface irradiance, but high spatial and temporal variability was observed and it ranged from 0.02% to 69% with a median value of 9% (Fig. 3). The spatial and temporal distribution of bottom irradiance shows that some sampling dates have very low values in all sampling sites and that low bottom irradiance is more frequent in the central areas of the lagoon than at the edges of the transects (Fig. 3) due to the deeper depths.
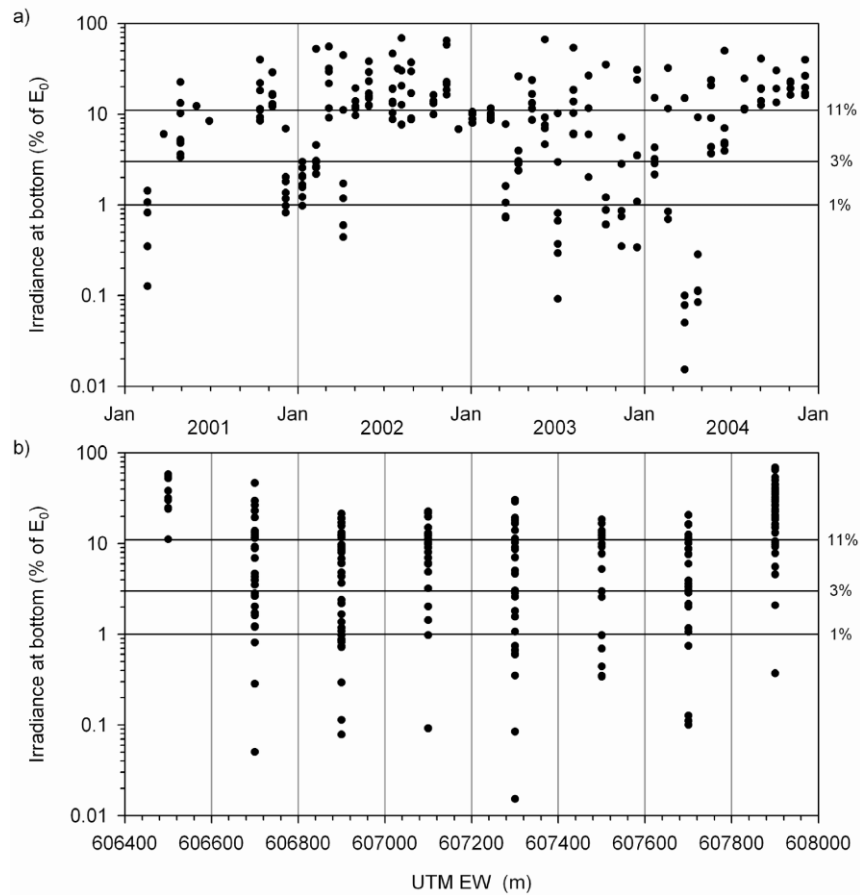
Figure 3. Temporal (a) and spatial (b) variation in the bottom irradiance expressed as a percentage of water surface irradiance. Reference critical levels of 11%, 3% and 1% (euphotic depth) are shown.

