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Modelling seasonal dynamics of biomasses and nitrogen contents in a seagrass meadow (Zostera noltii Hornem.): application to the Thau lagoon (French Mediterranean coast)

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Abstract:

A numerical deterministic model for a seagrass ecosystem (Zostera noltii meadows) has been developed for the Thau lagoon. It involves both above- and belowground seagrass biomasses, nitrogen quotas and epiphytes. Driving variables are light intensity, wind speed, rain data and water temperature. This seagrass model has been coupled to another biological model in order to simulate the relative contributions of each primary producer to: (i) the total ecosystem production, (ii) the impact on inorganic nitrogen and (iii) the fluxes towards the detritus compartment. As a first step in the modelling of seagrass beds in the Thau lagoon, the model has a vertical structure based on four boxes (a water box on top of three sediment boxes) and the horizontal variability is neglected until now. This simple box structure is nevertheless representative for the shallow depth Z. noltii meadows, spread over large areas at the lagoon periphery.

After calibration, simulation results have been compared with in situ measurements and have shown that the model is able to reproduce the general pattern of biomasses and nitrogen contents seasonal dynamics. Moreover, results show that, in such shallow ecosystems, seagrasses remain the most productive compartment when compared with epiphytes or phytoplankton productions, and that seagrasses, probably due to their ability in taking nutrients in the sediment, have a lower impact on nutrient concentration in the water column than the phytoplankton. Furthermore, in spite of active mechanisms of internal nitrogen redistribution and reclamation, the occurrence of a nitrogen limitation of the seagrass growth during summer, already mentioned in the literature, have also been pointed out by the model. Finally, simulations seems to point out that epiphytes and phytoplankton could compete for nitrogen in the water column, while a competition for light resources seems to be more likely between epiphytes and seagrasses.

Keywords: Seagrass ecosystem; Box model; Oxygen cycle; Nitrogen cycle; Thau lagoon

1. INTRODUCTION:

The Thau lagoon is one of the about thirty lagoons located on the French Mediterranean coast around the Lion Gulf. With a surface of 70 km^2 (maximum length 19.5 km and maximum width 4.5 km) and a mean depth of 4 m, Thau lagoon is a semi-confined ecosystem with two narrow openings towards the sea located at its extremities: the canals of Sète city and the « Grau de Pisses Saume » near the Marseillan village (see figure 1). The climate imposes a wide range of temperatures and salinities (minima in February with 5°C and salinity near 27, and maxima in August with 29°C and salinity about 40). Rainfall 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 5 on Beaufort scale; data from Météo-France), playing an important role in the lagoon hydrodynamics (Lazure, 1992).

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 with an annual oyster production of about 15 000 tons).

During the last fifteen years, several survey and research programmes – EcoThau (Amanieu et al., 1989), OxyThau (Deslous-Paoli et al., 1995) – have been conducted on the Thau lagoon and have contributed to a best understanding of the lagoon ecosystem. In 1997, the Coastal Oceanography National Programme "Mediterranean Lagoons" (PNOC programme) was launched, with the development of hydrodynamic and ecological models as one of its main objectives. This work is a part of this programme.

Several mathematical models have been developed or are in development for the Thau lagoon and the different compartments concerned are: hydrodynamics (Millet, 1989, Lazure, 1992), nutrient cycling (Chapelle, 1995), plankton food web (Chapelle et al., 2000) and oysters (Chapelle et al., 2000, Bacher et al., 1997). Nonetheless, the macrophyte populations have not been until now taken into consideration from the modelling point of view, in spite of: (i) their importance in terms of biomass and covered surfaces (10 073 ± 2 006 tons dry weight, spread over 70 % of the lagoon surface, Gerbal and Verlaque, 1995), (ii) the important role they play as primary producers (Sfriso and Marcomini, 1999), (iii) their impact on nutrient budgets (Sfriso et al., 1989, Ménesguen and Piriou, 1995, Viaroli et al., 1996, Touchette and Burkholder, 2000), all the more since they are located at the water-sediment interface, and (iv) their importance in the eutrophication and anoxic crisis processes (Frisoni et Cejpa, 1989, Ménesguen, 1992, Carreira et al., 1994, Viaroli et al., 2001).

Several studies allow a rather detailed vision of the composition of the macrophyte populations in the Thau lagoon (Ben Maiz, 1986, Gerbal, 1994, Gerbal and Verlaque, 1995, Laugier, 1998, Laugier et al., 1999), underlining seagrasses as they represent about 22 % of the total macrophyte biomass and are located on almost all the periphery of the lagoon excepted the oriental extremity (see figure 1). Two seagrass species have been found in the Thau lagoon, *Zostera marina* and *Z. noltii*. We chose to focus on the latter for the following reasons: this species covers wide areas, especially along the narrow sandy strand which separates the lagoon from the Mediterranean Sea (« le Lido », see figure 1), where it forms large monospecific meadows. *Z. noltii* is also important in terms of biomass: the map done within the framework of the PNOC programme ranked this species as the third biomass, accounting for about 13 % of the macrophyte total wet weight (Verlaque, Belsher and Deslous-Paoli, personal communication). Furthermore, if models for *Z. marina* meadows are rather abundant in the literature (Verhagen and Nienhuis, 1983, Wetzel and Neckles, 1986, Bach, 1993, Van Lent, 1995, Bocci et al., 1997), as far as we know, no model for *Z. noltii* has been published up till now. Finally, *Z. noltii* is present in various other temperate lagoons as Bages-Sigean, Ayrolle, Gruissan and Salses-Leucate (all situated in the Languedoc Roussillon region, Clanzig, 1987), Vaccares lagoon (Camargue region, Vaquer and Heurteaux, 1989), in Terschelling (Dutch Wadden Sea, Jacobs et al., 1981), in the Bassin d'Arcachon (Atlantic coast of France, Auby, 1991) and in the Palmones river estuary (South of Spain, Pérez Lloréns and Niell, 1993). A model developed for this species could probably become useful for the study of these ecosystems.

The aim of the present study was to develop a *Zostera noltii* ecosystem model, able to simulate the seasonal dynamics of biomasses and nitrogen contents and to estimate the contributions of the different primary producers (seagrasses, phytoplankton and epiphytes) to the nitrogen and oxygen cycle of such an ecosystem (oxygen production, nitrogen uptake and fluxes towards the detritus pool).

