Hydrobiologia
November 2005, Volume 551, Number 1, Pages 3-16
http://dx.doi.org/10.1007/s10750-005-4446-1

Short time scale changes in underwater irradiance in a wind-exposed lagoon (Vaccarès lagoon, France): Efficiency of infrequent field measurements of water turbidity or weather data to predict irradiance in the water column

D. Banas[1, 6, *], P. Grillas[1], I. Auby[2], F. Lescuyer[3], E. Coulet[3], J.C. Moreteau[4], B. Millet[5]

[1]Station Biologique de la Tour du Valat - Le Sambuc 13200 Arles - France.
[2]Centre d'Océanographie et de Biologie Marine - Université Bordeaux I - CNRS-URA 197 - 2 rue Pr. Jolyet - 33120 Arcachon - France.
[3]SNPN - Réserve Nationale de Camargue - France.
[4]LBFE - Université de Metz - Campus Bridoux - 57070 Metz Borny - France.
[5]Université de la Méditerranée - Campus de Luminy - Case 901 - 13288 Marseille cedex 09 – France.
[6]CNRS UMR.8079, Université Paris-Sud, Ecologie, Systématique et Evolution, Bât. 362, 91405 Cedex, Orsay, France (Present address)

*: Corresponding author : Banas D., email address : damien.banas@ese.u-psud.fr

Abstract:

High frequency water sampling in the wind-exposed Vaccarès lagoon revealed frequent and rapid changes in suspended solid (SS) concentrations in the water column. SS concentrations, sometimes higher than 800 mg l-1, were significantly correlated with antecedent wind conditions. Mean wind velocity during the 5-33 hours before water sampling or maximal wind velocity during the previous 8.5-22 hours were good predictors of SS concentrations in the water column. Underwater irradiance at canopy level was modeled (r2=0.66, n=7584) using the SS calculated from the relationship between SS and antecedent mean wind velocity and the surface irradiance data measured at the weather station close to the study site. On the other hand, we have shown that in this wind-exposed lagoon, mean underwater irradiance can not be effectively estimated using infrequent measurements of the optical properties of water.

Keywords: light, wind, submerged macrophyte, shallow lagoon

Introduction

Underwater irradiance is one of the most important factor determining the depth distribution, abundance and productivity of submerged aquatic macrophytes (Backman & Barilotti, 1976; Duarte, 1991; Zimmerman et al., 1994; Van Duin et al., 2001). The quantity of irradiance available for the submerged plants (i.e. photosynthetically active radiation = PAR), varies with water depth, density of particulate material (phytoplankton, sediment, etc.) and the concentration of dissolved substances (e.g. humic acids) in the water column.

In coastal wetlands, reductions of underwater irradiance due to anthropogenic or natural events (e.g. storms) may lead to the degradation of seagrass beds (Preen et al., 1995; Short & Wyllie-Echeverria, 1996; Cabello-Pasini et al., 2002). Worldwide anthropogenic nutrient inputs have resulted in progressively decreasing underwater irradiance available for rooted plants through increases of phytoplankton and periphyton (e.g. Giesen et al., 1990; Dennison et al., 1993). Biotic disturbances (e.g. bottom feeding fish) can also contribute to high turbidity levels (Blindow, 1992). In estuaries and shallow coastal lagoons, the complex dynamics of suspended solids (SS) in relation to the hydrodynamics can also play an important role in the spatial and temporal variations of turbidity. The resuspension of sediment by hydrodynamic processes (e.g. wave action, seiche, tides, currents) is particularly important (Arfi et al., 1993; Preen et al., 1995; Moore et al., 1997) and can affect dramatically seagrasses.

Many methods have been used to estimate underwater irradiance available to seagrasses (Carruthers et al., 2001). For example, instantaneous measurements of irradiance (Secchi disks or irradiance) taken at infrequent intervals have been used to establish the relationships between irradiance and submerged vegetation (Pérez & Romero, 1992; Koch & Beer, 1996; Laugier et al., 1999). These methods may provide biased estimates of water transparency through insufficient and unrepresentative sampling of the light environment. In addition, extreme turbidity events are often not sampled due to difficulties in accessing sites during storms. Regardless, irradiance requirements of submerged macrophytes have been calculated from the correlation between the maximum depth penetration of species and the mean irradiance attenuation coefficient (K) (Duarte, 1991; Middelboe & Markager, 1997; Carruthers et al., 2001). This method provides an integrated estimate of the irradiance budget for a species or a group of species (Duarte, 1991; Dennison et al., 1993). However, the predictive value of this correlation is weak for water depths of less than 10 m (Zimmerman et al., 1994) such as in some estuarine ecosystems. One of the limitations of the correlation between seagrass depth distribution and underwater irradiance availability is that it cannot take into account the temporal variation in irradiance. More recently, the importance of short-term changes in irradiance, and their significance on the survival and depth distribution of submerged macrophytes, have been recognized (Zimmerman et al., 1991; Dunton, 1994; Zimmerman et al., 1994; Moore et al., 1997; Longstaff & Dennison, 1999). However, few studies have focused on quantifying short-term changes in underwater irradiance that occur in response to changes in turbidity (Zimmerman et al., 1994; Hanlon et al., 1998; Alvarez-Cobelas et al., 2002; Cabello-Pasini et al., 2002).

The aim of our study was threefold. First, to describe the short-term variability of underwater PAR in a coastal Mediterranean lagoon. Secondly, to evaluate relationships between weather conditions and water turbidity to estimate underwater PAR in shallow aquatic systems. Thirdly, to evaluate the loss of quality in prediction of underwater irradiance using discrete, infrequent measurements of underwater PAR.

1. Materials and methods

1.1. Study site

The Vaccarès lagoon, located in Camargue (Rhône delta, South-France), covers 66 km^2 (Fig. 1) with a mean water depth of 1.4 m and a maximum depth of 2.1 m. Inter-annual water level fluctuations are generally limited to $\pm$ 0.3 m (Chauvelon, 1996). The main sources of water are direct rainfall, drainage of the catchment (317 km^2), and sea surges. The connection to the sea, which is through shallow lagoons (Etangs inférieurs), is diked. Water flows between the sea and the lagoons are regulated using gates located on the dam. The bottom sediments of the lagoon are covered with a 35 to 300 mm layer of unconsolidated fine particles (Vaquer & Heurteaux, 1989).
The sampling site for suspended solids (SS) concentrations and underwater irradiance was located at 800 m from the lagoon's east edge (43°32'29.6"N - 4°38'04.1"E; mean depth=1.33m, Fig. 1). It was equipped with a 2 m $\times$ 2 m platform where data loggers were housed. Bottom sediments were mainly composed of clay (18.4 %) and silt (39.7 %) with a low concentration (2 to 5 %; Grillas, unpub.) of organic matter and covered with *Zostera noltii* vegetation.

1.2. Field measurements

Meteorological data

The wind velocities (magnitude and direction measured at 10 m height) and irradiance (I_0, 2π sensor) were measured continuously and integrated over 0.5-h intervals at the Météo France climatic station located at 6 km of the south-eastern shore from the lagoon (Fig. 1).

Water level

Water level was recorded continuously at a station located 1.5 km from the sampling site.

Time series observations of irradiance

Underwater scalar PAR was recorded continuously between 16th December 1995 and 22nd May 1996 (159 days) using a spherical (4π) quantum sensor (LI-COR Model 193SA). The sensor was attached to a descending rod mounted 1 m off the south side of the station raft to minimise shading. The sensor was placed 0.36 m above the bottom sediment surface (z = depth which was just above the top of the *z. noltii*). The sensor was covered by at least 1.0 m of water at all times. Underwater PAR (Iz) was measured every five seconds and integrated over 0.5-h intervals and stored in a LI-COR Model 1000 data logger. The sensor was cleaned and the data loggers were switched by SCUBA divers at least twice a week and more often in spring. Accumulation of small amounts of fouling had no measurable effect on recorded values during the periods between cleanings, as evaluated by the difference in PAR immediately before and after cleaning.

Suspended solids concentrations in the water column

Water samples were collected during six episodes of 93 to 249 h (Fig. 2). Water samples (250 ml) water samples were collected each half hour and sets of four samples were composited before SS analyses. Sample water was pumped from 1 m above the sediment surface with an automatic sampler (SIGMA 9000) located on the platform. During six sampling trips, a total of 1544 individual samples were collected and groups of four consecutive samples were combined to produce 386 composite samples for analysis. Suspended solids (SS) concentrations were measured according to the French standard methods for water analysis (AFNOR, 1994), with GF/C filters dried at 105°C for a minimum of 24 h.