Temporal dynamics in K and water parameters in the period of 2003-2004

During the period of 2003-2004, K at the fixed central site averaged 1.59 m^{-1} and ranged from 0.75 to 3.58 m^{-1} (Fig. 4). Chlorophyll-a concentration was very high (mean 51 mg m^{-3}) and showed high temporal variability, peaking in March 2004 and July 2003 at 190 and 128 mg m^{-3} respectively. Phytoplankton concentration, inferred from the Chlorophyll-a concentration, was on average 39% of total suspended solids. Detritus and ISS were 40% and 21% of TSS on average. During the phytoplankton bloom observed in spring 2004, the weight contribution of Phytoplankton, Detritus and ISS to Total Suspended Solids was 47%, 50% and 3% respectively. The concentration of DOC showed a seasonal trend around high values, with values ranging from 7.8 to 12.8 mg L^{-1}. The minimum and maximum concentrations were observed in early spring and autumn, respectively.
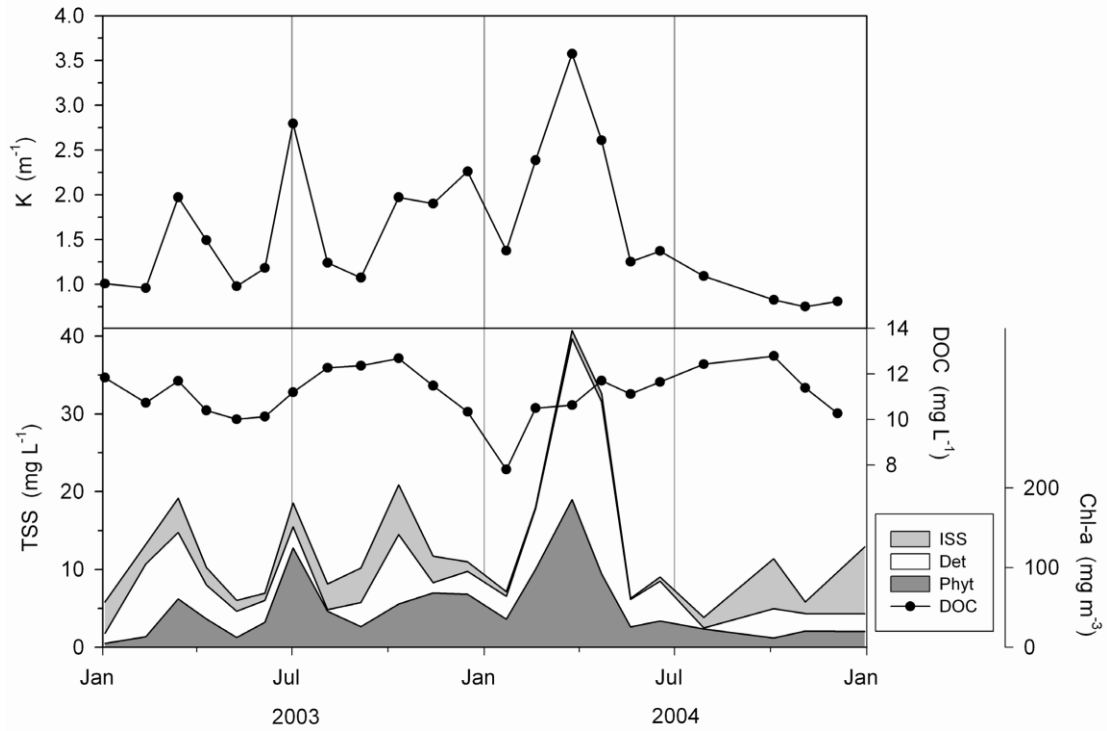
Figure 4. Temporal dynamics of K and water optically active components at the central sampling site for the period 2003-2004. For the concentration of phytoplankton, the equivalent scale in terms of Chlorophyll-a concentration is shown.

Partitioning of light attenuation

Significant positive correlation was observed between K and Chlorphyll-a, Detritus, OSS and Tripton and positive correlations were also observed between some water components (Table 1). A multiple regression of K versus Chl, ISS, Detritus and DOC was only significant in relation to Chlorophyll-a, and showed no significant relationship between K and DOC, ISS and Detritus. The same results were obtained if Tripton instead of its organic and inorganic fractions was considered in the model (regression between K and Chl, Tripton and DOC). The resulting model was:

$$K = 0.0163 \cdot [Chl] + 0.7627 \quad (R^2=0.93; n=22; p<0.001) \qquad \text{Eq. (6)}$$

The Root Mean Square Error (RMS) between the observed and the predicted values of K calculated with Eq. (6) was 0.21 m^{-1}, approximately 13% of the mean measured value. From Eq. (3) the value of the intercept (0.7627 m^{-1}) can be interpreted as the combined contribution of the non-phytoplankton components to light attenuation, i.e. $K_w + K_{doc} + K_{iss} + K_{det}$. By substituting the mean Chlorophyll-a concentration (51 mg m^{-3}) in Eq. (6), we get that the average contribution by Chlorophyll-a is 0.8313 m^{-1}, which is only the 52% of total attenuation at average conditions. The unspecified contribution of all the other components together accounts for 48% of total light attenuation on average.

The results of the second empirical method are shown in Fig. 5. The simple linear regression between K and TSS showed a significant relationship:

$$K = 0.0694 \cdot [TSS] + 0.6728 \ (R^2=0.68; \ n=22; \ p<0.001) \hspace{2cm} \text{Eq. (7)}$$
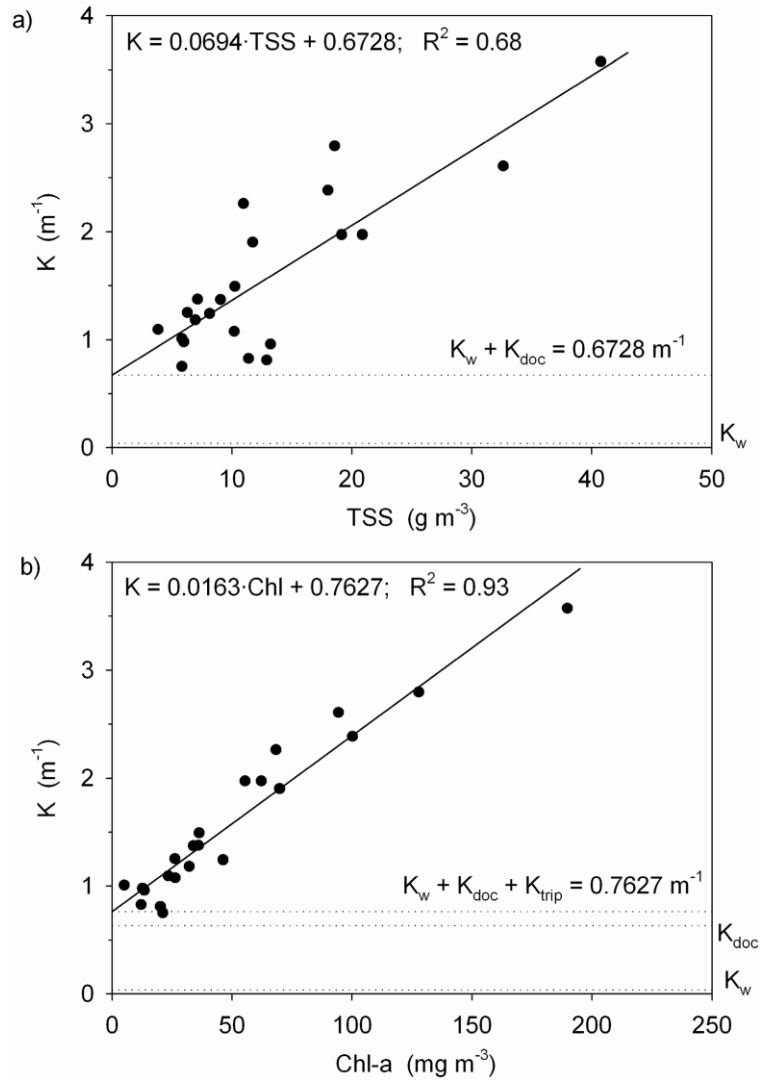
Figure 5. Simple linear regressions between K and a) Total Suspended Solids and b) Chlorophyll-a concentrations. From the constants of the fitted functions, the partial attenuation coefficients for DOC and Tripton are obtained (see text for details).

From K_w and the value of the constant in the model, 0.6728 m⁻¹, the resulting partial attenuation coefficient for DOC K_{doc} is 0.6344 m⁻¹. The specific attenuation coefficient for DOC, K'_{doc}, was not calculated because no significant correlation between DOC and K was observed (Table 1).

Table 1. Correlation matrix for the water components and the light attenuation coefficient. The mean and standard deviation of the water components during the studied period are also shown. ([*]: p<0.001; [**]: p<0.01)

| Component	Mean ± s.d.	Pearson r						
		Detritus	ISS	DOC	Tripton	OSS	TSS	K
Chlorophyll-a	51 ± 45 mg m^{-3}	0.63[**]	n.s.	n.s.	0.54[**]	0.88[*]	0.84[*]	0.96[*]
Detritus	5.3 ± 5.8 mg L^{-1}		n.s.	n.s.	0.92[*]	0.93[*]	0.91[*]	0.66[**]
ISS	2.7 ± 2.3 mg L^{-1}			n.s.	n.s.	n.s.	n.s.	n.s.
DOC	11.2 ± 1.1 mg L^{-1}				n.s.	n.s.	n.s.	n.s.
Tripton	8.1 ± 5.9 mg L^{-1}					0.84[*]	0.91[*]	0.56[**]
OSS	10.5 ± 9.3 mg L^{-1}						0.97[*]	0.88[*]
TSS	13.2 ± 9.1 mg L^{-1}							0.83[*]

In the next step a significant relationship between K and Chlorophyll-a concentration was obtained (Fig. 5b). The resulting equation is the same as Eq. (6) ($K = 0.0163 \cdot [Chl] + 0.7627$). The slope of the fitted function corresponds to the specific attenuation coefficient for Chlorophyll-a, 0.0163 m^2 mg^{-1} (Table 2). The average partial coefficient for Chlorophyll-a, K_{chl}, can be obtained by multiplying this value by the mean concentration of Chlorophyll-a, obtaining that $K_{chl} = 0.8313$ m^{-1}. From the constant in the fitted function, 0.7627, the partial attenuation coefficient for Tripton $K_{tripton}$ is calculated, and equals 0.0899 m^{-1}. The resulting average specific coefficient for Tripton , $K'_{tripton}$ is then 0.0111 m^2 g^{-1} (Table 2).