2. MODEL DESCRIPTION

The models developed for *Zostera marina* by Verhagen and Nienhuis (1983), Zimmerman et al. (1987), Bach (1993) and, more recently, those by Van Lent (1995) and Bocci et al. (1997) have been used as references for the development of our *Z. noltii* ecosystem model (hereafter called MEZO-1D).

The conceptual diagram of the model is presented on figure 2. Five state variables represent the seagrasses: the aboveground biomass (hereafter noted LB), the belowground biomass (RB), the density of shoots (LD), the aboveground and the belowground nitrogen pool (respectively LN and RN). Production of epiphytes growing on seagrass leaves is difficult to measure, nevertheless some studies have demonstrated that it is far from being negligible with respect to the whole system production (Penhale, 1977, Harlin, 1980, Heijs, 1984). Thus, we decided to introduce a state variable representing the epiphyte biomass (EB).

MEZO-1D has been thought as a coupling unit for the model developed for the Thau lagoon by Chapelle et al. (2000) built with the ELISE software (Ménesguen, 1990), and involving phytoplankton, zooplankton, oysters, detritus and dissolved inorganic nitrogen (with mineralization processes and fluxes at the water-sediment interface). All variables and processes have been kept in the model excepted the processes linked to oysters, because the *Zostera noltii* beds are located outside the shellfish cultivation areas (see figure 1). As nitrogen is the limiting factor in the Thau lagoon (Picot et al., 1990), the model deals with nitrogen: two state variables of dissolved inorganic nitrogen, ammonia (NH_4^+) and nitrate (NO_3^-), are defined in the water column and the sediment.

Four boxes compose the model's vertical structure: a water box (box n°1, 1.4 m depth) on top of three sediment boxes (box n°2, 0.5 cm depth; box n°3, 1.5 cm depth and box n°4, 38 cm depth). The division of sediment into three boxes allows on one hand, the oxygen and nutrient fluxes at the water-sediment interface (first centimetres), and on the other hand, a sufficient thickness to prevent nutrient exhaustion due to rhizomes and roots uptake. Horizontal variability is neglected for now, we thus consider the homogeneity of the seagrass meadow on the horizontal plan (the model box surfaces are 10 m^2).

Such a simple ecosystem, composed of a shallow water column and its sediment with seagrasses, epiphytes, phytoplankton, zooplankton, detritus compartment (expressed as organic particulate nitrogen) and dissolved inorganic nitrogen, is representative of the shallow depth *Z. noltii* beds which are located at the Thau lagoon periphery.

2.1 Elementary processes description

All processes linked to seagrasses and epiphytes are presented in tables 1 to 4. For mineralization of organic matter, nitrification, reaeration at the sea-surface and processes concerning phytoplankton and zooplankton (photosynthesis, respiration, grazing, excretion, …), please refer to Chapelle et al. (2000).

Seagrass photosynthesis (table 1):

Light and temperature are the two most important factors in controlling seagrass photosynthesis (Zieman and Wetzel, 1980, Dennison and Alberte, 1982, Evans et al., 1986, Bulthuis, 1987, Pérez and Romero, 1992). However, since temperature acts directly on the physiological processes (biochemical reaction acceleration with temperature), the effect of light not only depends on photosynthetic capacities but also on the seagrass bed morphology (self-shading effect) and on the shading due to epiphytes. Pérez and Romero (1992) showed that a seagrass model (*Cymodocea nodosa*) only based on temperature and light measured at the top of the seagrass canopy tends to overestimate the production, while taking into account the self-shading effect seriously improves the model results. Plus et al. (2001) found moreover, a correlation between *Z. noltii* beds production (*in situ* benthic bell jars measurements) and the intercepted light by the canopy.

The production model we have built is based on the so called « big leaf » model (Daudet and Tchamichian, 1993) developed for graminaceae, and allowing the calculation of the light really intercepted by the seagrasses knowing on one hand, the light reaching the top of the canopy and on the other hand, the seagrass bed leaf area index (LAI). In MEZO-1D, seagrass canopy is divided in ten elementary layers and the overall photosynthesis is given by the sum of the photosynthesis in each layer. The photosynthesis in a layer is calculated using a Jassby and Platt (1976) equation, with the maximum production parameter dependent on temperature. LAI is calculated by means of a linear function of leaf biomass (Pérez-Llorénz and Niell, 1993, Plus et al., 2001) and the canopy height is considered constant, equalling 30 cm. The light reaching the canopy is a function of the light measured at the sea surface, decreased by the extinction due to the water itself (Beer's law) and by the epiphytes shading (based on the Fong and Harwell model, 1994).

Seagrass respiration (table 1):

Seagrass respiration is usually modelled as an exponential function of temperature (Verhagen and Nienhuis, 1983, Bach, 1993, Pérez and Romero, 1992, Van Lent, 1995). If exponential type equations with temperature seem to fit quite well the respiration of *Zostera marina* or *Cymodocea nodosa* species (Bulthuis, 1987, and above cited models), as far as we know, no measurement of the impact of temperature on *Zostera noltii* respiration has been published yet. However, recent measurements of leaf and rhizome/roots respiration for *Z. noltii* at different temperatures (ranging from 7 to 20 °C) have been conducted and seem to show linear relationships between respiration and temperature (Auby, personal communication). We used such linear relationships in the model, due to the fact that these measurements have been performed on *Z. noltii* shoots from the Thau lagoon.

In the Thau lagoon, the oxic layer of the sediment is quite thin (a few centimetres, Mesnage, 1994, Deslous-Paoli, personal communication), thus we assume in the model that rhizomes and roots respiration imposes an oxygen demand in the water column, through the medium of the leaves.

Nitrogen uptake by seagrasses (table 2):

In the model nitrogen is split into ammonia and nitrate, but in the sediment, due to high reduction rates which impose very low concentrations of nitrate, we suppose that ammonia is the only source of nitrogen for the roots. Conversely, for the seagrass leaves both nitrogen forms are available in the water column.

