Factors influencing primary production of seagrass beds (Zostera noltii Hornem.) in the Thau lagoon (French Mediterranean coast)

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Abstract:

The primary production and the respiration of Zostera noltii beds in the Thau lagoon were studied by means of the benthic bell jar technique. Concurrently, environmental data (temperature, light and nutrients) as well as morphological data of seagrass meadows (leaf width and height, density of shoots, above/below-ground biomass ratio) were collected with the purpose of explaining most of the observed variations in metabolism. Seagrass plus epiphyte respiration rates were influenced mainly by the water temperature, showing a typical exponential response to an increase in temperature. Surprisingly, measurements of production rates were not related to incoming light intensities recorded at the seagrass canopy level. An equation frequently used for terrestrial standing crops, involving the leaf area index (LAI) and the characteristics of the canopy architecture (parameter K, depending on leaves optical and geometrical properties), was applied to the seagrass ecosystem in order to estimate the light energy actually available for the plants, i.e. the light intercepted by the seagrass canopy (Qabs). Linear relationships were then validated between gross production rates and calculated Qabs for Z. noltii beds, and the best fits were obtained with K values nearing 0.6, confirming the similarities between terrestrial graminaceae and seagrasses. A linear regression model for primary production is proposed, involving the calculated Qabs, the water temperature and the leaf nutrient content.

Keywords: Primary production; Seagrass ecosystem; Intercepted light by canopies; Temperature; Nitrogen contents

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Introduction

Environmental factors controlling seagrass bed dynamics have been studied several times from the ecological viewpoint (Sand–Jensen 1975, Backman and Barilotti 1976, Jacobs 1979, Pérez-Lloréns and Niell 1993 a, Philippart 1995, Laugier *et al*. 1999) as well as the metabolism of these plants, through laboratory experiments (Evans *et al*. 1986, Short 1987, Pérez and Romero 1992, Terrados and Ros 1995). Fewer studies have been dedicated to the entire complex ecosystem (Murray and Wetzel 1987, Moncreiff *et al.* 1992, Barranguet and Alliot 1995, Ziegler and Benner 1998) but they have enabled the contribution of different factors to be quantified: microphytobenthos, macrophytes and the organisms in the water column. Finally, studies on sediment metabolism have allowed the calculation of oxygen and nutrient fluxes at the water-sediment interface (Hopkinson and Wetzel 1982, Nowicki and Nixon 1985, Vidal *et al*. 1989, Chapelle 1995, Mazouni *et al*. 1996 and Plante-Cuny *et al*. 1998).

The use of the benthic bell jar technique to study the primary production dynamics in seagrass communities is common (Lindeboom and Sandee 1989, Barranguet and Alliot 1995, Viaroli *et al.* 1996, Plante-Cuny *et al.* 1998, Erftemeijer and Stapel 1999). It allows the isolation of an ecosystem fragment thus avoiding the problems caused by advection and gas exchanges. Moreover, it is possible to reduce the problems caused by containment and its impact on metabolism by ensuring a good homogenization inside the chambers and by limiting the experiment duration (Ziegler and Benner 1998).

Zostera noltii is widely distributed from south Norway to Mauritania and can spread over quite wide areas (up to 70 km^2 in Arcachon Bay, Auby 1991). In the Mediterranean zone, *Z. noltii* has been mentioned both in poïkilohaline (lagoons and estuaries) and

euryhaline environments (open sea), where it can be found in mixed seagrass beds with *Z. marina* (Laugier *et al*. 1999) or *Cymodocea nodosa* (Loques *et al*. 1990).

The aim of the present study was to estimate production and respiration of a *Z. noltii* community over several seasons using dissolved oxygen measurements in benthic chambers, to compare these data with other seagrass beds and to establish the main biotic (seagrass bed morphology, physiology of photosynthesis) and abiotic parameters (temperature, light and nutrients) which correlate with the observed variations.

Study site

The Thau lagoon is a brackish shallow lagoon (25 km long, 5 km wide and about 4 m mean depth) located on the French Mediterranean coast (see Fig. 1). The catchment area is small (280 km²) and drained by numerous little streams with intermittent flows. The lagoon is a semi-confined ecosystem with two narrow openings towards the sea and the climate imposes a wide range of temperatures and salinities (minima in February with 5°C and a salinity near 27, and maxima in August with 29°C and a salinity of 40). Precipitation also shows large interannual variation (from 200 to 1000 mm.year^{-1}) and the wind is often strong (a mean of 118.5 days per year above Beaufort force 5; data from Météo-France), particularly when coming from the northwest (the so called « Tramontane »). Both play an important role in the lagoon hydrodynamics (Lazure 1992). The annual average vertical attenuation coefficient, outside the oyster culture tables, is 0.35 m^{-1} (Deslous-Paoli 1995).

Besides its ecological interest as a breeding and transit zone for some sea fish species, the lagoon has a notable economic importance due to shellfish cultivation (highest production in the Mediterranean).

The whole macrophytobenthos biomass in the Thau lagoon has been estimated at 8742 ± 2795 tons dry weight with a significant proportion of seagrasses (22 %), represented by two species : *Zostera marina* L. and *Zostera noltii* Hornem. (Gerbal 1994), both located in different areas on almost all the lagoon periphery between 0 and 5 m depth (Fig. 1).

All the measurements were carried out in a homogeneous perpetually submerged *Zostera noltii* stand, situated against a narrow sandy strand which separates the lagoon from the Mediterranean Sea. At the study site, the water depth ranges from 1.2 to 1.6 m and the sediment is sandy (fraction 200 µm - 2 mm > 85 % dry weight and the organic matter quantity is 1.2 ± 0.2 % dry weight ; Deslous-Paoli, personnal communication). Seven *in situ* experiments were performed over a two year period; July 1996, April, August and October 1997, February, May and August 1998.

Materials and methods

Benthic chambers.

The day before each experiment, six PVC rings (0.38 m internal diameter) were gently pushed into the sediment in order to isolate some eelgrass shoots. Just before the measurements, six identical metacrylate hemispheres, the benthic chambers, were placed on the seagrasses and attached to the PVC rings by SCUBA divers, eliminating trapped molluscs or crustaceans if necessary. Three of the chambers were transparent (production measurements) and the other three were opaque (respiration measurements). Each *in situ* measurement lasted three hours and was repeated the following day, when the transparent and

opaque chambers were interchanged. Consequently, both respiration and production data were recorded for each isolated ecosystem fragment. Because of the shallow depth in the study site, the two experiments were started at the same hour in order to reduce differences in temperature. Homogenization inside the chamber was ensured by a magnetic stirrer and a surgical glove (acting as an expansion volume) allowed water sampling without the entry of sediment pore water. The whole installation never exceeded 20 min.

Dissolved oxygen and nutrients.

Dissolved oxygen was recorded inside the bell jars by YSI 5739 polarographic probes previously calibrated in the air at 100 % saturation, linked to YSI model 58 recorders on the boat. Two sets of seven water samples were collected (1 outside and 6 inside the benthic chambers), one at the beginning and the other one at the end of each experiment. After filtration (Whatman GF/F), samples for ammonium were analysed immediately, following the indophenol coloration method (Koroleff 1969, completed by Aminot 1983), whereas samples for other nutrients (nitrite, nitrate and phosphate) were frozen for further analysis on a segmented flow analyser according to the technique of Tréguer and Le Corre (1975).

Temperature, light and salinity.

Incoming light variation, i.e. the photosynthetic photon flux density (PPFD in the waveband 400-700 nm, expressed in µmol photons.$m^{-2}.s^{-1}$), provided by a LI-COR spherical waterproof sensor placed at the top of the seagrass canopy level, was recorded for three hours, concurrently with the dissolved oxygen measurements. Temperature and salinity were measured with a WTW LF 197-S conductimeter (accuracy 0.5 %), at the beginning and at the end of each experiment.