1.3. Relationships between wind and suspended solids concentrations

In this manuscript, wind velocity integrated during each half-hour interval is called integrated wind (W_{int}). The highest W_{int} measured during a time lapse greater than 0.5 h (range = 0-48 h) was called maximal velocity (W_{max}). The average of W_{int} measured during a range of time (0-48 h) was called Mean Velocity (W_{mean}).
Thus, W_{int} integrated during the time window contained between 1.5 h and 2 h before the water sampling is called $W_{int\ 2h}$. Highest W_{int} recorded during the time window contained between 0 and 16 hours before the water sampling is called $W_{max\ 16h}$.

The best relationships (linear, exponential, power and logistic) between SS concentrations and wind variables (W_{int}, W_{max}, W_{mean}) were examined using various time windows during the 48 hours before the water sampling. Thus, SS concentrations collected at time t=0 were correlated where:
W_{int} recorded between t=0 h and t=-0.5 h; t=-0.5 h and t=-1 h; …; t=-i h and t=-(i+½) h; …; up to between t=-47.5 h and t=-48 h.
W_{max} and W_{mean} recorded between t=0 h and t=-0.5 h; t=0 h and t=-1 h; …; t=0 h and t=-i h; …; up to between t=0 h and t=-48 h.
The time windows with the highest r^2 value (best fit) were then used to further investigate changes in PAR.
Several other types of relationships between wind velocity and SS were tested. Linear relationships on both sides of a wind velocity threshold (Somlyódy, 1981; Bengtsson & Hellström, 1992; Hanlon et al., 1998) were tested. The importance of fetch (distance covered by wind from edge to sampling site) on resuspension of sediment was tested with multi-variables relationships including wind velocity and fetch, such as CERC model (CERC, 1977) developed for coastal marine ecosystems. The fetch at the study site was calculated for 10° intervals in wind direction. Complementary details on that method can be found in CERC (1977), Luettich et al. (1990), and Arfi et al. (1993).

1.4. Estimation of underwater PAR from infrequent measures of irradiance

Charles-Edwards et al. (1986) have shown that the daily integral of irradiance intercepted by canopy is linearly correlated to macrophyte productivity. Based on the sinusoidal daily pattern of solar irradiance variability, the daily integral of irradiance which can reach canopy (or another depth) can be estimated theoretically from a single daily measure of the maximum irradiance at solar noon (Kirk, 1983; Thornley & Johnson, 1990; McBride, 1992) and the single equation:
$DI = I_N \sin (\pi * (t/D)$ (equation 1)
where DI is Daily integral of irradiance, I_N is Irradiance at solar noon, t is the time since sunrise in hours, and D is the photoperiod in hours.

For the whole study period, the sum of daily integrals of PAR at depth z (ΣDI), was calculated by either integrating underwater PAR measured by the sensor (ΣDI_{meas}) or using equation 1 and I_N measured by the sensor between 11:30 and 12:00 (ΣDI_{calc}). Calculated ΣDI was estimated using daily measurements of I_N or less frequent measures (range 1-30 days sampling intervals).
Day lengths at the study site were obtained from the astronomical data issued from the “Bureau Des Longitudes” (http://www.bdl.fr).

1.5. Estimation of underwater PAR from meteorological data and using relationships between wind and SS

PAR just beneath the water surface (Iz_0)

Iz_0, corresponding to the PAR immediately beneath the water surface was calculated from the equation:
$Iz_0 = I_0 \cdot C_{sph} \cdot m_0 \cdot m_1$ (equation 2)
where
I_0 is Incident total solar irradiance measured with a 2π sensor at the weather station;

C_{sph} is the mean spherical correcting coefficient (1.27) as recommended by Stefan et al. (1983) to adjust irradiance measured with a flat plate sensor into irradiance measured with a spherical (4π)sensor;
m_0 is the PAR coefficient =0.45 (Capblancq, 1995) to take into account only photosynthetically active radiation of the total solar radiation;
m_1 is the albedo coefficient = 0.94 (Lemmin, 1995) to take into account the mean loss of PAR due to reflectivity at the water surface.

Calculation of PAR just above the seagrass canopy (Iz)

PAR at 0.36 m above the sediments (Iz) was calculated according to the Lambert-Beer's Law of the form:

$$Iz = Iz_0 \exp[-Kd \cdot z] \qquad \text{(equation 3)}$$

where
Iz_0 is PAR just below the water surface, Iz is PAR at depth z (0.36 m above the bottom sediments), and Kd is the irradiance attenuation coefficient for PAR.

Estimation of irradiance attenuation coefficient in the water column (Kd)

Kd can be computed as the addition of specific attenuation coefficients due to different sources of water-column irradiance attenuation. Attenuation due to water and coloured substances can be combined into the same specific attenuation coefficient K_{WC} whereas Chlorophyll and SS are both linearly correlated to their respective concentrations (Kirk, 1983; Stefan et al., 1983; Alvarez-Cobelas et al., 2002).
Chlorophyll concentrations in the Vaccarès were fairly constant and generally lower than 15 µg l^{-1} (De Groot & Golterman, 1999; Grillas, unpub.). Chlorophyll can be taken into account in the K_{WC} coefficient as other coloured substances using the following equation:

$$Kd = K_{wc} + E_{SS} \cdot [SS_{comp}] \qquad \text{(equation 4)}$$

where K_{wc} (expressed in m^{-1}) is specific attenuation coefficient due to water, coloured dissolved substances, and chlorophyll pigments. E_{SS} is specific attenuation coefficient due to suspended solids (expressed in m^2 g^{-1}), and $[SS_{comp}]$ are SS concentrations (expressed in g m^{-3}) calculated from the best relationship found between wind velocity (measured at the weather station) and SS concentrations measured in the water samples.

K_{wc} and E_{SS} were estimated from the following equation derived from equations 3 and 4, and using non-linear least square estimation procedure following the Levenberg-Marquardt algorithm from the non-linear-model package of STATISTICA (Marquardt, 1963 in Statsoft, 2002).

$$Iz = Iz_0 \exp[-(K_{wc} + E_{SS} \cdot [SS]) \cdot z]$$

where [SS] are suspended solids concentrations measured in water samples, and Iz_0 and Iz were measured simultaneously for each water sample collection.

E_{SS} and K_{WC} were estimated either for the whole study period (from the 386 SS measures) or for each of the six SS sampling episodes. Next, underwater PAR was simulated using either constant specific attenuation coefficients for the whole study period, or various specific coefficients estimated from each SS sampling episode and a linear adjustment of coefficients were done between two episodes.

2. Results

2.1. Wind

The dominant wind, called Mistral, is oriented from North-North-West to South-South-East (Fig. 1). During the study period, the Mistral occurred 46 % of time and SSE wind 19%. These values were close to the 1988-1997 mean values, respectively 42 and 17 % for NNW and S-SE wind directions (Chauvelon, unpublished data). The other wind directions were less frequent. During the study period, average wind velocity (W_{mean}) was 4.4 m s^{-1} and maximal wind velocity (W_{max} = 18 m s^{-1}) was observed on 1st March, during a Mistral event.

2.2. Suspended solids

Relationships between wind velocity and SS concentrations

Mean SS concentrations measured at the sampling point was 98.4 mg l^{-1} (SD=141.5; n=386). These high concentrations fluctuated between 5 and 817 mg l^{-1} (Fig. 2).
When all samples were considered, statistically significant relationships (linear, power, exponential, and logistic) were found between various wind variables (W_{int}, W_{mean}, and W_{max}) and SS concentrations (Fig. 3 and Table 1). Considering antecedent wind conditions (regardless of the relationship used), the strongest relationships between SS concentrations and wind was found using either W_{int} measured during the period 1.5 to 2 hours before water sampling, or W_{mean} measured during the previous 16 hours, or W_{max} during the previous 14 hours. Results from these optimal time windows were not significantly different (p<0.05, n=386) using W_{int}, W_{mean} or W_{max} recorded for 0 to 7 h, 5 to 33 h, and 8.5 to 22 h before sampling, respectively.
Using exponential, power and logistic relationships, r^2 were always significantly greater (t test, p<0.05, n=386) than r^2 obtained with linear relationships. Whatever wind variables used, best fit (r^2) was obtained using power relationships but the efficiency of model was not significantly different (n=386, p<0.05) from exponential, or logistic relationships.

Regarding wind variables used, best power relationships were:

$$[SS] = 15.633 + 1.41305 \cdot W_{int\ 2h}^{2.284} \quad (r^2 = 0.56, p<0.001) \quad \text{(equation 5)}$$

$$[SS] = 20.398 + 0.25784 \cdot W_{mean\ 16h}^{3.161} \quad (r^2 = 0.71, p<0.001) \quad \text{(equation 6)}$$

$$[SS] = 14.270 + 0.02331 \cdot W_{max\ 14h}^{3.674} \quad (r^2 = 0.74, p<0.001) \quad \text{(equation 7)}$$

where [SS] are SS concentrations measured in the water samples, $W_{int\ 2h}$ is Wind velocity measured between 1.5 and 2 h before water sampling, $W_{mean\ 16h}$ is mean wind velocity measured during the period 0 to 16 h before water sampling, and $W_{max\ 14h}$ is maximal wind velocity measured during the period 0 to 14 h before water sampling.