Nitrogen uptake is defined in the model by the saturation degree of the internal quota, *i. e.* the internal quota relative to its upper and lower limits (Zimmerman et al., 1987, Van lent, 1995). Taking into account the plant internal quotas allows to separate growth from external nitrogen concentration. Thus, high growth rates remain possible (for a certain time) even when nutrient concentrations are low in the external medium.

Nitrogen redistribution and reclamation (table 2):

Seagrasses are well known to be quite well adapted to poor nutrient environments (Zimmerman et al., 1987, Hemminga et al., 1991, Pedersen and Borum, 1992 and 1993). Then, internal nitrogen redistribution (from belowground parts to leaves and *vice versa*) and reclamation (from old to young tissues) seem to play an important role in the plant nitrogen budget. Pedersen and Borum (1993) have estimated the contribution of internal recycling to meet 27 % of the annual nitrogen requirements for *Zostera marina*. MEZO-1D takes into account these mechanisms. Differences in saturation degree between leaves and belowground tissues internal quotas determine the nitrogen transfer direction and speed. A reduction coefficient for the nitrogen loss by mortality allows the reclamation calculation and thresholds avoid that quotas overpass the defined maxima.

Seagrass growth (table 3):

Total seagrass growth is calculated on the base of net production (gross production minus above and belowground respirations) multiplicated by a limitation function due to leaf internal quota. The transformation of production (expressed in terms of oxygen) into growth (expressed in terms of carbon), is done using a photosynthetic quotient of 1.1 $molO_2.molC^{-1}$ (Clavier et al., 1994). A photosynthetic quotient (PQ) greater than 1, allows to take into consideration that carbohydrates are not the only products of photosynthesis (PQ=1 meaning that one mole of oxygen is produced for each mole of carbon fixed), but that for example lipids are also produced.

Belowground growth depends on: (i) the part of carbon fixed by the leaves and translocated to the rhizomes and roots and (ii) the internal quota of belowground organs. Aboveground growth is then calculated by subtracting belowground growth from total seagrass growth.

Seagrass loss (table 2):

Mortality is defined in the model by two processes: on one hand a temperature-dependent mortality, the normal process of tissues senescence, and on the other hand a physical stress-dependent mortality, the leaves or shoots sloughing due to wave motion. The wind-induced stress decreases with increasing depth, following an exponential curve similar to those used by Verhagen and Nienhuis (1983) or Van Lent (1995).

Both mortality processes act on LB and LD state variables, while RB loss is only due to senescence.

Recruitment (table 3):

Laugier (1998) has shown that, for *Zostera noltii*, the effort devoted to sexual reproduction is almost nil in zones where this species is dominant. Moreover, the observation of scorpioïd rhizomes extremities is very rare (Laugier et al., 1999 and personal observations), which confirms that sexual reproduction is, in these areas, of secondary importance in reproduction processes. In MEZO-1D, we thus only consider vegetative reproduction, the term recruitment being reduced to the apparition of new shoots from rhizomes.

In our model, the apparition of new shoots is controlled by temperature (as in Verhagen and Nienhuis, 1983), aboveground biomass (self-shading can affect young shoots growing under the canopy) and belowground biomass (Van Lent, 1995). Recruitment is considered as a matter transfer from rhizomes (RB) to aboveground biomass (LB). Thus, the initial biomass of new shoots is fixed at a constant weight and recruitment represents a sink term for RB and a source term for LB. The belowground limitation function is added in order to avoid a possible depletion of RB due to an intense recruitment.

Epiphytes (table 4):

Light, temperature and nutrient concentrations are often considered as the main factors controlling epiphytes seasonal dynamics (Short, 1980, Borowitzka and Lethbridge, 1989, Philippart, 1995, Nelson and Waaland, 1997). In MEZO-1D we suppose that epiphytic population is mainly composed of diatoms (Auby, 1991) and that epiphyte growth is controlled by light, temperature and inorganic nitrogen concentrations (nitrogen being the limiting factor in the Thau lagoon, according to Picot et al., 1990). Furthermore, in order to take into account the fact that fast growing leaves are generally free of epiphytes while old slow growing leaves are largely colonised, a leaf growth limitation function is added.

We also assume that wave-motion stress acts as well on epiphytes, and that epiphytes sloughed with leaves also pass in detritus compartment. Thus, epiphytes mortality equals to the specific leaf mortality rate multiplicated by the epiphytes biomass.

Nitrogen uptake due to epiphytes is calculated through epiphytes growth, assuming the molar quotient C:N = 9 molC.molN^{-1} defined by Lin et al. (1996). No preference for one of the two sources of nitrogen (NH_4^+ or NO_3^-) is considered, the uptake of each nitrogen form only depending on their concentrations.

Epiphytes photosynthesis (oxygen production) is calculated by means of the epiphytes growth, using a photosynthetic quotient of 1.1 molO$_2$.molC^{-1}. Epiphytes respiration is controlled by temperature (exponential function), as typically used for the phytoplankton respiration modelling (Bacher et al., 1997, Chapelle et al., 2000).

Tables 5 and 6 present all parameters used to calculate the above-described processes.

2.2 Differential equations

All state variables and their distribution in the box system are listed in table 7. The system of differential equations allowing the state variables time integration is presented below.

➢In the water column:

$$\frac{dNH_4}{dt} = \min \times N\det - LABS_{NH_4} \times \frac{LB}{D} - EABS_{NH_4} \times \frac{EB}{D}$$

$$\frac{dNO_3}{dt} = -LABS_{NO_3} \times \frac{LB}{D} - EABS_{NO_3} \times \frac{EB}{D}$$

$$\frac{dLB}{dt} = LGR + REC \times SB_0 \times SD - LM \times LB$$

$$\frac{dSD}{dt} = (REC - LM) \times SD$$

$$\frac{dLN}{dt} = \left(LABS_{NH_4} + LABS_{NO_3}\right) \times LB + REC \times SB_0 \times SD \times \frac{RN}{RB} + \left(R_{trans} - L_{trans}\right) \times LN$$
$$- \left(1 - LN_{rec}\right) \times LM \times LN$$

$$\frac{dEB}{dt} = (EGR - EM) \times EB$$

$$\frac{dN\,det}{dt} = \left(1 - LN_{rec}\right) \times LM \times \frac{LN}{D} + LM \times \frac{EB}{9 \times D} - \min \times N\,det$$

$$\frac{dO_2}{dt} = O_{rea} + Ptot \times f\,(LN) \times \frac{LB}{D} + EP \times \frac{EB}{D} - LR \times \frac{LB}{D} - RR \times \frac{RB}{D_{totsed}} - ER \times \frac{EB}{D} - O_{\min}$$