Plant treatment.

At the end of the second day, all the plants in the chambers were collected and brought to the laboratory where they were carefully rinsed and washed with tap water. The seagrasses were separated into individual plants, and divided into above and below-ground biomasses. Rhizomes and roots were considered alive when crispy and light brown in colour. The number of shoots per chamber was recorded as well as the length and the width of at least fifteen randomly-chosen shoots (all leaves were measured) from each chamber. These measurements allowed the calculation of the seagrass leaf area index (LAI, total leaf surface per unit ground surface, expressed in $m^2.m^{-2}$) for each isolated seagrass meadow. Then, leaves, rhizomes, roots and occasionally macroalgae, were dried in an oven to constant weight (80°C, 48 h) for biomass measurements. During 1998 and the beginning of 1999, the carbon and nitrogen content of *Z. noltii* leaves (epiphytes having been removed) and below-ground parts (previously lyophilized) were measured using a Perkin-Elmer CHNSO autoanalyser (elementary thermoanalysis method). We assume that nutrient contents vary seasonally but that year to year, for the same season, variability is low. This hypothesis is supported by experiments done on *Z. noltii* in the Thau lagoon (in a site close to our) by Laugier (1998). Consequently, we will consider that nutrient contents in plants sampled in 1996 and 1997 are close to those measured for the same season in years 1998 and 1999. An epiphyte biomass estimate was made during August 1997 when, on a visual basis, epiphyte biomass was maximum. Epiphytes were carefully scraped from seagrass blades and dried to constant weight for biomass measurement.

Calculation of Metabolic Rates.

Respiration and production rates inside the chambers (expressed in $mgO_2.m^{-2}.h^{-1}$) were defined as the slope of the linear regression between oxygen concentration and time of

incubation (Hopkinson and Wetzel, 1982, Grenz *et al*., 1991). In the opaque chambers, the linear regressions were calculated at the beginning of the measurements, *i.e.* before the oxygen concentration fell below 50 % saturation, thus reducing the problems linked to oxygen depletion inside the chambers. In the transparent chambers, calculations of production were restricted to periods when incoming light intensity was stable for at least one hour. This was always calculated with oxygen concentrations below an upper limit of oxygen saturation fixed at 200 %. Total respiration rate of a dark chamber was added to net apparent production rates of the same ecosystem (clear chamber measurement done the day before or the day after) in order to calculate the gross production.

The complex ecosystems isolated inside the chambers may be divided into five groups : i) the seagrasses, their epiphytes and sometimes macroalgae, ii) the organisms living in the water column (phytoplankton and zooplankton), iii) the microphytobenthos, iv) the bacterial and invertebrate communities living at the surface and inside the sediment (responsible for the sediment biological oxygen demand) and v) the sediment chemical oxygen demand.

Neither the plankton communities nor the microphytobenthos were taken into account in the calculation of the production rates inside the chambers because they have a minor effect on the oxygen fluxes inside the benthic bell jars compared to the seagrass productivity (see Barranguet and Alliot 1995, Plante-Cuny *et al*. 1998 ; experiments carried out in the Thau lagoon).

Light intercepted by the seagrass meadows.

Light measurements inside the canopy could not be carried out due to the low height of *Zostera noltii* leaves. However, many studies have been conducted on the existing relationships between light, crop structure and primary production for aerial plants (Pearce et al. 1965, Sivakumar and Virmani 1984, Varlet-Granchet *et al*. 1993) and one can use the

similarities between graminaceae and seagrasses in order to estimate, for example, their shading effect (Sinoquet H., pers. comm.). The efficiency of PPFD interception by a plant meadow (denoted ε) is related to its leaf area index as in the following relationship (Varlet-Granchet *et al.*, 1989) :

$$\varepsilon = \varepsilon_{max} \times \left[1 - \exp^{(-K \times LAI)} \right] \qquad (2)$$

According to Varlet-Granchet *et al.* (1989) again, the maximum value for the interception efficiency, ε_{max} can be considered as a constant ($\varepsilon_{max}=0.95$) in the waveband 400-700 nm and coefficient K for light interception depends on the leaves optical properties and their orientation. Values for K have been published for a wide range of aerial species but, as far as we know, only the publication of Pérez-Llorénz and Niell (1993 b) gives an estimate of K for seagrasses (K = 0.97 for *Zostera noltii*). In this study, in addition to the K reported by Pérez-Lloréns and Niell, different K values for terrestrial graminaceae have been tested. In the air, parameter ε multiplied by the PPFD at the canopy level gives the radiation absorbed by the leaves (Qabs) but, in aquatic environments, light absorption both by the plants and by the water itself enhances total light reduction. In order to take the light reduction between the surface and the seagrass beds into account, we used the light measured underwater at the seagrass canopy (Qcan) for the Qabs calculation :

$$Qabs = Qcan \times \varepsilon \qquad (3)$$

Statistical analysis.

All means are given with standard errors ($\pm\ t_{95} \times \frac{s}{\sqrt{n}}$) and comparisons of data sets were performed using non parametric tests (Wilcoxon, Kruskall-Wallis). Relationships between all benthic chamber results and environmental conditions were tested using least square linear regressions and proposed here after checking the normality of residuals. To test

the linear model likehood (in the case of multiple regression), a Cp statistic has been used to see if the model is not improved by dropping any term. All statistics were performed using S-Plus 4 software (S-Plus 1997).

Results

Environmental variables and seagrass beds morphology (table 1 and 2).

As expected, the maximum water temperature is reached in summer (21.6 to 26.8 °C) and the minimum in winter (9.3 °C in February 1998, deemed a mild winter) while spring and fall exhibit roughly the same temperatures (around 14°C). The salinity ranged between 31.2 (April 1997) and 38.6 (August 1998), well within the tolerance range of *Zostera noltii* (minima 3.5-5, no maxima found in the literature, Auby 1991). Conditions of light reaching the seagrass canopy were highly variable, even over a very short period, as they depend on season and cloudiness as well as on water transparency.

Nutrient concentrations remained rather low throughout the experiments (ammonium, nitrates plus nitrites and phosphate concentrations never exceeded 5 $\mu mol.l^{-1}$, see Table 1), even following a strong increase in October 1997 (NH_4^+ = 4.3 ±0.83 $\mu mol.l^{-1}$; $NO_2^- + NO_3^-$ = 2.7 ±0.13 $\mu mol.l^{-1}$ and PO_4^{3-} = 0.95 ±0.03 $\mu mol.l^{-1}$).

The highest shoot density of all seven experiments (3593 ±753 shoots.m^{-2}) occurred in July 1996, but without reaching the highest LAI value, probably due to the rather low leaf height and width. In April, August and October 1997, no significant differences in density were found but leaf length was the highest in August (38.6 ±1.3 cm), and resulted in a very high LAI (3.6 ±0.86 m^2.m^{-2}). In April 1997, the LAI reached values very near those of July 1996 owing to a relatively high leaf length and width (22.8 ± 0.4 cm and 1.8 ±0.2 mm, respectively). Conversely, shoots were particularly short in October (leaf height = 12 ±0.2

cm). The measurements of February 1998 were conducted on a seagrass bed with low density (1061 ±165 shoots.m^{-2}) and little leaves, leading to the lowest LAI value (0.5 ±0.08 m^2.m^{-2}). Shoot density was also relatively low in May 1998 when the leaves were the shortest and the thinnest (8.5 ±0.2 cm and 1.2 ±0.01 mm, respectively), resulting in a very low LAI (0.6 ±0.06 m^2.m^{-2}). Finally, the last measurements (August 1998) were done on a seagrass meadow with low density and leaf lengths around 15 cm, so the LAI reached only 0.8 ±0.05 m^2.m^{-2}.