SS calculated from these equations are shown in Figure 4. Even if r^2 obtained with equation 7 was greater than with equation 6, difference between the two r^2 was not significant (p>0.05, n=386).

Other models including linear relationships with threshold and CERC model, did not improve the prediction of SS. Considering that the relationships between SS and wind velocity were linear above a wind velocity threshold which correspond to a wind velocity above which bottom sediment could be resuspended, r^2 values for the correlation between SS and wind velocity never exceeded 0.56. In the same way, the r^2 value of the correlation between the calculated shear stress generated by the wave (CERC method) and the SS never exceeded 0.41.

2.3. Irradiance

Specific attenuation coefficients

Based on the 159 suspended solids concentrations measured simultaneously with an underwater irradiance greater than zero (necessary to compute attenuation coefficient), the mean absorptivity for suspended solids (E_{SS}), and the mean attenuation coefficient for coloured dissolved matters (K_{wc}) were 0.027 m^2 g^{-1} and 0.683 m^{-1}, respectively.
Attenuation coefficients calculated for each of the six episodes of SS sampling covered a large range of values for these variables (0.026 to 0.038 for E_{SS} and 0.49 to 1.04 for K_{wc}).

Underwater PAR variability

Underwater PAR was strongly dependent on incident solar irradiance (I_0) (r^2=0.42, p<0.001, n=7584). During the study period, water depth (z) at the sampling point varied between 1.36 m and 1.89 m with

a mean depth of 1.61 m. We computed the depth of the 4π underwater sensor for each measurement period and used the mean attenuation coefficient previously estimated (K_{wc} = 0.683 m^{-1}) to predict PAR at the sensor. Incident solar irradiance explained 44 % of the variability in the measured underwater PAR.
The attenuation coefficient of irradiance between the surface (Iz_0) and the sensor (Iz), calculated using equation 2, showed a high degree of variability (Fig. 5). Although a significant relationship was observed between attenuation coefficients compared day to day (r^2=0.21, p<0.01, n=137), there was no clear seasonal pattern in the variance component of this variable. Mean daily attenuation coefficients measured on two successive days can be highly different and variation can reach a factor three. Attenuation coefficients were highly correlated to SS concentrations (r^2=0.79, n=386, p<0.001).

Estimation of underwater PAR from infrequent measures of irradiance

Daily integrals of radiation measured at depth z (DI) were highly correlated to irradiance (I_N) measured between 11:30 and 12:00 (r^2=0.91, p<0.001, n=159). Over the 159 days of the study in the Vaccarès, the calculation method for underwater PAR based on the sinusoidal fluctuation of irradiance could lead to high bias in ΣDI when measurements of I_N were infrequent (Fig. 6). Differences between calculated ΣDI and measured ΣDI were lower than 38 % when I_N measuring frequency was less than every five days. In contrast, using sampling intervals of two weeks or more, the differences can reach 200 %.

Estimation of underwater PAR from relationships between wind and SS

The underwater irradiance (Iz=PAR at depth z) calculated from I_0, E_{SS}=0.027 m^2 g^{-1} and K_{WC}=0.683 m^{-1}, and the following equations 2, 3, 4, and 6, is shown in Figure 7. The coefficient of determination (r^2) between measured and calculated Iz reached 0.66. If Iz was calculated with specific attenuation coefficients calculated for each SS sampling episode, r^2 was significantly higher (r^2=0.70) (p<0.001, n=7584). A month-to-month study showed that the lowest correlation between measured and calculated Iz was observed in February (r^2=0.42 with n=1344) and the best correlation was observed in January (r^2=0.76 with n=1488). During February, I_0 explained only 15 % of measured Iz variability. Irradiances calculated for the period contained from 15th February to 15th March were greatly overestimated (Fig. 7). This overestimation was considerably reduced (Fig. 8) using monthly specific attenuation coefficients (calculated for each SS sampling episode) compared to results calculated from mean coefficients (calculated from the whole 159 days study period).

3. Discussion

3.1. Suspended solids

During our study period, the SS concentrations measured in the lagoon was high, and light penetration into the water column was limited. Regarding studies carried out on other large shallow lakes (Luettich et al., 1990; Somlyódy & Koncsos, 1991; Van Duin et al., 1992), the Vaccarès can be characterized as highly turbid.
Suspended matter in the water column of lentic systems have various allochthonous origins (inputs from tributary, runoff, aerosols, etc.) or autochthonous (production or resuspension). Because of the low ratio of watershed area to lagoon area for the Vaccarès lagoon (Ad/Ao=4.8), allochthonous inputs were expected to be low and autochthonous particles to be the main source of SS. Water inputs from the Rhône River or outflow into the Rhône were regulated artificially and SS input or output were low with respect to standing mass of SS in the Vaccarès water column (Chauvelon, 1996). Our results (Table 1) highlight the dominant role of wind velocity in controlling the concentrations of suspended solids in the lagoon. Low concentrations of chlorophyll pigments generally measured in the Vaccarès (De Groot & Golterman, 1999) suggest that phytoplanktonic productivity could represent only a minor source of autochthonous suspended matter. Suspended matter in the water column was mainly resuspended sediment particles.

Relationships between wind and suspended solids are often observed in shallow systems because the bottom particles can be easily mobilised by waves (Aalderink et al., 1984; Bengtsson & Hellström, 1992; Arfi et al., 1993). In this study, the best relationship between SS and wind data (wind velocity

integrated over ½ hour periods) was found using the Velocity of wind measured between 1.5 and 2 hour ($W_{int\ 2h}$) before the water sampling (equation 5). However, because of the high autocorrelation of wind velocity between successive 0.5h time periods, results were not significantly different ($p<0.05$) using W_{int} measured between 0 and 6.5 hours before sampling. Hanlon et al. (1998) in Lake Okeechobee and Arfi et al. (1993) in a tropical lagoon measured both a 3 hours lag time between wind speed increase and sediment resuspension. These few hours of delay could be attributed to the time necessary for progressive building up of the waves and the resuspension of the bottom sediments.
In the Vaccarès, the variations of SS was better explained by the mean of wind velocity during the previous 16 hours (equation 6) or using maximal wind velocity measured during a 14-hour period before SS sampling (equation 7). The best explanations of SS variance obtained with longer delays and mean or maximal wind velocity can be explained by the lapse of time during which the majority of resuspended particles remained in the water column for a period of time that is dependant upon their settling velocities. Kinetics of the resuspension and deposition of particles was consequently taken into account in equation 6 and 7 and was incorporated into the simulation. The lag time taken into account in equations 5 to 7, will probably differ in other aquatic system depending on morphometry (surface area, depth), water salinity and to the composition of bottom sediment (organic matter content and particle-size distribution). In Lake Balaton, it was shown that the 24-hour antecedent wind velocity had a major impact on SS, irradiance, and phytoplankton (Somlyódy & Koncsos, 1991).
Despite the high r^2 value for equation 7, the use of $W_{max\ 14h}$ as a predictor can cause abrupt changes (Fig. 4c) in simulated SS that are not consistent with the smooth, continuous changes of observed SS within the pond in response to wind events. The use of averaged predictors, $W_{int\ 2h}$ and $W_{mean\ 16h}$, in equations 5 and 6 result in smoothed simulations that are more consistent with observed behavior. Similar relationships were found in the ocean (Denman & Miyake, 1971) or in Lake Tämnaren (Sweden, 35 km^2 area, 1.5 m mean depth) (Hellström, 1991), where the increase of suspended matter and irradiance attenuation were found to be proportional to wind velocity to the third power.
In the literature, other relationships used to explain SS variability take into account both wind velocity and fetch (CERC, 1977; Otsubo & Muraoka, 1988). Despite the large range of fetches found at our study site (located near the East edge), wind direction had little impact on SS concentrations. Bottom shear stress induced by waves, computed from empirical CERC equations (CERC, 1977), were poorly correlated with SS measured in the Vaccarès. The same results were obtained by Hanlon et al. (1998) who showed that CERC equations were inappropriate to estimate resuspension of bottom sediments at a muddy location of Lake Okeechobee. In a shallow lake, Aalderink et al. (1984) showed that among four resuspension models tested, the two models using wind velocity alone better matched the measured SS than did the two resuspension models using fetch. In a micro-tidal estuary, the best simulation of SS concentrations were also obtained with model using wind velocity alone (Pejrup, 1986). Two hypotheses may explain the weak correlation between wave models and suspended solids in the Vaccarès. These equations were developed for marine open coastal systems and do not take into account the size of bottom particles. They might be difficult to use in aquatic systems where the bottom sediment is made of very small and poorly cohesive particles (Hanlon et al., 1998). Furthermore in closed and relatively small systems such as lagoons or lakes, rapid wind-induced horizontal advection of suspended solids (Millet 1989) could contribute to reduce the importance of fetch (Gons et al., 1986). If these hypotheses were verified, the prediction of SS in lagoons using wave hydrodynamics models would require improved and revised equations for these variables.
Somlyódy (1981), Bengtsson & Hellström (1992) and Hanlon et al. (1998) found a threshold of wind velocity above which bottom sediments were resuspended. In the Vaccarès, the variance of the suspended solids concentration was better explained by wind velocity using continuous functions (exponential, logistic or power) and no threshold could be identified. Because of the small size of bottom particles in the Vaccarès, sediment was probably easily resuspended even when wind velocity was low. Furthermore, when sediments are frequently resuspended, such as in the Vaccarès, the critical shear stress for initiation of erosion may be lower than with consolidated sediments (Bengtsson & Hellström, 1992).