➢In the sediment:

$$\frac{dRB}{dt} = RGR - REC \times SB_0 \times SD - RM \times RB$$

$$\frac{dRN}{dt} = RABS_{NH_4} \times RB - REC \times SB_0 \times SD \times \frac{RN}{RB} + \left(L_{trans} - R_{trans}\right) \times RN - \left(1 - RN_{rec}\right) \times RM \times RN$$

$$\frac{dNH_4}{dt} = b\min \times \frac{1 - poro}{poro} \times N\,det - \frac{RABS_{NH_4}}{D_{sed} \times poro} \times RB$$

$$\frac{dNO_3}{dt} = bnitr \times NH_4 \text{ - } bdenitr \times NO_3$$

$$\frac{dN\,det}{dt} = \frac{(1 - RNrec) \times RM}{D_{sed} \times (1 - poro)} \times RN - b\min \times N\,det$$

$$\frac{dO_2}{dt} = -O_{b\,\min}$$

Mineralization processes (min and O_{min}), benthic mineralization processes (bmin and O_{bmin}), nitrification (nitr and bnitr) and denitrification processes (denitr and bdenitr) and reaeration process at the sea surface (O_{rea}) are described in Chapelle et al. (2000). Contrary to the epiphytes, mainly composed of diatoms (in the case of *Zostera noltii,* Auby, 1991) and having a mineralization rate close to the phytoplankton one, the seagrasses are submitted to a slow-working decomposition process (Rice and Tenore, 1981, Pellikaan, 1982, Pellikaan, 1984, Auby, 1991, Bourguès et al., 1996). Thus, mineralization processes have been empirically divided by 5 for seagrass tissues (leaves, rhizomes and roots), while epiphytes mineralization rate remains the same as phytoplankton. SB_0 is the initial biomass of a new shoot, poro is the sediment porosity (fixed at 80 % in the model), D is the water box depth, D_{sed} and D_{totsed} are respectively the thickness of the concerned sediment box and the total thickness of sediment assumed in the model (40 cm).

3. SIMULATION CHARACTERISTICS

The model is closed at its limits excepted for oxygen (through reaeration at the sea surface) and nitrate (through watershed inputs) state variables. Nitrogen inputs in the lagoon are not well known (Chapelle et al., 2000) due to the highly variable flows of rivers and little streams, responsible for complex mud and organic matter resuspension phenomenons. Watershed nitrogen inputs are nonetheless taken into consideration in MEZO-1D, following the same way as in Chapelle et al. (2000): daily nitrogen inputs are calculated multiplying the total nitrogen quantity flowing into the Thau lagoon during one year (estimated by Pichot et al., 1994, and corrected by the $\frac{\text{water box}}{\text{Thau lagoon}}$ volume ratio) by the percentage of total yearly rain which has fallen that day. Furthermore, we consider that nitrate is the only nitrogen form brought by the watershed.

Time step is 0.01 day and the model is run thanks to ELISE software (Ménesguen, 1990), using an empirical diffusion coefficient in order to calculate vertical exchanges between the different boxes.

Simulations were run for years 1994 and 1995. During these two years, a *Zostera noltii* bed from the south edge of the Thau lagoon has been monthly sampled (Laugier, 1998 and Laugier et al., 1999), and therefore allowed comparison between simulations and *in situ* data. MEZO-1D was firstly calibrated on year 1994 *in situ* data, and then run for year 1995, without changing any parameter, in order to compare the model results with data from year 1995. Before running the model for year 1995, the calculated detritus concentration in box n°4 has been empirically divided by 5 in order to keep detritus accumulation in this box reasonable, *i. e.* close to values reported in the literature (organic matter concentrations range 1.1-17.6 % of sediment dry weight in the Thau lagoon, data compilation from Laugier, 1998 and Deslous-Paoli, personal communication). Taking the December 31st of 1994 values in order to initialise each state variable (except for detritus in box n°4) on January 1st of 1995, the model results could be separated from data right from the start, allowing simulation-measurements comparison relevant all along the year.

At the end of each day during 1995 simulation, the contributions of the three different primary producers (epiphytes, seagrasses and phytoplankton), to the total ecosystem production, the uptake of nitrogen and the fluxes through detritus compartment, have been recorded in order to assess their respective impacts on nitrogen and oxygen cycles.

For driving variables (see figure 3), we used light intensity data provided by Météo France (Fréjorgues station), wind speed and rain data measured in Sète city and water temperature data measured weekly in the Thau lagoon.

In order to get a good overview of the model, a sensivity analysis has been performed. Two variations of +10% and -10% have been applied to each parameter and the model was at each time re-launched (90 simulations in total). Then, a sensibility index (IS, expressed in %) could be calculated for each parameter using the following equation:

$$\mathrm{IS} = \frac{100}{p \times n} \times \sum_{i=1}^{n} \frac{\left| X_i - X_i^{ref} \right|}{X_i^{ref}}$$

Where p is the variation of the parameter (± 10 %), n, the total duration of the simulation (expressed in days), X_i, the new value of the observed state variable and X_i^{ref}, the reference value of the observed state variable (simulation done without changing any parameter). Each IS was afterwards averaged on the two simulations. In order to observe every state variables, sensivity indexes have been calculated for the water box.

4. RESULTS AND DISCUSSION

Figures 4 to 7 present the simulation results as well as some data from Laugier (1998). The following discussion and comparisons between simulation and data will focus on year 1995 simulation, year 1994 having been used for the model calibration.