Number of leaves per shoot did not show large variations (mean 2.8 ±0.16) except perhaps in February 1998 when mean number of leaves per shoot was the lowest (2.6 ±0.1).

The above / below-ground biomass ratio ranged between 0.6 ±0.04 (April 1997) to 1.9 ±0.25 (October 1997) with values relatively high in fall and winter and low in spring. The biomass of algae in the benthic chambers remained very low (in some instances Rhodophyta, *Gracilaria spp.,* and/or Chlorophyta, *Chaetomorpha sp.* and *Cladophora sp.*, were found amongst the eelgrass shoots) in all seasons, never exceeding 3 % of total plant biomass. Nevertheless, it is notable that the highest biomasses of algae were always found in summer. Maximum epiphyte contribution to seagrass blade plus epiphyte biomass was around 10 % and averaged 13.7 g DW.m^{-2} in August 1997.

Seasonal patterns of carbon and nitrogen contents show a minimum at the end of spring and in summer and a maximum in winter with a stronger seasonality for nitrogen content (see table 3). C and N contents of leaves are significantly different from C and N content of below-ground parts ($p < 0.01$ and $p < 0.0001$ respectively). Although the carbon content in both parts of the plant remain close, the nitrogen content in leaves is roughly twice that of rhizomes and roots. Leaf C:N ratio was maximum in spring and minimum in winter but the variations remained low, contrary to the belowground parts which showed big C:N ratio variations during the year.

Benthic metabolism.

An example of observed dissolved oxygen variation in two benthic chambers (one dark and the other clear) is given in figure 2. For this experiment, two production rates were calculated, one for the first hour and a half at low incoming light level and one for the last hour at high light availability. Figure 3 shows the gross production and mean respiration rates measured in the ball jars during each experiment.

- Respiration :

Oxygen consumption in dark chambers ranged from 52.5 to 483.7 $mgO_2.m^{-2}.h^{-1}$. The highest values were measured in summer as the benthic respiration is closely related to the temperature ($p<0.001$), following an exponential curve (see fig. 4). Salinity, nutrient concentrations in the water column, and plant nitrogen content did not show any significant correlation with respiration.

- Production :

Net oxygen production rates (NPR) in the clear chambers ranged from -93.7 (August 1997) to 670.3 $mgO_2.m^{-2}.h^{-1}$ (July 1996). No significant relationship could be found between either environmental (temperature, salinity, seawater nutrient concentrations) or biotic factors (nutrients internal content, LAI, Qabs) and NPR. After adding the respiration rates to obtain gross production rates (GPR), relationships between GPR and other variables could be examined. A linear regression between GPR and seagrass leaf biomass was evident (Fig 5b) and a very slight positive effect of temperature on GPR (Fig 5a). Finally, although the data did not show any significant relation between GPR and Qcan (fig 5c), the calculation of absorbed PPFD by the canopy (Qabs) showed good linear correlations with GPR (see fig 6a and b). No significant relationship could be demonstrated between either seawater nutrient concentration or salinity and GPR.

Though no effect of either the temperature or the nutrient content alone on the production rates could be confirmed, a multiple regression grouping Qabs, temperature and leaf nitrogen content was attempted, and is presented here as it improves the percentage of explained GPR variation :

$$\text{GPRcal} = 0.59 \times \text{Qabs} + 17.47 \times \text{Temp} + 410.33 \times \text{Ncont} - 976.63 \qquad (4)$$

$r^2 = 0.604$, n = 49 and

parameter	Qint	Temp	Ncont
p value	< 0.0001	< 0.0001	$= 0.0001$

residual standard error = 125.1 $\text{mgO}_2.\text{m}^{-2}.\text{h}^{-1}$

Where GPRcal is the calculated gross production rate in $\text{mgO}_2.\text{m}^{-2}.\text{h}^{-1}$, Qabs is the light absorbed by the canopy in $\mu\text{mol photons}.\text{m}^{-2}.\text{s}^{-1}$, Temp is the water temperature in °C and Ncont is the leaf nitrogen content in % dry weight.

The addition of the seagrass leaf biomass as a new variable did not improve the model. Figure 7, indicates the accuracy of the model, *i. e*. how well the calculated values for GPR relate to measured values.

Discussion

These seven benthic chamber experiments were conducted in a warm temperate coastal lagoon, at shallow depths involving a wide range of climatic conditions, and on seagrass beds which have shown big morphological variations (leaf height and width, belowground biomass, shoot density) throughout the study period. LAI is a good index for estimating standing crop on a unit ground surface basis, nonetheless, in isolation it would not give us a good indication of the morphological characteristics of a seagrass bed. For example,

measurements of meadows in February and May 1998 are quite different regarding the density and leaf length but they exhibited almost the same LAI). As seagrass beds were not chosen at random, their morphological characteristics cannot be used to describe the temporal variations of seagrasses in the Thau lagoon. Nevertheless, general patterns of above/belowground biomass ratio can be compared to other *Z. noltii* beds. This ratio always remained below 2, with some values lower than 1, pointing out the importance of rhizome and root biomass for this species as already described by Auby (1991) in the bay of Arcachon (French Atlantic coast). Furthermore, it seems that the observed seasonal variations of the above/belowground biomass ratio corroborate the ones found by Philippart (1995) in the western Wadden Sea (Netherlands) with a maximum in late summer and a minimum in spring. In fact, our study site, in addition to the low organic matter content in the sediments (1.2 ± 0.2 % of sediment dry weight), is subject to intense hydrodynamics due to strong northwesterly winds (« Tramontane ») which occur frequently throughout the year (Lazure 1992, Laugier *et al*. 1999). Thus, the enhanced development of below-ground parts of the plant may be due to both the low nutrient availability in sandy sediments as well as to the hydrodynamics of the water column (resistance to up-rooting).

With regard to nutrients in the water column, the observed concentrations were within the range of low values previously reported for the Thau lagoon by Casellas *et al*. (1990) and Picot *et al*. (1990). This was probably due to the location of our study site, being outside the shellfish farming areas and at the same time relatively far from watershed inputs (north fringe of the lagoon) and from the cities; the three most important nutrient sources of the lagoon.

The spring and summer nitrogen concentrations in leaves are 20-25% less than winter values and the same pattern have been found for rhizomes and roots nitrogen content (40% less than winter values). This summer minimum has been previously described for *Z. noltii* by Laugier (1998; Thau lagoon), by Pérez-Llorens and Niell (1993; Palmones river estuary), by

Pirc and Wollenweber (1998) and for *Z. marina* by Sfriso and Marcomini (1999; Lagoon of Venice).

The measured respiration rates were close to ranges previously described in the literature for temperate seagrass beds (see table 4). A good exponential relationship with temperature could be fitted, confirming the importance of temperature in this aspect of metabolism. Thus, the high temperatures recorded during summer could explain why our measured maximum respiration rates were above those previously reported in the literature. However, considering that the seagrass biomass, compared to other components of the ecosystem inside the benthic chambers, was always the greatest, we made the assumption that seagrasses and their epiphytes were mainly responsible for the variations in respiration. Thus, the high mean respiration rate measured in August 1997, can be explained by the highest seagrass biomass (leaves + rhizomes and roots) throughout the experiments (see figure 3 and table 2).

Gross production rates are within the range previously reported for other temperate seagrass beds (table 5). Variation in incoming light has a rapid, short-term effect on photosynthesis as shown in Fig. 2a, when a strong increase of available light led to an immediate response in fluxes of oxygen. However, when determining the parameters responsible for the variation in ecosystem primary production (figures 5 and 6), the light measured at the seagrass canopy could not explain, surprisingly, the observed variations in ecosystem gross productivity. In fact, the photosynthetic photon flux density measured at the seagrass canopy was always very high, as only one measurement was recorded below the intensity of saturation (Ik $\approx$ 300 µmol photons.m^{-2}.s^{-1}, Jiménez *et al*. 1987) in all seven experiments. Futhermore, a few authors have already mentioned the importance of the self-shading effect in the photosynthetic response of seagrasses (Short 1980, Pérez and Romero 1992). These observations led us to calculate the light not only available but actually

intercepted by the canopy (Qabs) using equations (2) and (3), derived from the Monsi and Saeki studies frequently used for terrestrial plants (Varlet-Granchet *et al*. 1989, Pérez-Lloréns and Niell 1993 b).