Table 2. Partitioning of light attenuation by the simple linear regression method with the mean percent contribution of each component during the studied period.

Component	Specific attenuation coefficients (K')	Partial attenuation coefficients (K)	Mean percent contribution
Chlorophyll-a	0.0163 m^2 mg^{-1}	0.8313 m^{-1}	44%
Tripton	0.0111 m^2 g^{-1}	0.0899 m^{-1}	6%
DOC	-	0.6344 m^{-1}	47%
Kw	-	0.0384 m^{-1}	3%

These results were used to describe the partial contribution of water components for each date because the effect of Tripton and DOC are included. The average contribution of each component was estimated as the mean of the contribution for all the sampling dates. Phytoplankton (expressed as the concentration of Chlorophyll-a) accounted for 44% of total attenuation, DOC for 47%, Tripton for 6% and water for 3% (Table 2).

To evaluate the relative importance of the water constituents over the entire range of variation of K and not only on the average values, the percentage contribution of each component for each sampling date was plotted against total attenuation in Fig. 6. At low values of K, DOC accounted for the 60- 75% of total attenuation, whereas Phytoplankton only accounted for 10-35%. The opposite situation was observed at high values of K, the contribution of DOC diminished to the 15% and Phytoplankton accounted for up to the 80% of total light attenuation. Tripton had a constant contribution around 6%.
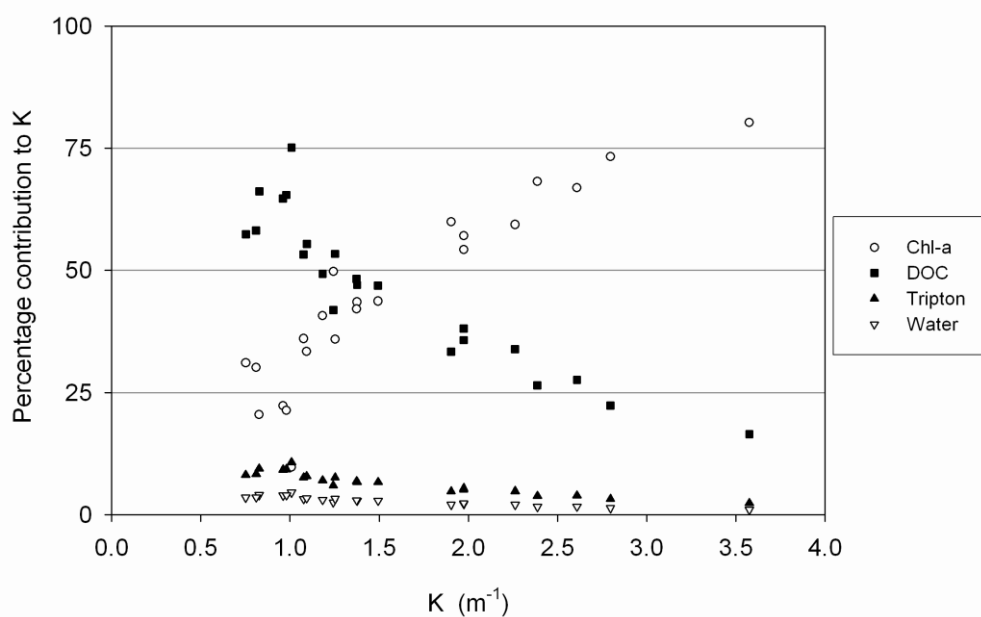
Figure 6. Partial contributions of water components to light attenuation over the entire range of light attenuation observed during the studied period. The contribution of each component is expressed as a percentage of total attenuation.

Discussion

Light availability

During the studied period the lagoon was spatially uniform with respect to light attenuation, and had higher variability on a temporal basis than on a spatial basis. The light attenuation coefficients had a mean of 1.42 m^{-1}, but large variation was observed. Even though the minimum observed euphotic depth was shallower than the average depth of the lagoon, the average euphotic depth was deeper than the maximum depth most of the time (75% of sampling dates, Fig. 2). This suggests that light limitation would not play an important role in controlling the planktonic primary production of the lagoon except during the very turbid events such as the observed in March 2004.