3.2. Underwater PAR

Underwater PAR variability

In the Vaccarès lagoon, a large part of underwater PAR fluctuations was due to the variance of irradiance attenuation coefficient which was mainly explained by SS concentrations (r^2=0.79). Few studies have focused on the estimation of short time scale variability of underwater PAR in shallow lakes or lagoons (Hanlon et al., 1998; Alvarez-Cobelas et al., 2002). In marine environments, studies have showed that transparency of estuarine water columns can be highly variable with time (Stross & Sokol, 1989; Pinckney & Zingmark, 1993; Zimmerman et al., 1994). Day to day variations of mean daily attenuation coefficient for irradiance can reach a factor of five in the Monterey Bay (Zimmerman et al., 1994). These authors stressed the impact of numerous specific processes (wind, tide, phytoplankton blooms) contributing to the apparent chaotic variability of underwater PAR. In the Vaccarès, although a correlation between attenuation coefficients compared from one day to the next was observed (r^2=0.21, $p<0.01$), attenuation coefficients measured on two successive days could vary by as much as a factor of three (Fig. 5). Therefore, an attenuation coefficient measured on one day is a poor predictor of the attenuation on the following day. Consequently, in this wind-exposed shallow system, infrequent measurements of underwater PAR are poor predictors of the mean optical quality of the water column.

Computation of Integral underwater PAR from infrequent measurements of irradiance

The daily integral of PAR reaching the canopy (DI) is a major factor for plant productivity (Charles-Edwards et al., 1986). DI can be computed from irradiance measured at solar noon (I_N) adjusted using a sinusoidal function for intra-day variation of irradiance intensity (Thornley & Jonhson, 1990 ; McBride, 1992). Application of this method to our data from the Vaccarès lagoon showed that for I_N measured every four days or more frequently, errors in the calculation were less than 38 % with respect to measured values of ΣDI. However, despite the good correlation between I_N (measured between 11h30 and 12h00 in our test) and DI measured by the sensor (r^2=0.91), the calculated ΣDI was unrealistic when I_N was measured infrequently (Fig. 6). Furthermore, we had probably underestimated the magnitude of errors induced by this method because:
first, we have used the mean value of I_N measured between 11:30 and 12:00 (this value was probably more representative of the mean daily conditions than a single measurement taken at noon as this is often done in aquatic survey program);
secondly, we had simulated a regular measurement frequency during the whole study period without taking into account the inaccessibility of the study site during windy days.

Zimmerman et al. (1994) have shown that irradiance at noon (I_N) was not a reliable predictor of daily integrated irradiance in Monterey Bay where correlation between I_N and the daily irradiance integral reached only 58 %. These authors concluded that coastal marine survey programs based on infrequent measurements of optical water quality were not useful for managing macrophyte populations.

Many studies on relationships between underwater PAR and macrophyte productivity were based on infrequent (weekly or monthly) measures of optical water qualities (e.g. Pearsall, 1920; Canfield et al., 1985; Pip & Simmons, 1986; Johnstone & Robinson, 1987; Pérez & Romero, 1992; Koch & Beer, 1996; Laugier et al., 1999; Longstaff & Dennison, 1999). In most lentic freshwater systems, phytoplankton productivity is the main factor contributing to irradiance extinction in the water column (Kirk, 1983 ; Van Duin et al., 2001). Changes in phytoplanktonic communities are generally less chaotic and slower than changes in SS concentrations resulting from wind action. In these systems, at time scales shorter than those necessary to significantly change the phytoplanktonic community, the water column turbidity is often considered as relatively constant. In other shallow lakes, Alvarez-Cobelas et al. (2002) showed that optical-water properties that affect light attenuation varied following a seasonal pattern and were due to changes in gilvin concentrations arising from the decomposition of reeds. Thus, in shallow aquatic systems, two main trends can be observed. Changes in underwater irradiance attenuation can be linked either to phytoplankton or gilvin concentrations at seasonal time scale, or to SS at shorter time scales (days-weeks) especially in wind exposed systems (Van Duin et al., 2001).

Computation of integral underwater PAR using relationships between wind and SS

Underwater PAR at depth z was calculated using specific attenuation variables (E_{SS} and K_{WC}) and SS calculated from the relationships observed between wind velocity and measured SS (equations 5 to 7). Mean values of specific attenuation coefficients (K_{wc}=0.683 m^{-1} and E_{SS} =0.027 m^2 g^{-1}) estimated

from all SS sampling episodes were within the range of values measured in shallow lakes with bottom sediments having low organic matter contents (Kirk, 1983; Davies-Colley, 1993).
During our study period, 42 % of underwater PAR variability was explained by incident solar irradiance. Explanation of PAR variability was increased by 24 % (r^2=0.66) if irradiance attenuation along the water column was simulated taking into account SS variability calculated from wind velocity (Fig. 7). Using this relationship based only on weather data, error in predicting the sum of daily integrals of irradiance (ΣDI) reaching depth z over the whole study period was lower than 19 % (Fig. 6). In this shallow system, mean wind conditions seems to be a relevant tool for the evaluation of underwater irradiance conditions.

Between mid-February and mid-March, calculated PAR was over-estimated whereas it seems to be under-estimated after the 10 April (Fig. 7). For all simulations, constant specific attenuation coefficients were used. However, these coefficients depend on optical qualities of water, and notably on organic matter content of resuspended particles (Kirk, 1983; Davies-Colley, 1993). Using various specific attenuation coefficients estimated for each of the six SS sampling episodes, explanation of the irradiance variance was improved by 4 %. Over-estimation of calculated PAR during February and March was mainly due to the use of mean specific coefficients. Using specific coefficients estimated from SS collected in February, calculated values of PAR were close to the measured PAR values (Fig. 8). However, estimation of specific attenuation coefficients requires water sampling and SS analyses. Simulations using variable coefficients should be consequently more difficult and costly to use in survey programs unless the pattern of changes of the attenuation coefficient is known. Future development of research should focus on this issue.

At the end of the study period, the under-estimation of calculated PAR using our equations could be attributed to the development of *Zostera* cover in spring which can reduce resuspension by dampening wave energy (Gregg & Rose, 1982; Dieter, 1990; Madsen et al., 2001, Banas et al., 2002). Consequently, the water was less turbid and our model under-estimated irradiance reaching the canopy.

Conclusions

In wind-exposed lagoons, SS concentrations and underwater PAR can be highly variable for short time scales on the order of a day or a few days. Continuous measurement of irradiance, if available, or frequent measurements that are unbiased with respect to meteorological conditions seem necessary to obtain realistic estimates of mean irradiance in the water column of these systems. However, we have shown that a good approximation of underwater PAR, and thus of growth conditions for macrophytes at our study site, can be obtained from readily available weather data (wind velocity and solar irradiance).
Depending on the plant species growing in the aquatic system being studied and on their sensitivity to irradiance attenuation, monitoring of weather data could be useful for evaluating the impact of wind events on macrophyte populations. This method, based on simple relationships (easily developed from data collected in survey programs) between weather data and SS can be effective tool for studying and managing aquatic systems in which SS composition is relatively constant. Furthermore, the continuous measurement of attenuation of underwater irradiance and the analysis of the causes of short term (intra-day to a few days) and medium term (weeks and months) changes permit a better understanding of processes operating at a given site. The information gained on processes and the calibration values for various variables will be developed further in a latter project stage and introduced into deterministically coupled models combining hydrodynamics and primary production.

Acknowledgements

We thank R. L. MILLER for reviewing and improving the manuscript and the second anonymous reviewer for his valuable remarks. We also thank Dr A. Charpentier and Dr H. L. Golterman who provided helpful comments and suggestions on an earlier version of this paper and Dr. P. Chauvelon who provided us with the meteorological data. This project was funded by Fondation Sansouire and Fondation MAVA.