Different values for K were then tested and the best regression was obtained with K near 0.55 (see figure 6). Our data do not permit the establishment of an exact K coefficient value for *Zostera noltii*. Nevertheless, it seems that Pérez-Lloréns et al. (1993 b) slightly overestimated its value. One hypothesis might be that the K value was determined in an experiment which didn't account for the orientation of leaves but only the optical properties. In table 6, we can see that K values close to 1 are typical for plants with horizontally disposed leaves while graminaceae with vertical leaves exhibit lower values.

Notably, in Fig. 5c, the values for GPR recorded in May 1998 at high light intensities (1382 and 1453 µmol photons.m^{-2}.s^{-1}) were especially low. Photoinhibition might explain such low production rates but we have rejected this hypothesis, owing to the data from Jiménez *et al.* (1987) who incubated leaves of *Z. noltii* in up to 6000 µmol photons.m^{-2}.s^{-1} without stimulating any photoinhibition, and from Leuschner and Rees (1993) who have calculated a light saturation value of 1831 µmol photons.m^{-2}.s^{-1} for the same species during emersion**.** A plausible explanation could be given using the nutrient content data : in the Thau lagoon, the minimum nitrogen content actually occurs in late spring and summer (1.9 and 2.05 % of leaf dry weight and 0.93 and 0.77 % of rhizomes/roots dry weight, respectively), with values nearing the threshold value for nitrogen limitation (1.8 % of dry weight) published by Duarte (1990).

A multiple linear regression model has been proposed (see equation 4), allowing an estimation of the gross primary production based on three parameters : Qabs, water temperature and leaf nitrogen content. We consider that the leaf nitrogen content (measured at the end of the experiments) is an independent parameter. In fact, at the end of each

experiment we calculate the sum ($N_{t+\delta t}$) of i) the leaf nitrogen content immediately before the measurement (N_t) and ii) the balance between nitrogen gain and loss occurring during the three hour measurement (δN). We assume in this theoretical model that δN is not significant with respect to N_t and thus, that $N_{t+\delta t} \approx N_t$.

This empirical model must however be considered carefully, as its formulation is only acceptable in the ranges of temperature and leaf area indices tested (9 to 26.8 °C and 0.5 to 3.6 $m^2.m^{-2}$ respectively). Furthermore, the percentage of explicated variance by the model (60 %) was rather low and should be improved appreciably by multiplying measurements at different times of the year (different temperatures, light levels and nutrient contents).

Under these restrictions the theoretical model proposed here can be used to make predictions knowing the standard error of estimate (125.1 $mgO_2.m^{-2}.h^{-1}$), and be compared with the respiration calculated by means of the exponential model (see Figure 4). It is then possible (within the limitations exposed above), under a given set of environmental parameters (light and temperature) and knowing the leaf area index and the leaf nitrogen content of a seagrass bed, to elucidate whether the community is autotrophic or heterotrophic. It appears that

Conclusion

The choice of benthic bell jars to study primary production and respiration of a seagrass ecosystem leads to the formulation of a simplified hypothesis as the fragment ecosystem isolated is still complex. Nevertheless, it is evident that the principal parameters responsible for the observed variations in the metabolism of Thau lagoon *Z. noltii* meadows are : temperature, light and nutrient content. However, in our opinion the measurement of

incoming light alone is not sufficient, as it overestimates the effective available light for photosynthesis. Actually, as results of the interaction of crop structure and light microclimate are already available for terrestrial species, we thought that using the similarities between aerial graminacea and seagrasses could be very useful. Thus, the use of the light intercepted by the canopy, calculated as a function of the leaf area index, has been proposed here, allowing the construction of a linear regression model (also involving water temperature and leaf nitrogen content) to estimate the primary production of *Zostera noltii* beds.

Considering the importance of seagrass biomass in the Thau lagoon, we may deem this work as a first step in accounting for macrophytes in the study of the whole ecosystem oxygen cycle.