The percentage of light reaching the bottom is used in this study as an indicator of light limitation for macrophytes, and it results from the effect of light attenuation in the aquatic medium and the depth of the water column at each site. The spatial distribution of bottom irradiance (Fig. 3) shows that

benthic light limitation is presumed to take place during the most turbid periods in the central area of the lagoon due to the higher depths found there. This is in accordance with the observed distribution of macrophytes in the lagoon, which are usually scarce or absent in the central areas (Obrador et al. 2007).
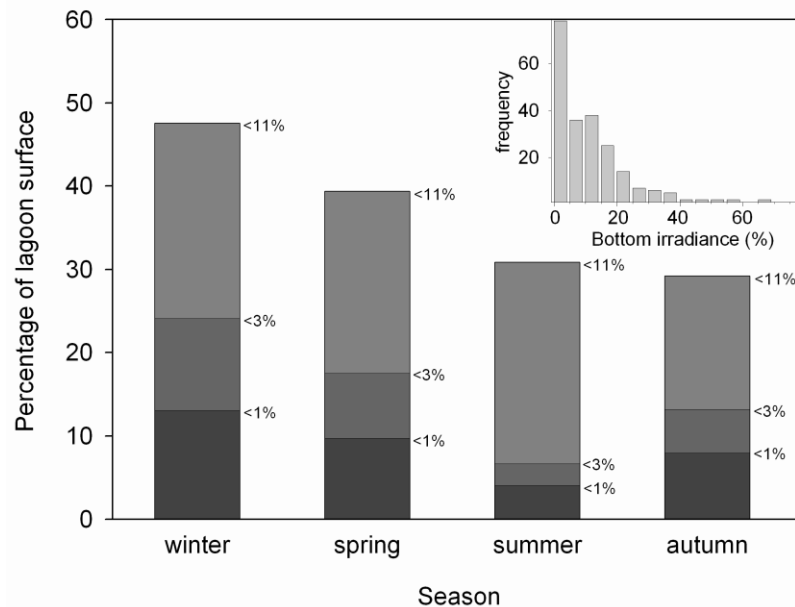

Figure 7. Percentage of the lagoon surface with expected light limitation. The average area with bottom irradiance lower than the critical levels of 11% (upper specification), 3% (intermediate specification) and 1% (lower specification) of surface irradiance is shown for each season in relation to the surface area of the lagoon. The overall frequency distribution of the percentage bottom irradiance in the 221 vertical profiles is also shown (inset).

The evaluation of the mean bottom irradiance for each date shows that light limitation of macrophyte growth was expected to occur on 16% of the sampling dates if the specific light requirement for *R. cirrhosa* is considered, and up to 43% of the sampling dates if we consider the more general reference value of 11% for seagrasses (Fig. 3). Seasonally, winter is the period with the lowest values of benthic light availability independently of whether the 11% or the 3% critical level is considered (Fig. 7). During the winter months, up to 24% and 48% of the lagoon area had bottom irradiance lower than 3% and 11% respectively (Fig. 7). It must be noted that throughout the annual cycle, at least 30% of the benthos of the lagoon was expected to receive less than 11% of surface irradiance on average (Fig. 7). Spring and summer are the main growing period for *R.cirrhosa* in the Albufera des Grau, but it can occasionally extend to autumn (Obrador et al. 2007). Considering the 3% critical value for *R. cirrhosa*, 17% of the lagoon is expected to be light limited in spring (Fig. 7). Summer would be the optimal growth period in relation to benthic light availability, but even then 7% of the lagoon was observed to have benthic light limitation.

From these results, light limitation is expected to play an important role in the primary production

and spatial distribution of benthic primary producers in the lagoon during certain periods of the year. The specific effect on the distribution and abundance of each macrophyte species should be examined in detail, especially during the growing season.