4.1 Seagrasses and epiphytes (figure 4)

The unimodal pattern of the *Zostera noltii* beds in the Thau lagoon (both for biomass and density) is well reproduced by MEZO-1D (see figure 4). Maximal aboveground biomass, in spite of being slightly lower than observed data (190 $gDW.m^{-2}$ instead of 230 ± 30 $gDW.m^{-2}$), is reached at the same moment as the latters (end of July), and is followed by a decrease all along autumn and winter periods. Furthermore, the variation magnitude between minimum and maximum biomasses is well reproduced by the model. Such unimodal pattern has been widely reported both in experimental and model studies (Verhagen and Nienhuis, 1983, Pérez and Romero, 1992, Bach, 1993, Auby, 1995, Zuppo et al., 1997) and thus, can be considered as typical for temperate seagrass meadows.

Belowground biomass data are unfortunately not available for year 1995. Nevertheless some *in situ* data (aboveground and belowground biomasses) collected during years 1996 to 1998 (Plus et al., 2001, *Zostera noltii* beds from the same area) allowed the comparison for $\frac{\text{above} - \text{ground}}{\text{below - ground}}$ biomasses ratios (hereafter noted $R_{above/below}$) at every seasons. Table 8 presents the comparison results. It appears that excepted for autumn season simulated and observed data differ significantly. MEZO-1D probably underestimates the belowground biomass variations, which could explain such high $R_{above/below}$ ratio simulated during summer period. This hypothesis should nevertheless be tested using more precise data.

Epiphytes growth is important during summer period, when light intensity is still high and the leaf renewal is less rapid than in spring. Maximal epiphyte biomass (28.3 $gDW.m^{-2}$) is reached in the beginning of September (see figure 4), and equals to 14.7 % of vegetal total biomass (seagrass leaves plus epiphytes). This percentage increases up to 30 % by the end of the year, when seagrass leaves fall down but inorganic nitrogen concentrations are still high and support the epiphytes growth. In spite of the fact that no measurement was available for the epiphytes biomass in the Thau lagoon, the model results could be compared with Philippart (1995) measurements in *Zostera noltii* beds from the Dutch Wadden Sea: epiphytes biomass ranged between 27 to 50 % of the total biomass (leaves plus epiphytes). Model simulations are in accordance with such values. No evidence of competition between seagrasses and epiphytes for nitrogen could be shown, belowground nitrogen uptake, redistribution and reclamation mechanisms allowing an increase of seagrass internal nitrogen contents during autumn and winter periods (even when the percentage of epiphytes is at its maximum). On the contrary, it seems that competition for light availability can be important, model results showing a 80 % decrease of available light for seagrass leaves when epiphytes:leaves biomasses ratios are maximum.

Seasonal variations of shoot density (figure 4) follows the same general pattern as aboveground biomass and model simulations are close to Laugier (1998) measurements. Vegetative recruitment is active during spring and the beginning of summer, increasing shoot density from 750 shoots.m^{-2} in winter to about 3000 shoots.m^{-2} in summer. During autumn and winter periods shoot density is submitted to a drastic decrease mainly due to high sloughing rates induced by wave motion. In his model, Nielsen (1997) found similar results for *Zostera marina* beds (Roskilde Fjord, Danemark), arguing that: "*…a considerable amount of biomass had to be removed during the autumn in order to simulate the observed pattern*."

4.2 Oxygen, dissolved inorganic nitrogen and internal nitrogen quotas (figure 5 and 6)

Oxygen concentrations simulated in the water column are relatively stable all along the year. The general pattern of oxygen evolution shows nevertheless a minimum in summer (7.46 mg.l^{-1}), probably due to both a decrease in oxygen solubility and an increase of mineralization and respiration processes at high temperatures (Chapelle et al., 2000). The annual mean oxygen concentration corresponds to 153.3 % (minimum 130 % and maximum 175.1 %) of the saturation point (Weiss, 1970), which remains higher than other values reported in summer for the Thau lagoon outside from seagrass beds: 100.4 % according to Plante-Cuny et al. (1998) and 102.1 % (minimum 83.5 % and maximum 134.7 %) according to Gasc (1997). It seems that the over-saturation calculated by the model can be explicated by the active seagrass production, coupled with epiphyte production, which cannot be compensated neither by respiration nor mineralization. Thus, MEZO-1D seems to put in light one of the impacts of seagrass beds on such shallow depth ecosystems, *i. e.* an increase of oxygen concentrations all along the year, particularly noticeable in summer.

The inorganic nitrogen concentrations simulated by the model can be separated into two periods. Low concentrations are simulated in summer, 1.3 µmol.l^{-1} on average (NH_4^+ plus NO_3^-, minimum 0.6 µmol.l^{-1} and maximum 2.7 µmol.l^{-1}), due to an active nitrogen uptake by seagrasses and epiphytes and low watershed inputs. Higher concentrations are simulated in winter (NH_4^+ plus NO_3^-, mean 4.8 µmol.l^{-1}, minimum 2 µmol.l^{-1} and maximum 7.6 µmol.l^{-1}) because of a lower uptake coupled with greater watershed inputs. Simulated concentrations are in good accordance even if situated within the lower range of those reported in the literature (see table 9). This could be explained by the location of some measurement sites, close from the influence of river nitrogen inputs.

Internal nitrogen quotas remain all along the year close to measurements from Laugier (1998), showing a summer minimum (0.04 molN.molC^{-1} for the leaves and 0.03 molN.molC^{-1}

for the rhizomes and roots). The seasonal variations in nitrogen content are in the same range as those described for *Zostera marina* in Venice lagoon (Italy) and Øresund (Danemark), by Bocci et al. (1997) and Coffaro and Bocci (1997). Nevertheless both leaf and belowground internal simulated quotas present a slightly overestimated minimum in summer. The sediment characteristics described by Laugier (1998) at his study site (in percentage of dry sediment: grain size < 100 µm = mud 0.6 %, 100 µm < grain size < 1.5 mm = sand 87.6 %, grain size > 1.5 mm = shell fragment 11.7 %, and organic matter 2,2 %, De Casabianca et al., 1997) can maybe explain these differences: the high ammonia concentrations simulated in the sediment (see figure 6, NH_4^+ mean concentration in interstitial waters is 260 µmol.l^{-1}) are probably higher than the concentrations one can expect in sandy sediment. This explanation is nevertheless to be confirmed by interstitial waters analysis. Anyway, the simulated summer minimum could indicate a nitrogen limitation of seagrass growth during this period. Indeed, this minimum corresponds to a leaf $\frac{\text{nitrogen}}{\text{dry weight}}$ mass ratio of 1.2 % (calculation made with a $\frac{\text{carbon}}{\text{dry weight}}$ mass ratio equals to %, Plus et al., 2001), which is under the threshold value for nitrogen limitation (1.8 %) published by Duarte (1990). This hypothesis is moreover supported by *in situ* (benthic bell jars measurements, Plus et al., 2001), and *in vitro* production measurements for *Zostera noltii* leaves collected in the Thau lagoon (polarographic measurements, Auby, personal communication).