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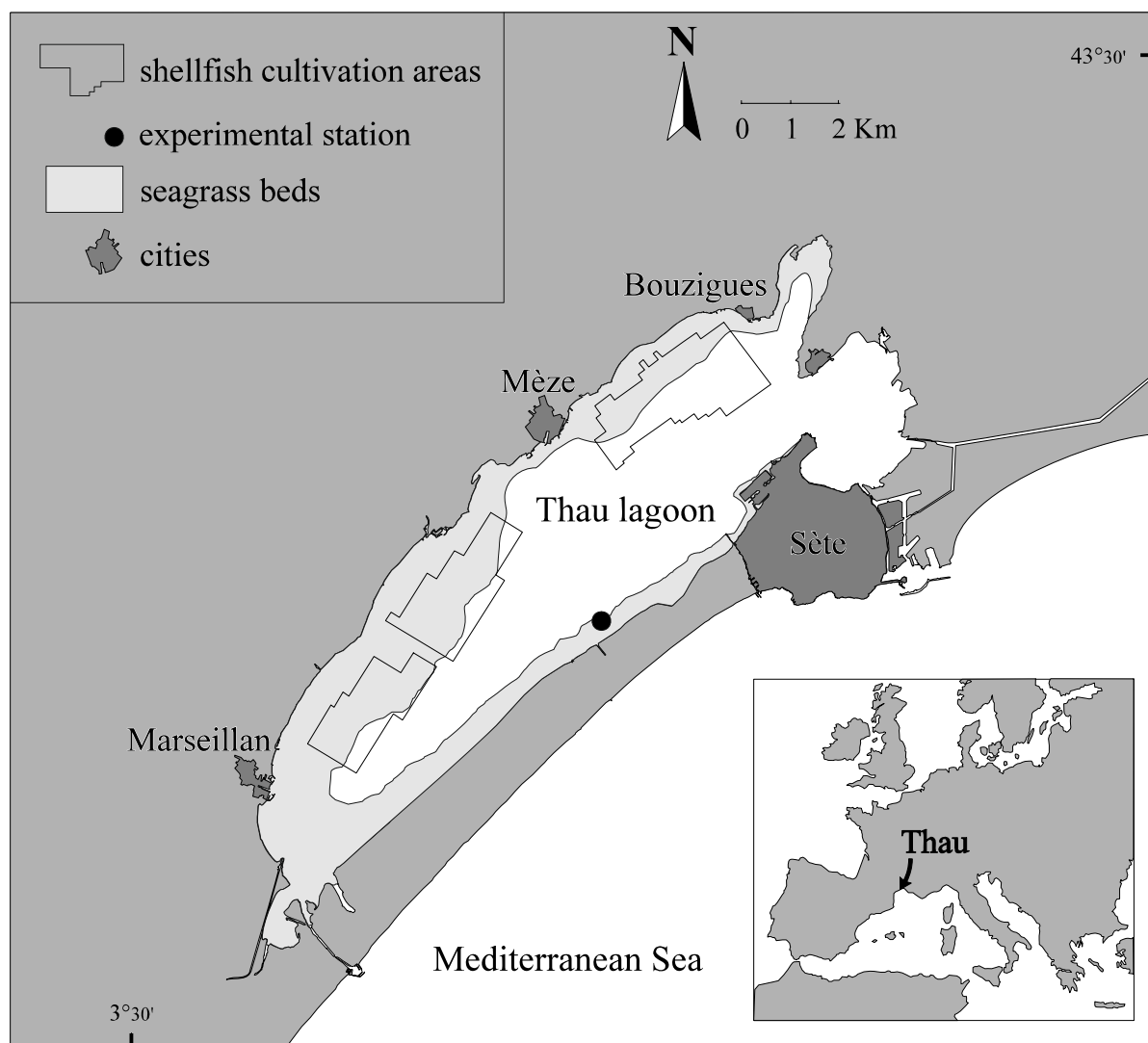
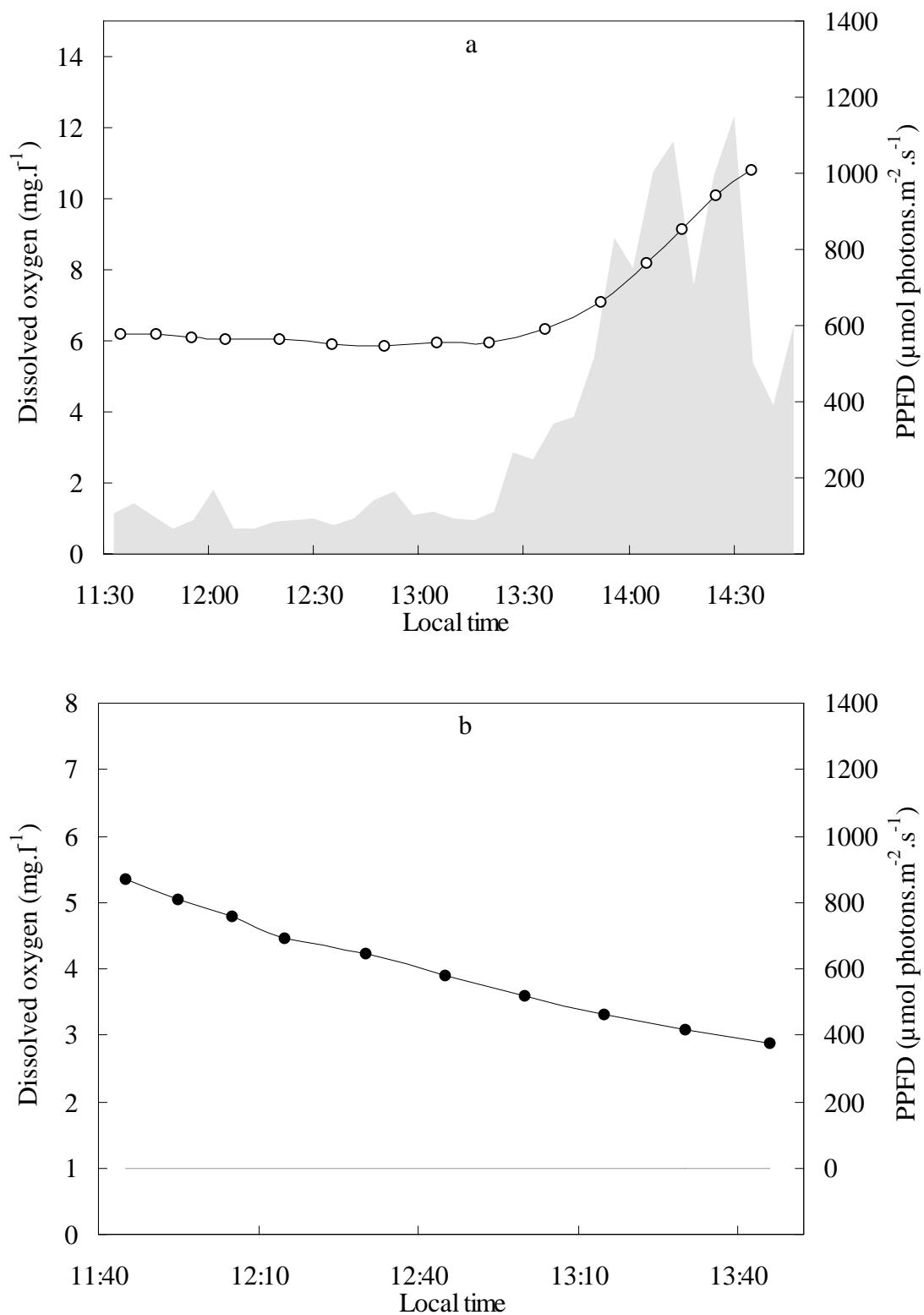Fig.1. The Thau lagoon. Distribution of seagrass beds and location of the experimental station.