For a given site benthic light limitation can result from either high light attenuation coefficients or high water levels in the lagoon. In order to assess the contribution of each factor to benthic light availability, the bottom irradiance values were plotted on a plane defined by the water level and the light attenuation coefficient (Fig. 8). The critical lines of expected light limitation (taking 3% of surface irradiance as a critical level) are shown for different depths. On the right of each reference   line, the points corresponding to that depth are expected to be light limited (bottom irradiance lower than 3%). Points on the left of the line will have bottom irradiance higher than 3%.
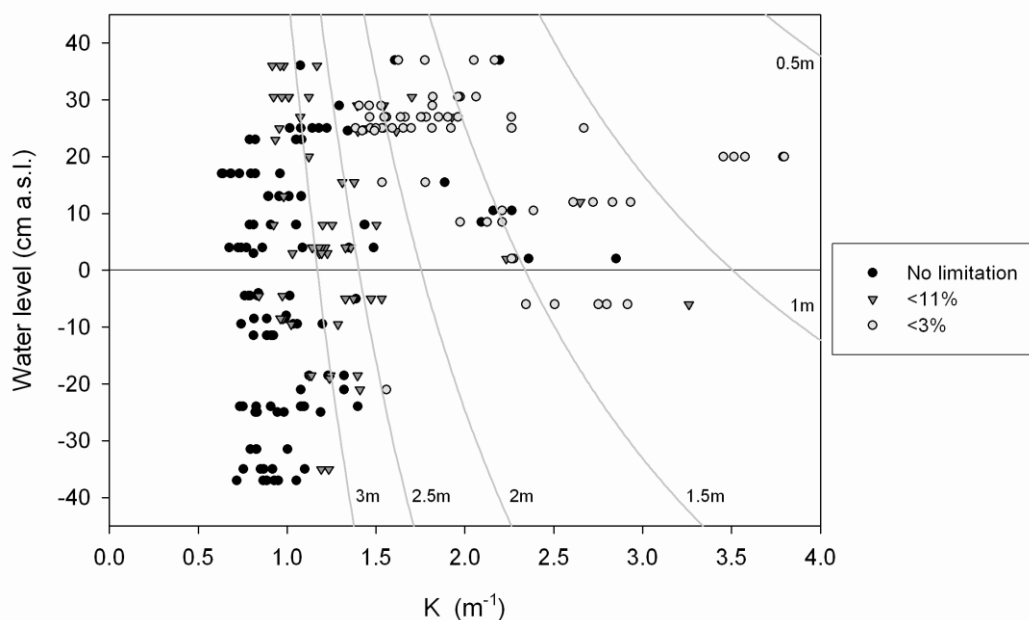
Figure 8. Pot of the benthic light availability in the plane defined by the water level of the lagoon (in cm above sea level) and the light attenuation coefficient (in m^{-1}). Each point corresponds to a vertical profile and the different symbols correspond to different values of bottom irradiance in relation to the critical levels of 3% and 11%. The critical lines of the 3% of surface irradiance are shown for different depths (see text for details).

As expected, bottom irradiances lower than 3% were mainly found in the upper-right quadrant of the plane, i.e. high K and high water level (Fig. 8). At low values of K (<1.3 m^{-1}), benthic irradiance was always higher than 3% independently of the water level of the lagoon. The lower-right quadrant of the plane (high K and low water level) was poorly represented in the data set. The slightly vertical distribution of the isolines of high depths (>2 m) suggests that light availability in the deepest areas of the lagoon is mainly driven by changes in light attenuation and not by changes in water level. The

shallower areas (<0.5 m), with a more oblique isoline at the top of the plane, would not be light limited for any combination of K and water level. The intermediate depths show oblique isolines, suggesting that benthic light limitation is influenced by both K and water level. The upper and lower cutting points of the 1.5 m-isoline are 1.8 m^{-1} and 3.3 m^{-1} respectively (Fig. 8). These points are defined from the water levels of 45 cm and -45 cm, which are not the maximum and minimum physical values of the lagoon but describe well the usual range of variation of water level in the lagoon (authors' unpublished data). These cutting points can be interpreted in the sense that for K higher than 3.3 m^{-1}, all areas deeper than 1.5 m are expected to be light limited, and for K lower than 1.8 m^{-1}, shallower areas will have bottom irradiance higher than 3%. The depth of 1.5 m is significant because the bathymetry of the lagoon distributes 47% of the surface in areas shallower than 1.5 m (authors' unpublished data). These results are assumed to include enough variance in both K and water level due to the temporal extension of the data set. However, the results should be interpreted carefully because the selection of a constant threshold in bottom irradiance is not an absolute but a suggestive measure of light limitation. Moreover, the temporal resolution of the data set does not include the short term variation in underwater irradiance, which is believed to play a role in the limiting effect of light on benthic primary producers (Banas et al. 2005).