References

Aalderink, R. H., L. Lijklema, W. Breukelman, W. Van Raaphorst & A.G. Brinkman, 1984. Quantification of wind induced resuspension in a shallow lake. Water Science and Technology 17: 903-914.

AFNOR, 1994. Qualité de l'eau. Association Française de Normalisation (AFNOR), Paris, pp. 862.

Alvarez-Cobelas, M., A. Baltanas, J. L. Velascos & C. Rojo, 2002. Daily variations in the optical properties of a small lake. Freshwater Biology 47: 1051-1063.

Arfi, R., D. Guiral & M. Bouvy, 1993. Wind induced resuspension in a shallow tropical lagoon. Estuarine Coastal and Shelf Science 36: 587-604.

Backman, T. W. & D. C. Barilotti, 1976. Irradiance reduction: effects on standing crop of the eelgrass *Zostera marina* in a coastal lagoon. Marine Biology 34: 33-40.

Banas, D., G. Masson, L.G., Leglize, L. & J. C. Pihan, 2002. Temporal variations of sedimentation in shallow freshwater systems. Archiv Fur Hydrobiology 153: 623-634.

Bengtsson, L. & T. Hellström, 1992. Wind-induced resuspension in a shallow lake. Hydrobiologia 241: 163-172.

Blindow, I., 1992. Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. Freshwater Biology 28: 15-27.

Cabello-Pasini, A., C. Lara-Turrent & R. C. Zimmerman, 2002. Effect of storms on photosynthesis, carbohydrate content and survival of eelgrass populations from a costal lagoon and the adjacent open ocean. Aquatic Botany 74: 149-164

Canfield, E. D., K. A. Langeland, S. B. Linda & W. T. Haller, 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. Journal of Aquatic Plant Management 23: 25-28.

Capblancq, J., 1995. Production primaire autotrophe. In: Limnologie générale. Pourriot, R. & M. Meybeck (Eds), Masson, Paris, pp. 228-252.

Carruthers, T. J. B., B. J. Longstaff, W.C. Dennison, E. G. Abal & K. Aioi, 2001. Measurement of irradiance penetration in relation to seagrass. In: Global Seagrass Research Methods. Short, F.T. & R. Coles (Eds), Elsevier Science B. V., pp. 369-392.

CERC, 1977. Shore protection manual. Vol. I, U.S. Army Coastal Engineering Research Center, Fort Belvoir, Virginia.

Charles-Edwards, D., D. Doley & G. M. Rimmington, 1986. Modelling plant growth and development. Academic Press, New York, pp. 350.

Chauvelon, P., 1996. Hydrologie quantitative d'une zone humide méditerranéenne aménagée: Le bassin de Fumemorte en Grande Camargue, delta du Rhône. Thesis, University of Montpellier, pp. 274.

Davies-Colley, R. J., 1993. Colour and clarity of natural waters: Science and management of optical water quality. Ellis Horwood Limited, Chichester, pp. 310p.

De Groot, C. J. & H. L. Golterman, 1999. Le risque d'eutrophisation de l'étang de Vaccarès et des marais de la Camargue (Delta du Rhône, France). Ecologie 30 (2): 91-100.

Denman, K. L. & M. Miyake. 1973. Upper layer modification at ocean station Papa: observations and simulation. Journal of Physical Oceanography 3: 185-196.

Dennison, W. C., R. L. Orth, K. A. Moore, J. C. Stevenson, V. Carter, S. Kollar, P. W. Bergstrom & R. A. Batiuk, 1993. Assessing water quality with submerged aquatic vegetation. BioScience 43: 86-94.

Dieter, C. D., 1990. The importance of emergent vegetation in reducing sediment resuspension in wetlands. Journal of Freshwater Ecology 5: 467-473.

Duarte, C. M., 1991. Seagrass depth limits. Aquatic Botany 40: 363-377.

Dunton, K. H., 1994. Seasonal growth and biomass of the subtropical seagrass *Halodule wrightii* in relation to continuous measurements of underwater irradiance. Marine Biology 120: 479-489.

Giesen, W. B. J. T., M.M. van Katwijk & C. Den Hartog, 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. Aquatic Botany 37: 71-85.

Gons, H. J., R. Veeningen & R. Van Keulen, 1986. Effects of wind on a shallow lake ecosystem: resuspension of particles in the Loosdrecht Lakes. Hydrobiological Bulletin 20: 109-120.

Gregg, W. W. & F. L. Rose, 1982. The effects of aquatic macrophytes on the stream micro-environment. Aquatic Botany 14: 309-324.

Hanlon, C. G., R. L. Miller & B. F. McPherson, 1998. Relationships between wind velocity and underwater irradiance in a shallow lake (Lake Okeechobee, Florida, USA). Journal of the American Water Resources Association 34 (4): 951-961.
Hellström, T., 1991. The effect of resuspension on algal production in a shallow lake. Hydrobiologia 213: 183-190.
Johnstone, I. M. & P. W. Robinson, 1987. Light level variation in Lake Tutira after transient sediment inflow and its effect of the submersed macrophytes. New Zealand Journal of Marine Freshwater Research 21: 47-53.
Kirk, J. T. O., 1983. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge, pp. 401.
Koch, E. W. & S. Beer, 1996. Tides, light and the distribution of Zostera marina in Long Island Sound, USA. Aquatic Botany 53: 97-107.
Laugier, T., V. Rigollet & M. L. De Casabianca, 1999. Seasonal dynamics in mixed eelgrass beds, Zostera marina L. and Z. noltii Hornem., in a Mediterranean coastal lagoon (Thau lagoon, France). Aquatic Botany 63: 51-69.
Lemmin, U., 1995. Limnologie physique. In: Limnologie générale. Pourriot, R. & M. Meybeck (Eds), Masson, Paris, pp. 60-114.
Longstaff, B. J. & W. C. Dennison, 1999. Seagrass survival during pulsed turbidity events: the effects of light deprivation on the seagrasses Halodule pinifolia and Halophila ovalis. Aquatic Botany 65: 105-121.
Luettich, R. A., D. R. F. Harleman & L. Somlyódy, 1990. Dynamic behavior of suspended sediment concentrations in a shallow lake perturbed by episodic wind events. Limnology and Oceanography 35: 1050-1067.
Madsen, J. D., P. A. Chambers, W. F. James, E. W. Koch & D. F. Westlake, 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia 444: 71-84.
Marquardt, D. W., 1963. An algorithm for least-squares estimation of non-linear parameters. Journal of the Society Industry Applied Mathematics 11 (2): 431-441.
McBride, G. B., 1992. Simple calculation of daily photosynthesis by means of five photosynthesis-light equations. Limnology and Oceanography 37: 1796-1808.
Millet, B., 1989. Fonctionnement hydrodynamique du bassin de Thau: Validation écologique d'un modèle numérique de circulation (programme Ecothau). Oceanologica Acta 12 (1): 37-46.
Millet, B. & O. Guelorget, 1993. Relationships between benthic communities and physical environment in a lagoon ecosystem. Journal of Coastal Research 9 (2): 378-389.
Moore, K. A., R. L. Wetzel & R. J. Orth, 1997. Seasonal pulses of turbidity and their relations to eelgrass (*Zostera marina* L.) survival in an estuary. Journal of Experimental Marine Biology and Ecology 215: 115-134.
Otsubo, K. & K. Muraoka, 1988. Field observation and simulation of sediment resuspension in a shallow lake. Water Science and Technology 20 (6/7): 263-270.
Pearsall, W. H., 1920. The aquatic vegetation of the English lakes. Journal of Ecology 8: 163-199.
Pejrup, M., 1986. Parameters affecting fine-grained suspended sediment concentrations in a shallow micro-tidal estuary (Ho Burt, Denmark). Estuarine Coastal and Shelf Science 22: 241-254.
Pérez, M. & J. Romero, 1992. Photosynthetic response to light and temperature of the seagrass Cymodocea nodosa and the prediction of its seasonality. Aquatic Botany 43: 51-62.
Pinckney, J. L. & R. G. Zingmark, 1993. Modeling the annual production of intertidal benthic microalgae in estuarine ecosystems. Journal of Phycology 29: 396-407.
Pip, E. & K. Simmons, 1986. Aquatic angiosperms at unusual depths in Shoal Lake, Manitoba-Ontario. Canadian Field-Naturalist 100: 354-358.
Preen, A. R., W. J. Lee Wong & R. G. Coles, 1995. Flood and cyclone related loss, and partial recovery, of more than 1000 km² of seagrass in Hervey Bay, Queensland, Australia. Aquatic Botany 52: 3-17.
Short, F. & S. Wyllie-Echeverria, 1996. Natural and man-induced disturbances of seagrasses. Environmental Conservation 23: 17-27.
Somlyódy, L., 1981. Modelling a complex environmental system: The Lake Balaton study. WP-81-108, IIASA, Laxenburg, Austria. pp. 14-19.
Somlyódy, L. & L. Koncsos, 1991. Influence of Sediment Resuspension on the Light Conditions and Algal Growth in Lake Balaton. Ecol. Model. 57 (3/4): 173-192.
StatSoft, 2002. STATISTICA. Statsoft, Inc., 6th Edition.
Stefan, H. G., J. J. Cardoni, F. R. Schiebe & C. M. Cooper, 1983. Model of light penetration in a turbid lake. Water Resources Research 19 (1): 109-120.