Figure 2. Variations of dissolved oxygen inside a clear (2a) and a dark (2b) benthic chamber and the available light at the seagrass canopy (PPFD, shaded grey surface) as a function of time. Date of experiments: 5th July 1996, temperature: 21.7 °C.
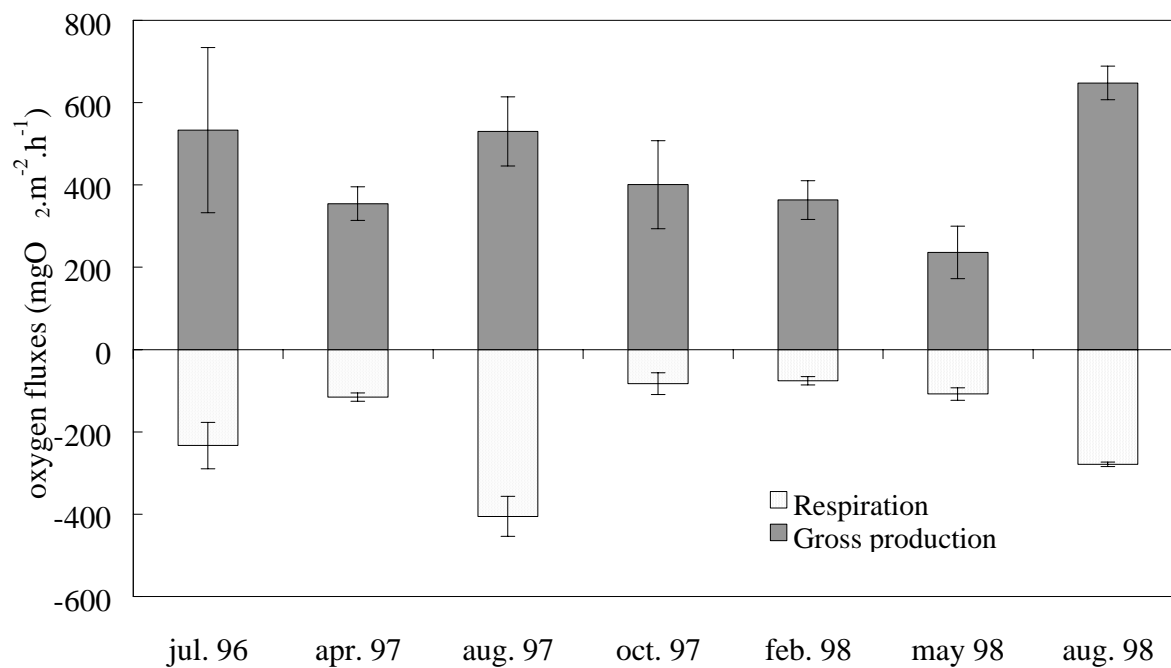
Figure 3. Mean (± 95 % confidence limits) oxygen fluxes measured inside the benthic chambers for each experiment (whatever the incoming light intensity). Negative values represent an uptake of oxygen (respiration in dark chambers) while positive values show an oxygen production (photosynthesis in clear chambers). The respiration was added to the net production measured in each chamber to give the gross production rates.
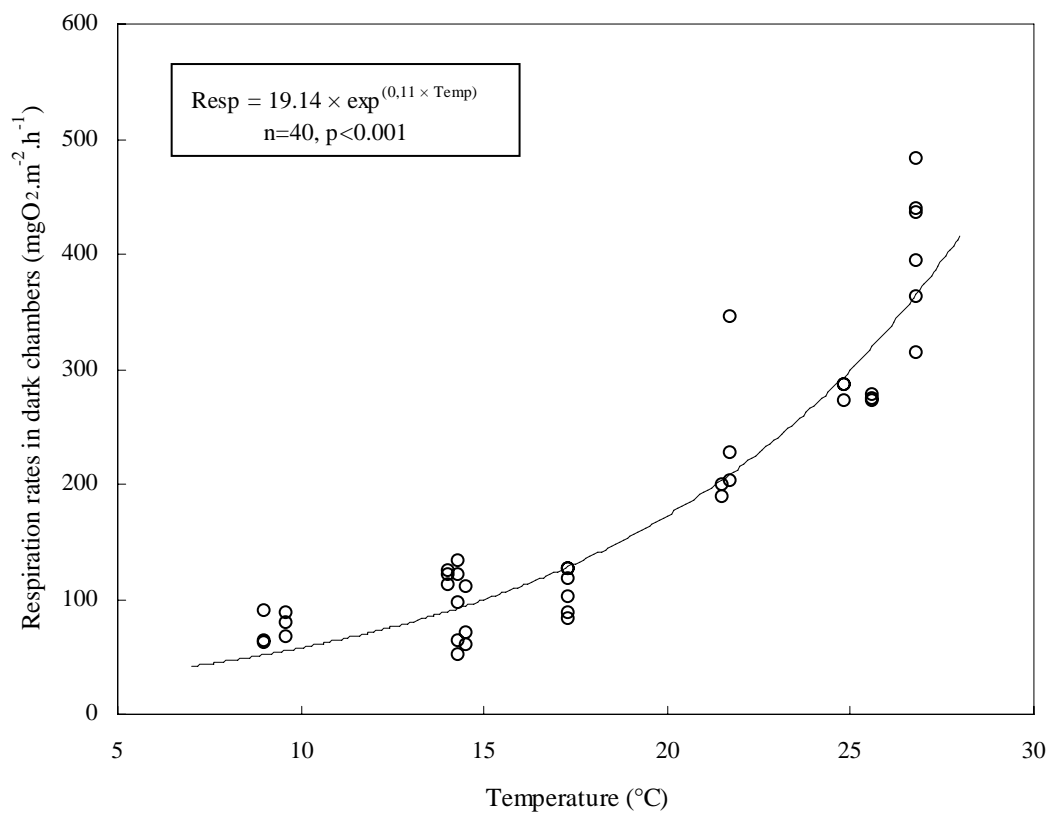
Figure 4. Ecosystem dark respiration (Resp) as a function of temperature (Temp). Equation and significance for the non linear regression line are given in inset.