Simulated dissolved oxygen in interstitial waters rapidly vanishes with depth. These results are in accordance with Brotas et al. (1990) measurements, showing that oxygen penetration is less than one centimetre even in sandy sediments. Chapelle (1995) also estimates, but for muddier sediments, that oxygen penetration does not exceed a few millimetres in the Thau lagoon.

MEZO-1D shows a detritus accumulation in the sediment (see figure 6). Probably because the aerobic mineralization, the only process included in the model, is not sufficient. Considering *a priori* that detritus concentrations remain roughly constant in the sediment, the model could probably be improved introducing anaerobic mineralization processes (the sediment being mainly anoxic) and disappearance of organic matter through burial and advection.

4.3 Impacts of the different primary producers to nitrogen and oxygen cycles (figure 7)

MEZO-1D allowed the comparison of the three different primary producers (seagrasses, phytoplankton and epiphytes) contributions to the total ecosystem simulated nitrogen and oxygen cycles (production, fluxes through detritus compartment and nitrogen uptake in the water column, see figure 7).

The model shows that more than 80 % of total production is done by the seagrasses mainly during spring and summer. Phytoplankton production is nonetheless not negligible, contributing to about 20 % of total production during the summer period, and up to 60 % during winter (February and March). The contribution of epiphytes to the ecosystem production remains always low (a maximum of 8 % reached in November) due to their low biomass when compared to seagrass or phytoplankton biomasses.

Nitrogen fluxes towards detritus pool due to seagrass mortality and sloughing are also the most important: the model estimates that about 69 % of total annual inputs in detritus compartment is due to the seagrasses. Contributions of phytoplankton and epiphytes are respectively 20 % and 11 %. These results put into light the importance of seagrass beds in the fluxes through the detritus pool, like already mentioned by Pergent et al. (1994) for the *Posidonia oceanica* beds in the Mediterranean. Oshima et al. (1999), also noticed the importance of seagrasses in the production of particulate organic matter (POM): their model results estimated that *Zostera marina* losses account for about 60 % while phytoplankton mortality account for 30 % of the total POM production. Due to differences in decomposition rates (Rice and Tenore, 1981, Pellikaan, 1982, Auby, 1991, Bourgues et al., 1996), the behaviour of detritus will probably be different if coming from seagrasses, phytoplankton or epiphytes. We can suppose that seagrass leaves detritus will probably be exported by advection to calmer zones (or on the shore) while dead epiphytes and phytoplankton will be decomposed rapidly (Zhuang et al., 1993, Duarte, 1995), thus participating to the regeneration into the seagrass bed. Model results for the detritus compartment are therefore to be taken with care, because detritus exportation due to advection is not taken into account.

Model results show also that phytoplankton is responsible for the main nitrogen uptake in the water column. It appears that this uptake is on average ten times higher than the seagrass leaves uptake during the whole simulation period. Using their model, Oshima et al. (1999), obtained similar results on shorter periods. These results are not surprising considering (i) that belowground uptake can respond to an important part of seagrasses nitrogen demand (Short and Mc Roy, 1984, Zimmerman et al., 1987, Pellikaan and Nienhuis, 1988) and (ii) that seagrasses have developed effective internal nitrogen redistribution mechanisms (Pedersen and Borum, 1992 and 1993). Seagrass high growth rates are thus not necessarily linked to high nitrogen uptakes, allowing seagrasses to maintain high growth rates during periods of nitrogen low availability. Model simulations show that competition for inorganic nitrogen between seagrasses and phytoplankton is unlikely, and thus, that when competition occurs in the Thau lagoon, it rather concerns light availability (a phytoplankton bloom producing an important increase of light extinction in the water column). Nitrogen uptake by the epiphytes remains very low when compared with other primary producers due to their low biomass. Its maximum (3.2 % of total nitrogen uptake in the water column) is reached when the simulated phytoplankton biomass is at its minimum (beginning of March). It is then possible that a competition for nitrogen occurs between phytoplankton and epiphytes, the latter having the same nitrogen dynamics (same uptake rate, rapid turnover, same nitrogen sources) than the former in the model. This hypothesis remains nevertheless to be confirmed.

4.4 sensivity analysis

The two state variables most sensible to parameter variations are NO_3^- and the epiphyte biomass, each parameter variation leading to a model variation greater than 1 %. Nonetheless, these model variations remain generally small (below 5 %), except for Θ_{LM} ($\overline{IS} = 11$ %) and for Θ_E ($\overline{IS} = 5$ %). Inversely, oxygen remains particularly stable regarding parameter variations (no sensivity index was found above 1%). Parameters linked to temperature (Θ_{LM}, Θ_E, Θ_{REC}, Θ_{Pmax}, …) are generally more sensitive, probably due to the fact that they are involved in exponential type equations. To sum up, the sensivity analysis put into light a need of accuracy for parameters Θ_{LM}, Θ_E, Θ_{Pmax} (effect of temperature on leaf mortality, epiphyte growth and seagrass production) and K_{LAI} (acts on seagrass production calculation). On the other hand, MEZO-1D is not very sensitive to parameters linked to nitrogen uptake (K_{LGR}, $RN_{quotmin}$, K_R, RV_M, δ_1, δ_2) and to seagrass and epiphyte respiration rates ($LR_{20°C}$, $RR_{20°C}$ and $ER_{20°C}$).

5. CONCLUSION

MEZO-1D has permitted correct simulations of the seasonal variations of biomasses, shoot density and nitrogen quotas for a *Zostera noltii* bed in the Thau lagoon. These results have been validated using comparisons with *in situ* measurements whenever it could be possible. The following model weak points remain nevertheless to be improved: (i) the model probably underestimates the seagrass rhizome and root biomass (RB state variable), and (ii) the absence of benthic detritus decomposition leads to an accumulation in the sediment.