Stross, R. G. & R. C. Sokol, 1989. Runoff and flocculation modify underwater light environment of the Hudson River Estuary. Estuarine Coastal and Shelf Science 29: 305-316.
Thornley, J. H. M. & I. R. Johnson, 1990. Plant and crop modeling: A mathematical approach to plant and crop physiology, Clarendon Press, Oxford, pp. 187.
Van Duin, E. H. S., G. Blom, L. Lijklema & M. J. M. Scholten, 1992. Aspects of Modeling Sediment Transport and Light Conditions in Lake Marken. Hydrobiologia, 235: 167-176.
Van Duin, E. H. S., G. Blom, F. J. Los, R. Maffione, R. Zimmermann, C. F. Cerco, M. Dortch & E. P. H. Best, 2001. Modeling underwater light climate in relation to sedimentation, resuspension, water quality and autotrophic growth. Hydrobiologia 444: 25-42.
Vaquer, A. & P. Heurteaux, 1989. Modifications récentes de la végétation aquatique de l'étang du Vaccarès (Camargue, france) liées aux perturbations anthropiques. Annales de Limnologie 25: 25-38.
Zimmerman, R. C., A. Cabello-Pasini & R. S. Alberte, 1994. Modeling daily production of aquatic macrophytes from irradiance measurements: a comparative analysis. Marine Ecology-Progress Series 114: 185-196.
Zimmerman, R. C., J. L. Reguzzoni, S. Wyllie-Echeverria, M. Josselyn & R. S. Alberte, 1991. Assessment of environmental suitability for growth of *Zostera marina* L. (eelgrass) in San Francisco Bay. Aquatic Botany 39: 353-366.

Table 1: Determination coefficient of linear, exponential, power and logistic relationships between SS concentrations in water and wind velocity measured before water sampling.

	Wind parameters correlated to SS concentrations in water (n=386)					
	W_{int}		W_{max}		W_{mean}	
Model	r^2	t (h)	r^2	t (h)	r^2	t (h)
linear	0.46	2	0.55	15.0	0.57	25.5
exponential	0.55	2	0.73	14.0	0.71	16.5
power	0.56	2	0.74	14.0	0.71	16.0
logistic	0.57	2.5	0.73	14.0	0.71	16.0

t: laps of time optimised to have the better determination coefficient. W_{int}: wind velocity integrated (over 0.5 hour) t hours before water sampling. W_{max}: maximal W_{int} measured during the t hours before water sampling. W_{mean}: Mean of W_{int} measured during the t hours before water sampling.

Figure legends:

Figure 1: Map of the Camargue region showing the location of the sampling site, the weather station, and the yearly wind direction pattern.

Figure 2: SS concentrations and wind velocity during the six episods of SS sampling.

Figure 3: Linear (3.a) and power relationships (3.b) between SS observed and antecedent wind velocity for hours 0 through 48. Circles indicate wind velocity (W_{int}), squares indicate maximal-wind velocity (W_{max}) and triangles indicate mean-wind velocity (W_{mean}). Results obtained with exponential and logistic relationships were not presented because of superimposing with power relationships.

Figure 4: Comparison between SS observed and SS calculated from power relationships with antecedent wind.

Figure 5: Time serie of mean daily attenuation coefficient measured between surface and depth z.

Figure 6: Integral of irradiance at depth z during the whole period (ΣDI) calculated from sinusoidal function and irradiances at noon (I_N) measured with various frequencies (one to 30 days), and expressed in percentage of ΣDI measured by the sensor. The cross shows ΣDI estimated from Iz calculated from power relationship between SS and wind.

Figure 7: Comparison between Iz measured at the sampling station and Iz estimated from SS computed on the basis of the equation 6 resulting from the best relationship between SS observed and antecedent wind conditions.

Figure 8: Details of computed and measured Irradiance (Iz) between 15 February and 15 March. (a) Using mean attenuation coefficients (E_{SS} and K_{WC}) estimated from the whole study period. (b) Using coefficients estimated from water samples collected in February.