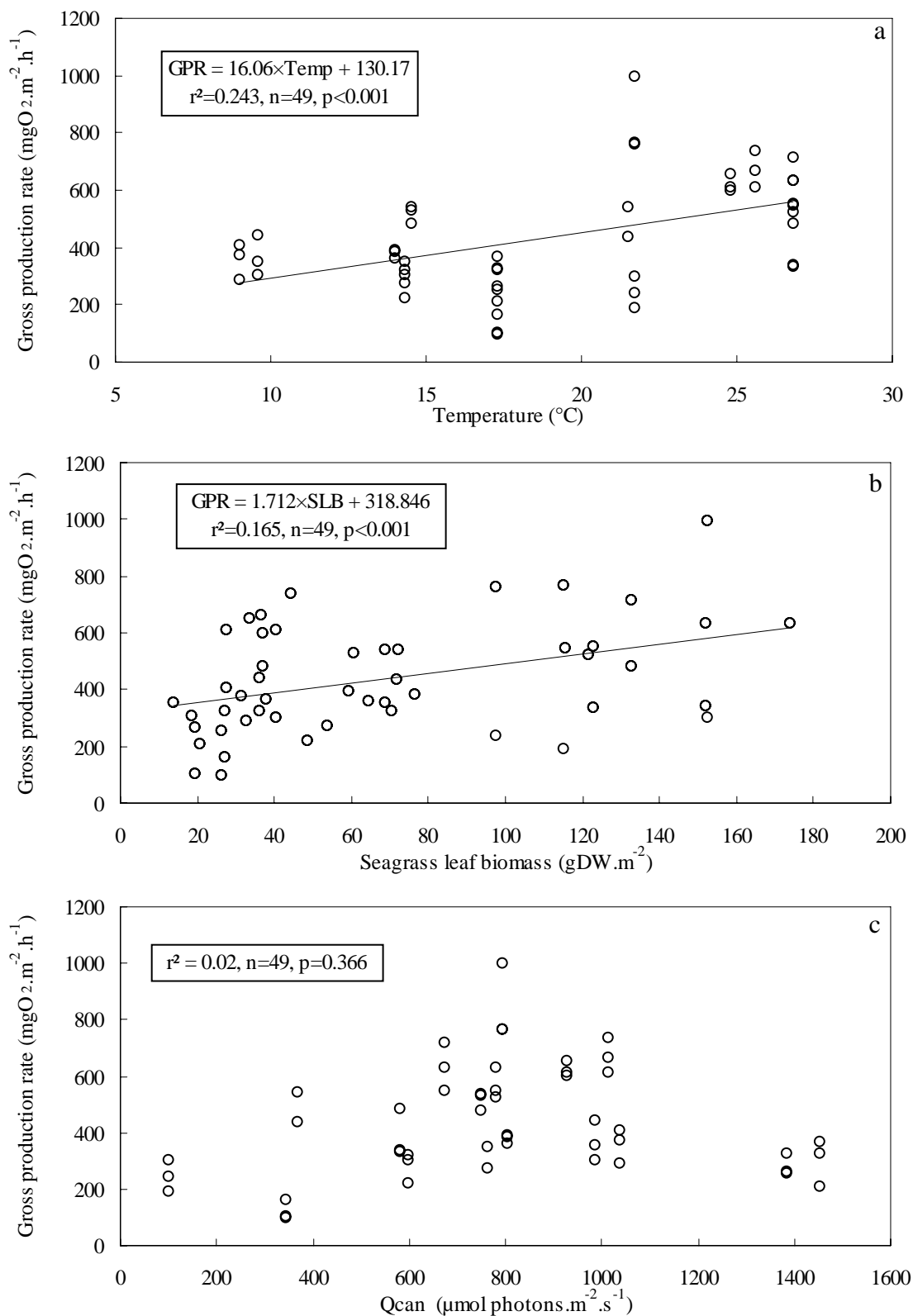
Figure 5. Relationships between gross production rates (GPR) and temperature (Temp, 5a), seagrass leaf biomass (SLB, 5b) and measured photosynthetic photon flux density at the canopy level (Qcan, 5c). Equation, R-squared and probabilities for regression lines are given in insets.
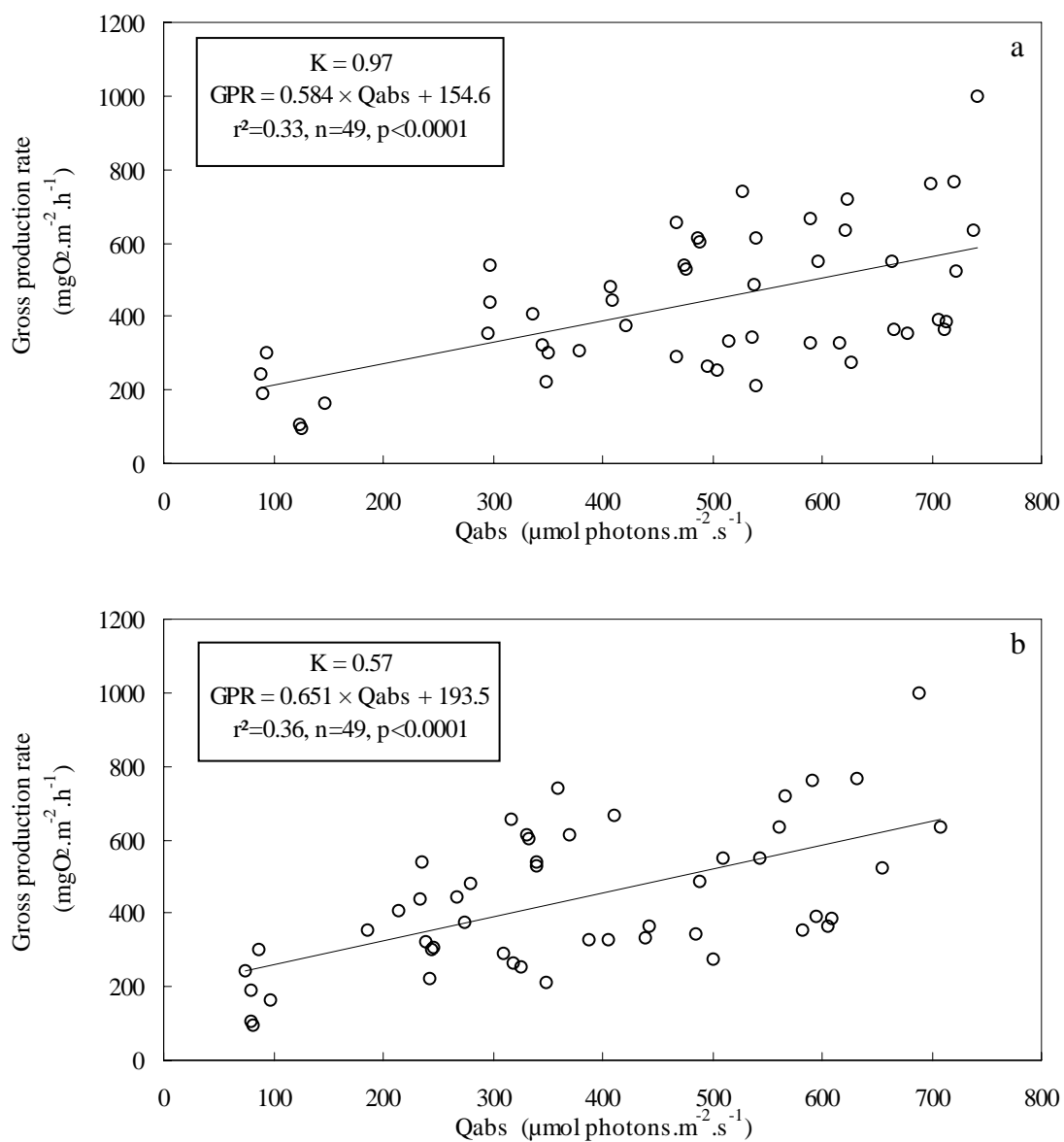
Figure 6. Relationships between the gross production rates (GPR) and the light intercepted by the seagrass canopy (Qabs). Calculations for Qabs with two different K values are presented : (a) K = 0.97 (*Zostera noltii,*Pérez-Lloréns & Niell 1993 b) and (b) K = 0.57 (*Festuca arundinacea*, Varlet-Granchet *et al.* 1989).
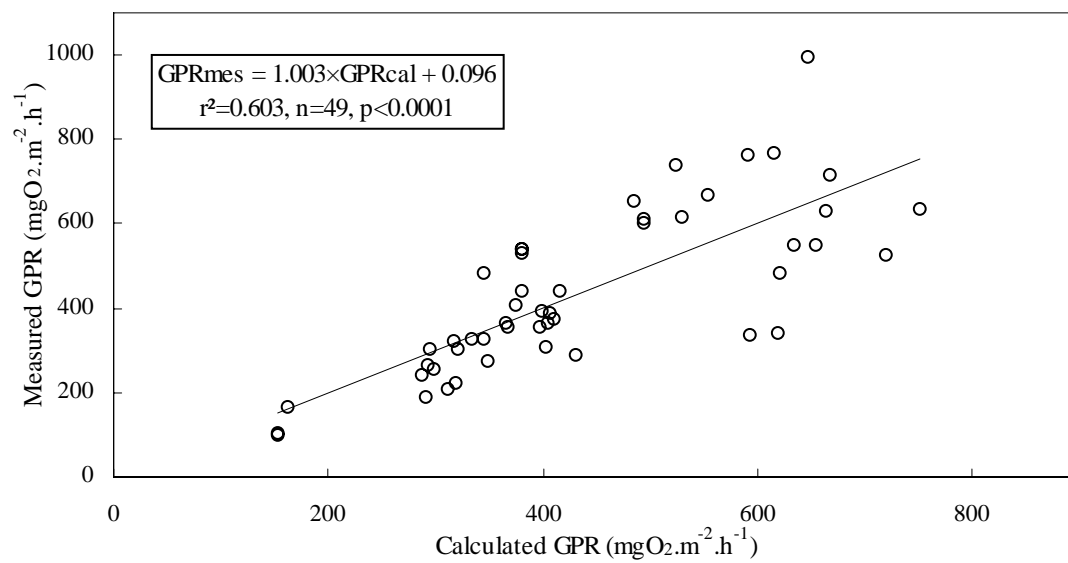
Figure 7. Calculated (GPRcal) against measured gross production rates (GPRmes).