Results for the nitrogen quotas seem to indicate that the seagrass growth could suffer from nitrogen limitation during summer period in spite of effective mechanisms of nitrogen redistribution and reclamation. These results are in accordance with measurements done on the same seagrass beds in Thau lagoon (Plus et al., 2001, Auby, personal communication).

Moreover, the importance of epiphytes in the seagrass ecosystem has been confirmed by the model, particularly considering a possible competition with seagrasses for light resources, when the $\frac{\text{epiphytes}}{\text{leaves}}$ biomass ratio is important. If the model did not show any competition for nitrogen between seagrasses and neither epiphytes nor phytoplankton, simulations seems to point out that due to their similar nitrogen dynamics, epiphytes and phytoplankton could compete for nitrogen in the water column.

MEZO-1D, coupled with the Chapelle et al. model (2000), allowed to simulate the impacts of three different primary producers on the oxygen and nitrogen cycles for a simplified ecosystem (the shallow depth *Z. noltii* meadows from the Thau lagoon edge). Within this simulated ecosystem, seagrasses are the most productive compartment in comparison with phytoplankton and epiphytes. Comparisons made between model results and oxygen saturation measurements at different locations in the Thau lagoon showed that the high seagrass production notably increases oxygen concentrations in the water column. Nevertheless, the ability of seagrasses in taking nitrogen from the sediment and the internal nitrogen recycling processes make their impact on dissolved inorganic nitrogen in the water column smaller than the phytoplankton’s one. Finally, the seagrass leaves exportation contributes more than phytoplankton or epiphyte mortality to the organic matter flux through the detritus compartment.

In conclusion, MEZO-1D must be considered as a first step in modelling the seagrass beds in the Thau lagoon, and beyond the above-mentioned results, an extension to a three-dimensional model could allow the simulation of seagrass beds variations in time and space, in order to evaluate the impact of such communities at the whole lagoon level.

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Table 1 : List of equations linked to seagrass photosynthesis and respiration processes. References : 1, Jassby and Platt (1976) ; 2, Varlet-Granchet et al. (1993) ; 3, Plus et al. (2001) ; 4, Pérez-Lloréns and Niell (1993) ; 5, Fong et Harwell (1993) ; tent. = tentative.

Process		**Equation**	**References**
Seagrass photosynthesis			
P_{tot}	total gross production ($gO_2.mmolC^{-1}.d^{-1}$)	$P_{tot} = P_{max} \times \int_{z=0}^{LAI} \tanh(\frac{Q_{can} \times f_2(l)}{I_{k1}}) \times dz$	1, 2
P_{max}	maximum production rate ($gO_2.mmolC^{-1}.d^{-1}$)	$P_{max} = \Theta_{P\max} \times t - P_{max}^{0°C}$	tent.
t	water temperature (°C)		measurements
LAI	leaf area index ($m^2.m^{-2}$)	$LAI = K_{LAI} \times LB$	3, 4
Q_{can}	light at the top of the canopy ($W.m^{-2}$)	$Q_{can} = I \times f_1(E) \times e^{(-K_1 \times (D-0.3))}$	tent.
I	PAR* at the sea surface ($W.m^{-2}$)		measurements
$f_1(E)$	limitation due to epiphytes (-)	$f_1(E) = e^{(-K_2 \times \frac{EB}{LB})}$	5
$f_2(l)$	part of the incoming light intercepted by the canopy (-)	$f_2(l) = e^{(-K_3 \times z)}$	2
I_{k1}	saturation light intensity ($W.m^{-2}$)	$I_{k1} = \frac{I_{k\max} + I_{k\min}}{2} + \frac{I_{k\max} - I_{k\min}}{2} \times \cos(2\pi \times \frac{d-110}{365})$	tent.
Seagrass respiration			
LR	leaf respiration ($gO_2.mmolC^{-1}.d^{-1}$)	$LR = \Theta_{LR} \times t + LR_{0°C}$	tent.
RR	rhizomes/roots respiration ($gO_2.mmolC^{-1}.d^{-1}$)	$RR = \Theta_{RR} \times t + RR_{0°C}$	tent.

* PAR = photosynthetic active radiation ; - = dimensionless

Table 2 : List of equations linked to nitrogen uptake and mortality processes. References : 1, Van Lent (1995) ; 2, Bach (1993); 3, Bocci et al. (1997) ; 4, Zimmerman et al. (1987) ; tent = tentative.

Process		**Equation**	**References**
Nitrogen dynamics			
$LABS_{NH_4}$	ammonium uptake by leaves ($mmolN.mmolC^{-1}.d^{-1}$)	$LABS_{NH_4} = LV_m \times \frac{NH_4}{(NH_4 + K_L)} \times (1 - LN_{sat})^{\delta_1}$	1, 3, 4
$LABS_{NO_3}$	nitrates uptake by leaves ($mmolN.mmolC^{-1}.d^{-1}$)	$LABS_{NO_3} = LV_m \times \frac{NO_3}{(NO_3 + K_L)} \times (1 - LN_{sat})^{\delta_1}$	1, 3, 4
$RABS_{NH_4}$	ammonium uptake by roots ($mmolN.mmolC^{-1}.d^{-1}$)	$RABS_{NH_4} = RV_m \times \frac{NH_4}{(NH_4 + K_R)} \times (1 - RN_{sat})$	1, 3, 4
Δ_{sat}	difference of nitrogen saturation between leaves and below-ground parts	$\Delta_{sat} = RN_{sat} - LN_{sat}$	tent.
L_{trans}	carbon transfer rate from the leaves towards the rhizomes ($mmolN.mmolC^{-1}.d^{-1}$)	$\text{if } \Delta_{sat} \rangle 0 \text{ and } LN_{sat} \langle 0.75 \Rightarrow \begin{cases} L_{trans} = 0 \\ R_{trans} = \tau \lvert \Delta_{sat} \rvert \end{cases}$ $\text{if } \Delta_{sat} \langle 0 \text{ and } RN_{sat} \langle 0.75 \Rightarrow \begin{cases} L_{trans} = \tau \lvert \Delta_{sat} \rvert \\ R_{trans} = 0 \end{cases}$	tent.
R_{trans}	carbon transfer rate from the rhizomes towards the leaves ($mmolN.mmolC^{-1}.d^{-1}$)	$\text{if } \Delta_{sat} = 0 \Rightarrow \begin{cases} L_{trans} = 0 \\ R_{trans} = 0 \end{cases}$	
LN_{rec}	part of nitrogen reclaimed inside the leaves (-)	$\begin{cases} LN_{rec} = \left[1 - (\frac{LN_{sat}}{S_{rec}})^2 \right] \times REC_{max} \\ LN_{rec} = 0 \quad \text{if} \quad LN_{sat} \rangle S_{rec} \end{cases}$	tent.
RN_{rec}	part of nitrogen reclaimed inside the rhizomes/roots (-)	$\begin{cases} RN_{rec} = \left[1 - (\frac{RN_{sat}}{S_{rec}})^2 \right] \times REC_{max} \\ RN_{rec} = 0 \quad \text{if} \quad RN_{sat} \rangle S_{rec} \end{cases}$	
Seagrass mortality			
LM	leaf loss rate (d^{-1})	$LM = LMR_{20°C} \times f_5(t) + f_6(v)$	1, 2, tent.
$f_5(t)$	mortality limitation due to température (-)	$f_5(t) = \Theta_{LM}^{(t-20)}$	1, 2
$f_6(v)$	leaf loss function due to wind generated currents and waves (d^{-1})	$f_6(v) = LMR_v \times \frac{V_{vent}}{10} \times e^{(-K_4 \times D)}$	tent.
V_{vent} , D	wind speed ($m.s^{-1}$) and depth (m)		
RM	below-ground loss rate (d^{-1})	$RM = RMR_{20°C} \times f_5(t)$	1