Figures

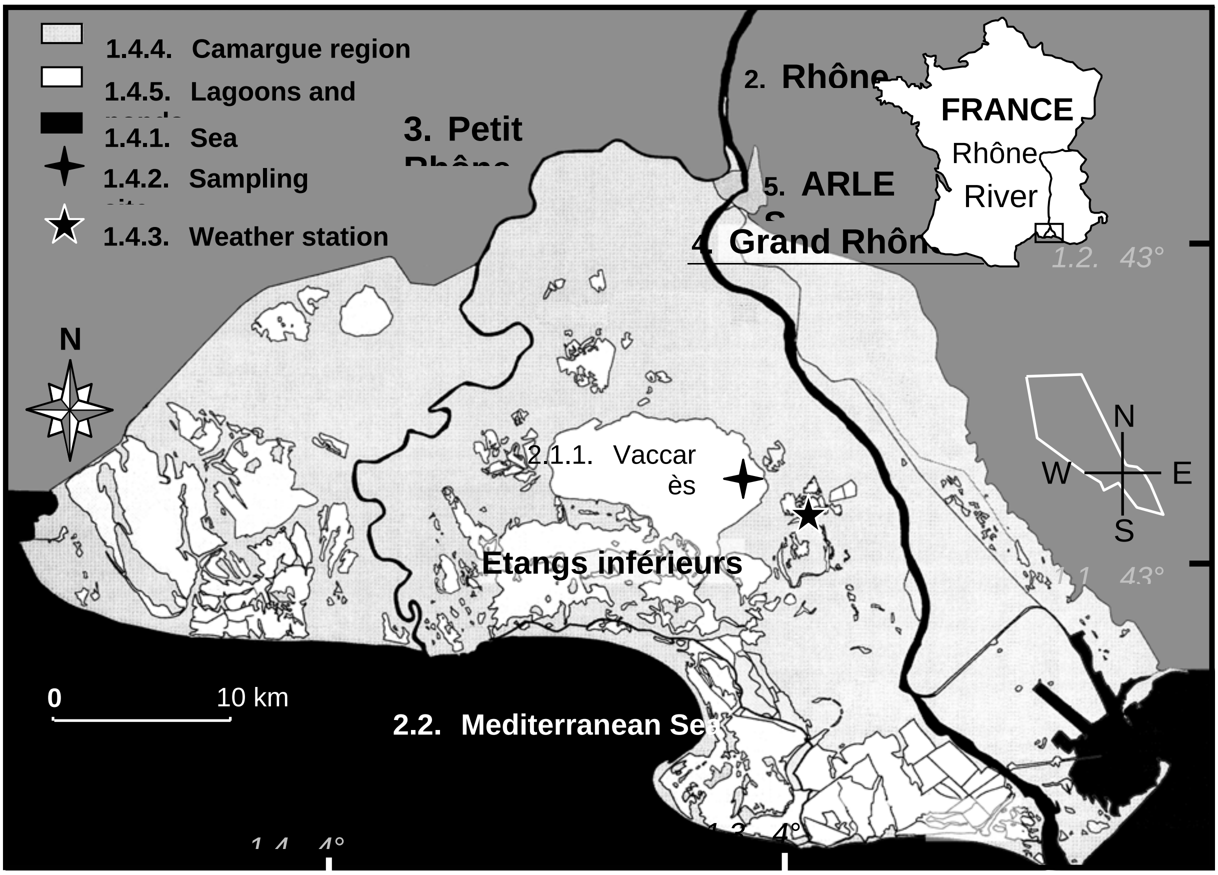


Figure 1

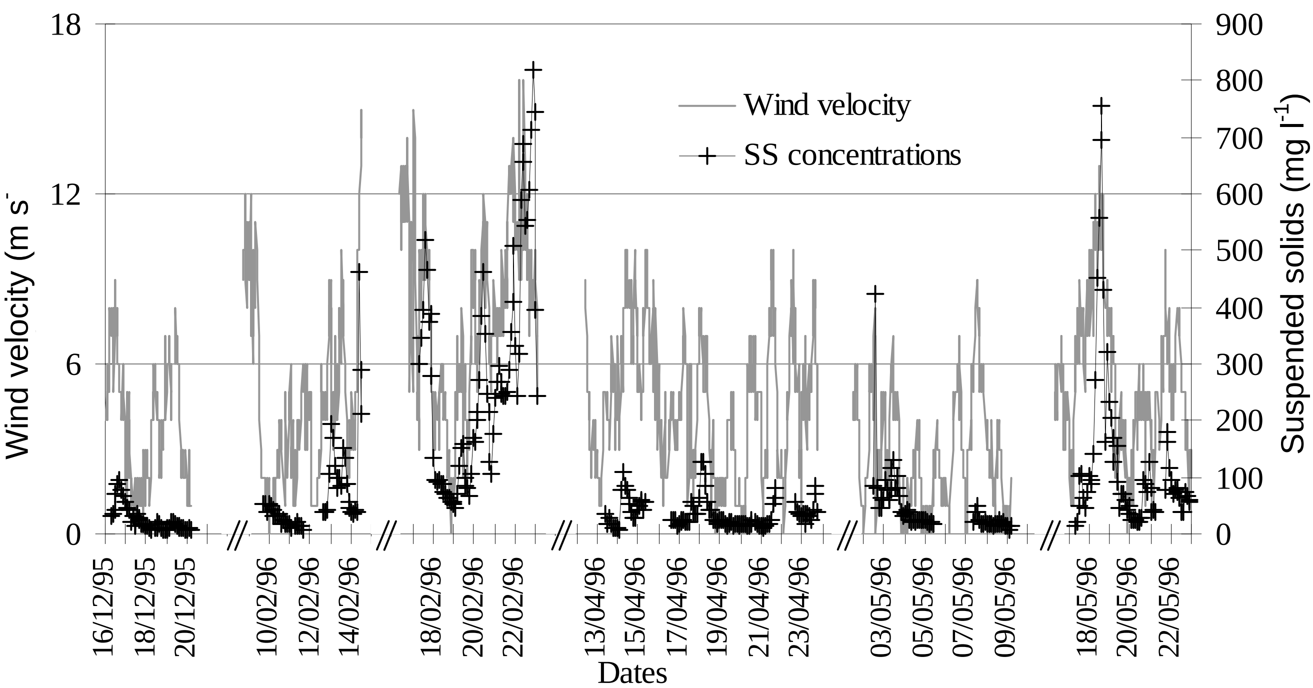

18
12
6
0
900
800
700
600
500
400
300
200
100
0
Wind velocity (m s-
Suspended solids (mg l-1)
Wind velocity
SS concentrations
16/12/95
18/12/95
20/12/95
10/02/96
12/02/96
14/02/96
18/02/96
20/02/96
22/02/96
13/04/96
15/04/96
17/04/96
19/04/96
21/04/96
23/04/96
03/05/96
05/05/96
07/05/96
09/05/96
18/05/96
20/05/96
22/05/96
Dates

Figure 2

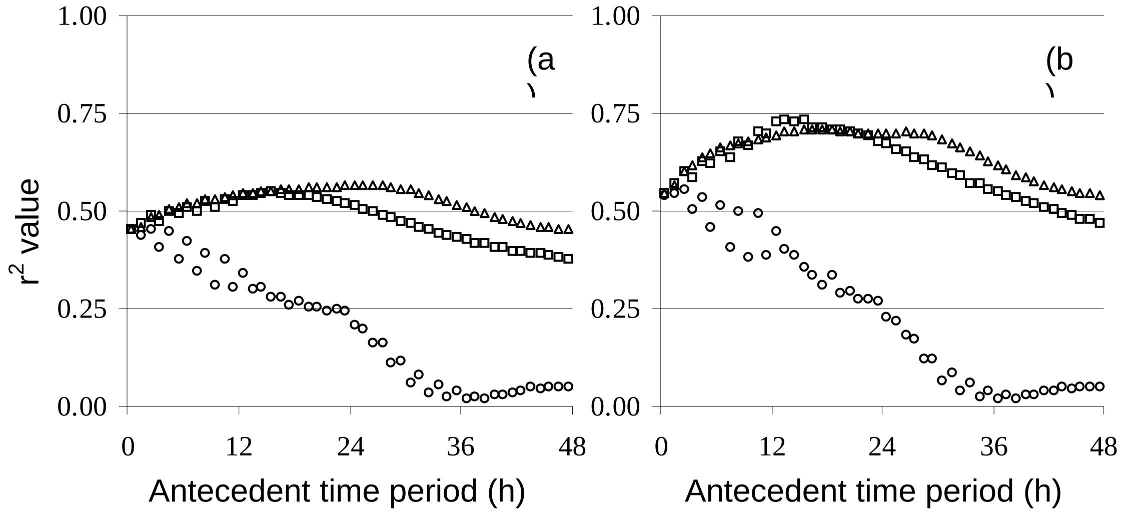
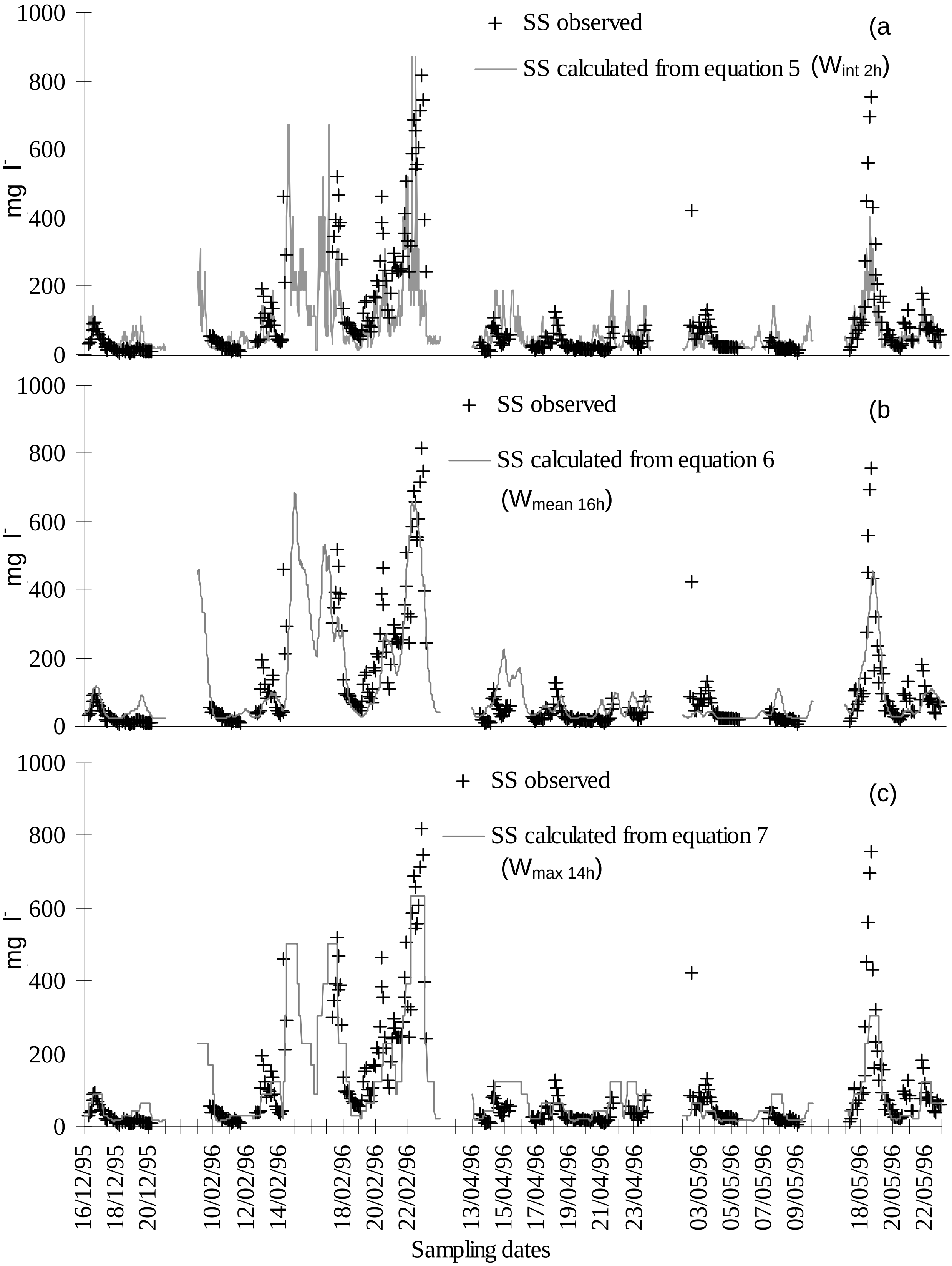

1.00
0.75
0.50
0.25
0.00
r^2 value
(a)
(b)
0
12
24
36
48
Antecedent time period (h)
Antecedent time period (h)