Components of light attenuation

The empirical partitioning of light attenuation in the Albufera des Grau resulted in a dominance of the phytoplanktonic component as the main driver of the temporal dynamics in light attenuation coefficients. The resulting specific attenuation coefficient for Chlorophyll-a (0.0163 m^2 mg^{-1}; Table 2) falls well between the previously reported values (Reynolds 1984; Phlips et al. 1995b; Kelble et al. 2005). An equation describing K as a linear function of Chlorophyll-a, Eq. (6), accounts for 93% of the variance. Available data of Chlorophyll-a for the period 2001-2002 (authors' unpublished data) allowed the validation of Eq. (6) on an independent data set (Fig. 9). This period was not included in the partitioning of light attenuation because data of suspended solids was not available. Observed and predicted values agreed well but explained less variance than for the period 2003-2004 (R^2=0.44; n=21; p<0.01). This could be due to the lower range of K and Chlorophyll-a concentration observed in the validation period (Fig. 9). The overall agreement between observed and predicted values for the whole period 2001-2004 was significant and explained 83% of the variance (R^2=0.83; n=43; p<0.001; Fig. 9). In conclusion, for modelling purposes Eq. (6) ($K = 0.0163 \cdot [Chl] + 0.7627$) is a useful equation to predict the light attenuation in the lagoon, but this equation should be used carefully especially on the lower range of concentrations and light attenuation coefficients used in the present study.
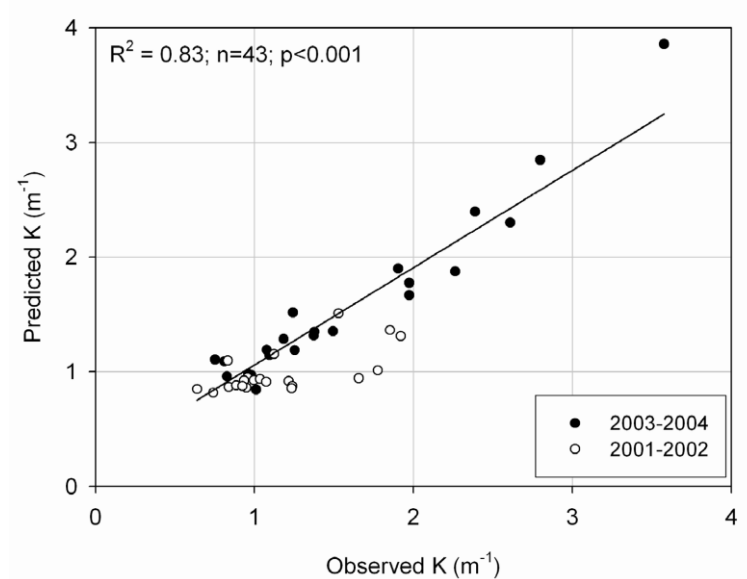
Figure 9. Observed versus predicted values of the light attenuation coefficient. The data sets used for the calibration (2003-2004) and for the validation (2001-2002) of Equation 6 are shown. The fitted line refers to the overall data set.

The results show that despite phytoplankton is the major driver of K, it only accounts for less than half of the total light attenuation on average (Table 2). The particulate component is responsible for 50% of light attenuation, whereas the dissolved matter accounts for 47%. The low Tripton contribution to light attenuation is not in accordance with other reported estuarine and lagoonal systems (Phlips et al. 1995a; Phlips et al. 1995b; Pfannkuche 2002; Christian and Sheng 2003; Lund-Hansen 2004; Kelble et al. 2005) or with the prevailing view of turbidity components in freshwater shallow lakes (van Duin et al. 2001; Jackson 2003). In this study the contribution of Tripton to light attenuation could not be separated into the inorganic (sediment) and organic (Detritus) fractions. By weight, the inorganic fraction of Tripton, ISS, averaged 21% of TSS and 33% of total Tripton, and it only occasionally contributed to more than 50% of total Tripton (Fig. 4). A shallow aquatic system located in a very windy location such as the north of Menorca, is expected to have high contribution of ISS to total Tripton due to sediment resuspension (Phlips et al. 1995a; van Duin et al. 2001; Banas et al. 2005). The origin of ISS in the Albufera des Grau could be assigned not only to wind-driven sediment resuspension but also to the clays entering the lagoon during torrential events. Such events drive the main hydrological pattern in water level fluctuations in this lagoon (authors' unpublished data). On the other hand, the high Chlorophyll-a concentration observed in the lagoon could explain the low contribution of inorganic Tripton to TSS by weight.

It must be noted that the organic fraction of Tripton corresponds to detritus originated from phytoplankton and macrophytes, which are both pigmented particles not easily differentiated from