Fig. 8. Net production rates (NPR) calculed by means of the two models (GPR$_{cal}$, Eq. (3) and Resp, fig. 4; NPR=GPR$_{cal}$-Resp). Model results are presented for temperatures ranging from 9°C to 27°C and for light intensities at the canopy level (Q$_{can}$) ranging from 100 to 1500 µmol photons m^{-2} s^{-1}; leaf area index is 2 m^2 m^{-2} and nitrogen leaf content equals to 1.9% PS. The community is autotrophic (NPR>0) above the shaded grey box showing the heterotrophic zone (NPR<0).

Table 1. Environmental characteristics for each experimental period. Temperature, salinity (noted Temp. and Sal. respectively) and average values (± 95 % confidence limits) for water nutrient concentrations (NH_4^+, $NO_2^- + NO_3^-$ and PO_4^{3-}) are based on the two measurements performed at the beginning and at the end of each experiments. PPFD is the photosynthetic photon flux density (in the waveband 400 to 700 nm), data given are arithmetic means (± 95 % confidence limits) over the periods considered for production rates calculation.

	Temp. (°C)	Sal.	Depth (m)	PPFD (μmol photons.m^{-2}.s^{-1}) surface	PPFD canopy	NH_4^+ (μmol.l^{-1})	$NO_2^- + NO_3^-$ (μmol.l^{-1})	PO_4^{3-} (μmol.l^{-1})
Jul 4, 96	21.5	33.0	1.5	nd	370 ± 20	0.88 ± 0.10	0.04 ± 0.01	0.78 ± 0.07
Jul 5, 96	21.7	33.4	1.5	nd	(1) 100 ± 13 (2) 793 ± 164	0.84 ± 0.07	0.06 ± 0.02	0.88 ± 0.22
Apr 8, 97	14.3	31.2	1.5	nd	761 ± 60	0.38 ± 0.03	0.21 ± 0.01	0.15 ± 0.01
Apr 9, 97	14.0	31.2		1703 ± 14	805 ± 7	0.36 ± 0.07	0.17 ± 0.02	0.17 ± 0.01
Aug 20, 97	26.8	36.0	1.5	nd	781 ± 11	0.77 ± 0.34	0.09 ± 0.02	0.77 ± 0.26
Aug 21, 97	26.8	36.2	1.5	nd	(1) 581 ± 73 (2) 673 ± 77	0.83 ± 0.04	0.07 ± 0.00	0.69 ± 0.07
Oct 29, 97	14.3	36.5	1.2	nd	597 ± 28	4.71 ± 1.37	2.77 ± 0.16	0.94 ± 0.05
Oct 30, 97	14.5	37.5	1.2	nd	750 ± 14	3.87 ± 0.94	2.62 ± 0.18	0.94 ± 0.06
Feb 25, 98	9.0	34.1	1.2	2399 ± 13	1036 ± 6	0.60 ± 0.17	0.24 ± 0.02	0.06 ± 0.01
Feb 26, 98	9.6	34.1	1.2	2353 ± 23	984 ± 14	0.36 ± 0.14	0.23 ± 0.15	0.10 ± 0.05
May 12, 98	17.3	36.2	1.2	2613 ± 36	1453 ± 26	0.57 ± 0.05	0.14 ± 0.04	0.15 ± 0.05
May 13, 98	17.3	36.2	1.2	(1) 2635 ± 96 (2) 784 ± 90	(1) 1382 ± 63 (2) 345 ± 43	0.39 ± 0.12	0.14 ± 0.09	0.16 ± 0.07
Aug 11, 98	24.8	38.4	1.6	2390 ± 63	928 ± 28	0.41 ± 0.29	0.12 ± 0.06	0.23 ± 0.02
Aug 12, 98	25.6	38.8	1.6	2450 ± 5	1012 ± 10	0.42 ± 0.05	0.06 ± 0.03	0.24 ± 0.02

"surface" refers to measurements in air and "canopy" indicates measurements at the seagrass canopy level. "(1)" and "(2)" : two periods of different irradiance could be differentiated in the same day. "nd" : not determined.

Table 2. Eelgrass abundance and morphology in the seven experiments. All values are means (± 95 % confidence limits) of the six chambers. Because of the undetermined leaf morphology in July 1996 (nd), the leaf area index (LAI) had to be calculated assuming a linear regression between LAI and leaf biomass (LB) of all the following experiments (LAI=0.0275×LB ; r^2=0.932 and p<0.0001). Different lettering for LAI values are significantly different (p<0.05). Last row present the percentage of macroalgae trapped within the seagrass shoots.

	Jul 96	Apr 97	Aug 97	Oct 97	Feb 98	May 98	Aug 98
Shoot density (shoots.m^{-2})	3593 ± 753	2288 ± 275	2175 ± 515	2251 ± 184	1061 ± 165	1917 ± 210	1241 ± 79
Leaf biomass (gdw.m^{-2})	99.9 ± 19.5	67.7 ± 8.8	136.3 ± 17.9	54.2 ± 11.5	26.6 ± 7.0	27.8 ± 6.2	36.4 ± 4.6
Rhizomes + roots biomass (gdw.m^{-2})	93.4 ± 21.4	106.9 ± 11.0	125.0 ± 16.5	30.0 ± 8.2	19.2 ± 3.3	34.4 ± 5.5	40.8 ± 3.3
Above/below-ground biom. ratio	1.1 ±0.14	0.6 ±0.04	1.1 ±0.19	1.9 ±0.25	1.4 ±0.23	0.8 ±0.09	0.9 ±0.11
Leaf height (cm)	nd	22.8 ± 0.4	38.6 ± 1.3	12.0 ± 0.2	14.8 ± 0.3	8.5 ± 0.2	15.7 ± 1.4
Leaf width (mm)	nd	1.8 ± 0.2	1.6 ± 0.1	1.3 ± 0.1	1.3 ± 0.02	1.2 ± 0.01	1.5 ± 0.05
Leaf area index (m^2.m^{-2})	2.8 ± 0.50 A	2.7 ± 0.33 A	3.6 ± 0.86 A	1.0 ± 0.08 B	0.5 ± 0.08 C	0.6 ± 0.06 C	0.8 ± 0.05 D
Number of leaves per shoot	nd	2.9 ± 0.2	2.7 ± 0.3	3.0 ± 0.1	2.6 ± 0.1	2.9 ± 0.1	2.9 ± 0.2
Algae (% of total plant biomass)	1.85 ± 0.56	0.00 ± 0.00	2.84 ± 1.87	0.73 ± 0.50	0.03 ± 0.02	0.01 ± 0.01	2.97 ± 3.30

Table 3. Carbon content , nitrogen content and C:N ratio of *Z. noltii* leaves and belowground parts (values expressed as % of dry weight). Data given are means and 95 % confidence limits of triplicate measurements.

	Leaves			Rhizomes and roots		
	Carbon	Nitrogen	C:N ratio	Carbon	Nitrogen	C:N ratio
	mean	mean	mean	mean	mean	mean
May 98	37.00 ± 0.05	1.90 ± 0.02	19.51 ± 0.14	31.11 ± 0.01	0.93 ± 0.05	33.57 ± 0.34
Jully 98	35.09 ± 0.03	2.05 ± 0.00	17.15 ± 0.02	31.87 ± 0.03	0.77 ± 0.01	41.27 ± 0.34
November 98	36.86 ± 0.02	2.20 ± 0.03	16.75 ± 0.15	35.97 ± 0.08	0.85 ± 0.02	42.49 ± 1.31
February 99	38.94 ± 0.08	2.60 ± 0.03	15.00 ± 0.13	35.74 ± 0.05	1.44 ± 0.02	24.87 ± 0.29

Table 4. Respiration rates (min – max) in relation to leaf biomass (min – max) of some seagrass species.

Species	Location	Leaf biomass $(gDW.m^{-2})$	Respiration rate $(mgO_2.m^{-2}.h^{-1})$	References
Zostera noltii	Arcachon Bay	81 – 101	78.7 – 252.8	Viaroli *et al*. (1996)
	Thau lagoon	13.6 – 173.8	29.9 – 429.6	Present study
Zostera marina	Thau lagoon	nd	11.4 – 92.6	Barranguet & Alliot (1995)
	Chesapeake Bay	20 – 116	30 – 360 *	Murray & Wetzel (1987)
Cymodocea nodosa	Adriatic Sea	8 – 147	1 – 155 *	Zavodnik *et al*. (1998)
Ruppia maritima	Chesapeake Bay	20 – 116	85 – 350 *	Murray & Wetzel (1987)

nd : not determined. * values estimated from graphic data.

Table 5. Gross production rates (GPR, min – max) in relation to leaf biomass (min – max) for some seagrass species.

Species	Location	Leaf biomass (gDW.m^{-2})	GPR (mgO$_2$.m^{-2}.h^{-1})	References
Zostera noltii	Arcachon Bay	81 – 101	280.9 – 474.6	Viaroli *et al*. (1996)
	Thau lagoon	13.6 – 173.8	97.5 – 1001.3	Present study
Zostera marina	Chesapeake Bay	20 – 116	30 – 615 *	Murray & Wetzel (1987)
Cymodocea nodosa	Adriatic Sea	8 – 147	5 – 320 *	Zavodnik *et al*. (1998)
Ruppia maritima	Chesapeake Bay	20 – 116	450 – 1150 *	Murray & Wetzel (1987)

nd : not determined. * values estimated from graphic data.

Table 6. K values reported for several terrestrial plants (after Varlet-Granchet *et al*. 1989).

Species	K coefficient	References
Triticum aestivum (common wheat)	0.66 – 0.91	Hodge & Kanemasu (1977), Hipps *et al*. (1983)
Festuca arundinacea (tall fescue)	0.57	Moulia (1986)
Oryza sativa (rice)	0.41	Hayachi (1972)
Helianthus annum (sunflower)	0.97	Rawson *et al*. (1984)
Vigna mungo (blackgram)	0.95	Muchow & Charles-Edwards (1982)
Medicago sativa (alfalfa, lucerne)	0.88	Gosse *et al*. (1982)