Figure 3



1000
800
600
400
200
0
mg l-
SS observed
SS calculated from equation 5 (W int 2h)
(a
SS observed
SS calculated from equation 6
(W mean 16h)
(b
SS observed
SS calculated from equation 7
(W max 14h)
(c)
16/12/95
18/12/95
20/12/95
10/02/96
12/02/96
14/02/96
18/02/96
20/02/96
22/02/96
13/04/96
15/04/96
17/04/96
19/04/96
21/04/96
23/04/96
03/05/96
05/05/96
07/05/96
09/05/96
18/05/96
20/05/96
22/05/96
Sampling dates

Figure 4

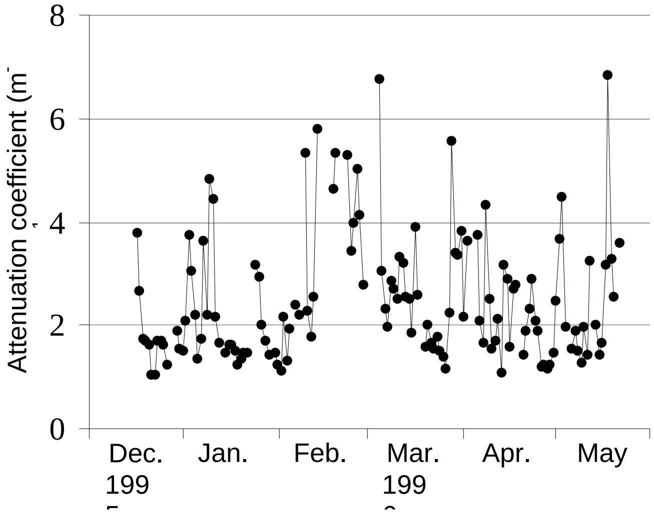
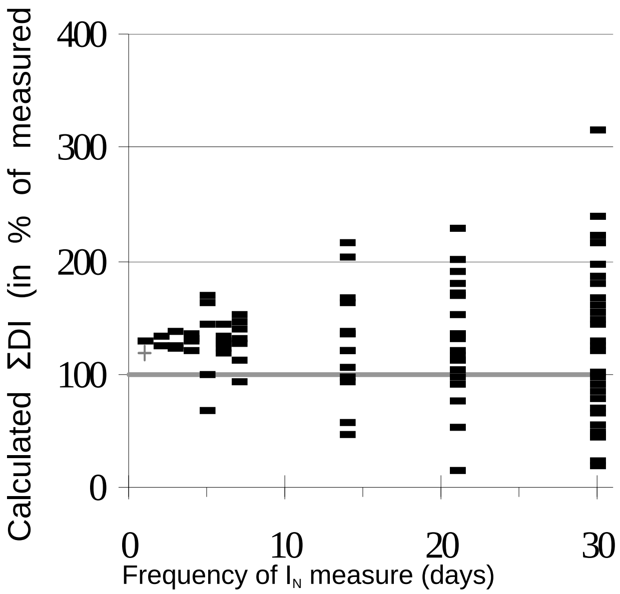
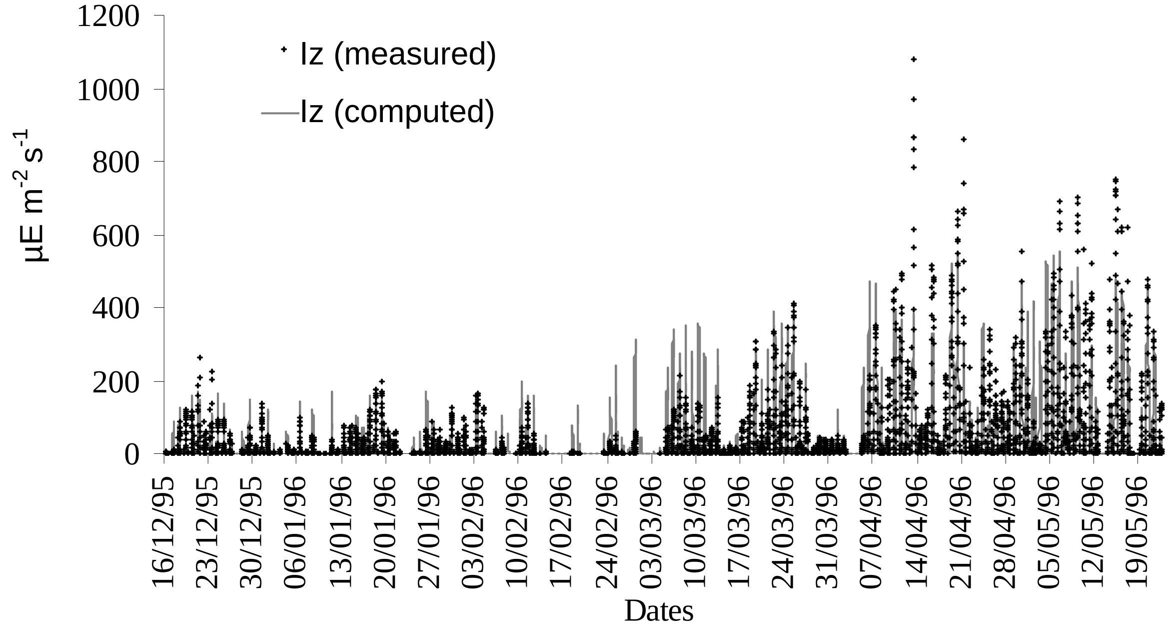

Attenuation coefficient (m-1)
0
2
4
6
8
Dec. 1995
Jan.
Feb.
Mar. 1996
Apr.
May

Figure 5



Calculated ΣDI (in % of measured
400
300
200
100
0
0
10
20
30
Frequency of I$_N$ measure (days)

Figure 6



1200
1000
800
600
400
200
0
Iz (measured)
Iz (computed)
µE m-2 s-1
16/12/95
23/12/95
30/12/95
06/01/96
13/01/96
20/01/96
27/01/96
03/02/96
10/02/96
17/02/96
24/02/96
03/03/96
10/03/96
17/03/96
24/03/96
31/03/96
07/04/96
14/04/96
21/04/96
28/04/96
05/05/96
12/05/96
19/05/96
Dates

Figure 7

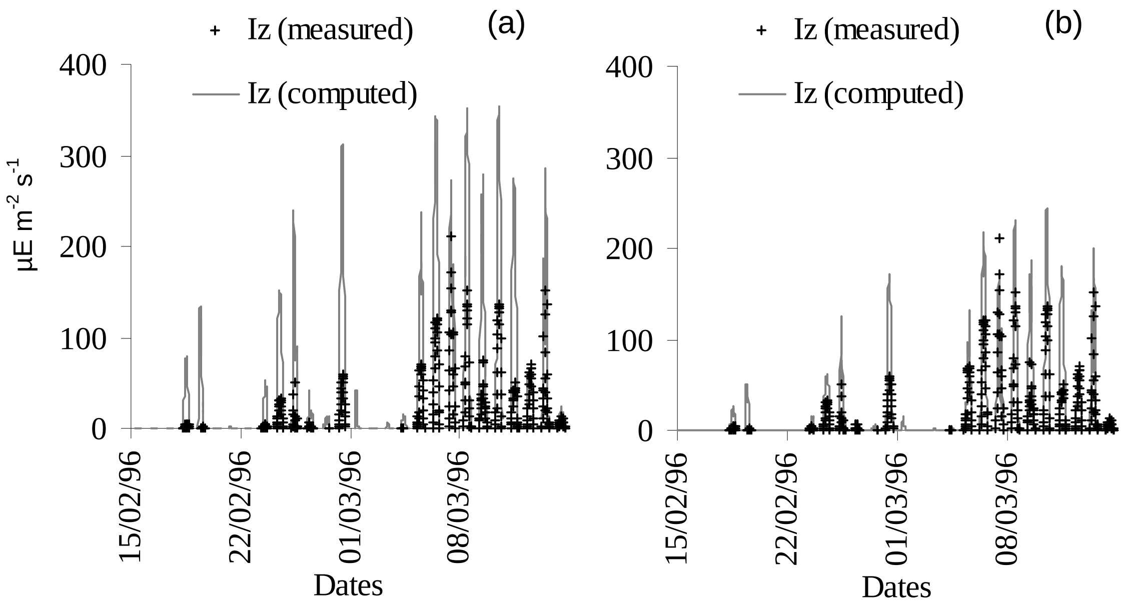

(a)
Iz (measured)
Iz (computed)
µE m-2 s-1
400
300
200
100
0
15/02/96
22/02/96
01/03/96
08/03/96
Dates
(b)
Iz (measured)
Iz (computed)
400
300
200
100
0
15/02/96
22/02/96
01/03/96
08/03/96
Dates

Figure 8