living phytoplankton. In this study Chlorophyll-a concentration was not corrected for phaeophytin following the suggestions of Stich and Brinker (2005). From the ratio 430:410 of the pigment extracts (Moss 1967), the presence of phaeopigments in the samples was expected to be 20-50% of total chlorophyll. Moreover, the conversion between Chlorophyll-a and phytoplankton with the fixed ratio 1:100 could be responsible for a misdetermination of the living and non-living fractions of the organic suspended solids. This could have resulted in an erroneous determination of the contribution of Tripton to total light attenuation. In order to check for this effect, the simple linear regression method was applied again on the directly measured variables that do not depend on the chlorophyll determination and on the conversion of chlorophyll to phytoplankton (i.e. DOC, ISS and OSS). Similarly as above, simple linear regressions were performed on TSS and OSS to obtain respectively the contributions by DOC and ISS from the constants of the fitted functions. Both regressions were significant at p<0.001 (R^2=0.68 and 0.76 respectively) and the results are summarised in Table 3. As can be seen the resulting partial contributions of OSS, ISS and DOC are 41%, 12%, and 44% respectively. These results are similar to the above conclusions in the sense that on average the particulate and the dissolved components account for half of light attenuation each one. The contradictory lower contribution of OSS (41%; Table 3) in relation to that of Clorophyll-a (44%; Table 2), may be assigned to a consequence of the assumed linear partitioning of K or to the inaccuracy in the determination of the Chlorophyll-a concentration due to the presence of phaeopigments. In relation to the low contribution of ISS to light attenuation, it must be noted that higher contribution would be expected if shorter time scales were considered (van Duin et al. 2001; Banas et al. 2005).

Table 3. Partitioning of light attenuation by the simple linear regression method applied on the directly measured water components.

Component	Specific attenuation coefficients (K')	Partial attenuation coefficients (K)	Mean percent contribution
OSS	0.0711 m^2 g^{-1}	0.7466 m^{-1}	41%
ISS	n.s.	0.1680 m^{-1}	12%
DOC	n.s.	0.6344 m^{-1}	44%
Kw	-	0.0384 m^{-1}	3%

The relative contribution of DOC to light attenuation is highlighted, specially considering that no correlation with K was observed. The lack of correlation between DOC and K could be a consequence of the use of DOC as an approximation to CDOM, because only the coloured fraction of the dissolved organic matter is related to light absorption (Ferrari et al. 1996). Further research on the variation of light attenuation including the different size fractions of DOC over a wide range of Chlorophyll-a

concentrations is needed. More mechanistic approaches based on the specific spectral variations in absorption and scattering must contribute to obtain a more precise partitioning of the light attenuation (Bracchini et al. 2005; Gallegos et al. 2005).

In the previous studies reporting high contribution of DOC to light attenuation an allochthonous origin of DOC from adjacent terrestrial systems is usually assumed, even for estuarine systems (Branco and Kremer 2005; Xu et al. 2005) or inland waters (Bukaveckas and Robbins-Forbes 2000; Álvarez-Cobelas et al. 2002). In the case of shallow lakes and lagoons, the autochthonous DOC released from submerged macrophyte meadows is believed to be significant (Bertilsson and Jones 2003). However, turbidity in these systems is typically attributed to phytoplankton and inorganic suspended solids (Cristofor et al. 1994; van Duin et al. 2001; Jackson 2003), and reports of high contribution of DOC to light attenuation are not frequent in the literature. In the few studies where high DOC contribution to light attenuation is reported in shallow lakes, an allochthonous origin of DOC is described (Squires and Lesack 2003; Bracchini et al. 2005; Loiselle et al. 2005). In the Albufera des Grau the dynamics of DOC seems to be related to the macrophyte cycle, with high DOC values during the decomposition period of the dense macrophyte meadows (authors' unpublished data[2]). Given the high contribution of DOC to total light attenuation described in this study, the hypothesized macrophytic origin of DOC would suggest the possibility of interference in the interaction between macrophytes and phytoplankton. Such extent should be explored and possible thresholds determined, especially in systems where wide variations in light attenuation and water components concentrations make them difficult to be classified in the classical optical water classifications (Morel and Prieur 1977; Reinart et al. 2003).

<u>Conclusions</u>

The underwater light environment in the Albufera des Grau coastal lagoon was characterised by high temporal variability in the light attenuation coefficient. Light limitation was expected to play an important role in the primary production and spatial distribution of the benthic primary producers. During the macrophyte growing season 7-17 % of the lagoon benthos was expected to be light limited. In the deepest areas of the lagoon (>2 m) changes in bottom irradiance were related more to variations in the light attenuation than to variations in water level, but at intermediate depths (1.5 m) water level appeared to play an important role in determining benthic light availability.

The phytoplanktonic component was the main driver of the temporal dynamics in light attenuation coefficients but only accounted for 44% of light attenuation on average. Despite no correlation between DOC and K was observed, the dissolved organic matter accounted for an important fraction of light attenuation. The partitioning of light attenuation resulted in a similar contribution of the

particulate and the dissolved water components, with a mean contribution of 50% and 45% to the light attenuation coefficient respectively.

<u>Acknowledgements</u>

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