- = dimensionless

Table 3 : List of equations linked to seagrass growth and recruitment processes. References : 1, Van Lent (1995) ; 2, Verhagen and Nienhuis (1983) ; 3, Bach (1993); tent = tentative.

Process		**Equation**	**References**
Seagrass growth			
TG	total net growth rate ($mmolC.m^{-2}.d^{-1}$)	$\begin{cases} TG = [Ptot \times f_3(LN) - (LR + RR)] \times \frac{LB \times 100}{32 \times \omega} \\ TG = 0 \quad \text{if} \quad TG \langle 0 \end{cases}$	1
$f_3(LN)$	nitrogen limitation function for leaves (-)	$f_3(LN) = LN_{sat}{}^{\varepsilon_1}$	1
LN_{sat}	saturation level of leaf nitrogen quota (-)	$LN_{sat} = \frac{LN_{quot} - LN_{quot\,min}}{LN_{quot\,max} - LN_{quot\,min}}$	1
LN_{quot}	leaf nitrogen quota ($mmolN.mmolC^{-1}$)	$LN_{quot} = \frac{LN}{LB}$	1
RGR	below-ground growth rate ($mmolC.m^{-2}.d^{-1}$)	$RGR = TG \times f_4(RN) \times K$	1, 2, 3
$f_4(RN)$	nitrogen limitation function for rhizomes/roots (-)	$f_4(RN) = RN_{sat}{}^{\varepsilon_2}$	1
RNsat	saturation level of below-ground nitrogen quota (-)	$RN_{sat} = \frac{RN_{quot} - RN_{quot\,min}}{RN_{quot\,max} - RN_{quot\,min}}$	1
RN_{quot}	below-ground nitrogen quota ($mmolN.mmolC^{-1}$)	$RN_{quot} = \frac{RN}{RB}$	1
LGR	leaf growth rate ($mmolC.m^{-2}.d^{-1}$)	$LGR = TG - RGR$	1
Recruitment			
REC	shoot recruitment rate (d^{-1})	$REC = REC_{max} \times f_7(t) \times f_8(LB) \times f_9(RB)$	1, tent.
$f_7(t)$	temperature limitation function for recruitment (-)	$\begin{cases} f_7(t) = 0 & \text{if} \quad t \langle 5°C \\ f_7(t) = \Theta_{REC}{}^{(t-12)} & \text{if} \quad 5°C \le t \le 22°C \\ f_7(t) = 2{,}8 & \text{if} \quad t \rangle 22°C \end{cases}$	tent.
$f_8(LB)$	self-shading limitation function for recruitment (-)	$\begin{cases} \text{if } lum_{fond} \langle 10\ W.m^{-2} \text{ then} : f_8(LB) = 0 \\ \text{else} : f_8(LB) = \frac{(lum_{fond}\ \text{-}10)}{(lum_{fond}\ \text{-}10) + K_{rec1}} \end{cases}$	tent.
$f_9(RB)$	below-ground limitation function for recruitment (-)	$f_9(RB) = \frac{RB}{(RB + K_{rec2})}$	tent.

- = dimensionless

Table 4 : List of equations linked to epiphytes processes. References : 1, Van Lent (1995) ; 2, Verhagen and Nienhuis (1983) ; 3, Bach (1993) ; 4, Bocci et al. (1997) ; 5, Zimmerman et al. (1987) ; tent = tentative.

PROCESS		**EQUATION**	**REFERENCE**
Epiphytes growth			
EGR	epiphytes growth rate (d^{-1})	$EGR = EGR_{max} \times f_{10}(l) \times f_{11}(t) \times f_{12}(N) \times f_{13}(LG)$	6, tent.
$f_{10}(l)$	light limitation function (-)	$f_{10}(l) = \tanh\left(\frac{\frac{Q_{can}}{f_1(E)}}{I_{k2}}\right)$	tent.
$f_{11}(t)$	temperature limitation function (-)	$\begin{cases} \text{if } t \langle 10°C & \text{then } f_{11}(t) = 0 \\ \text{if } 10°C \le t \le 27°C & \text{then } f_{11}(t) = \Theta_E^{(t-20)} \\ \text{if } t \rangle 27°C & \text{then } f_{11}(t) = 2 \end{cases}$	tent.
$f_{12}(N)$	dissolved inorganic nitrogen limitation function (-)	$f_{12}(N) = \frac{(NH_4 + NO_3)}{(NH_4 + NO_3) + K_E}$	6, tent.
$f_{13}(LG)$	leaf growth rate limitation function (-)	$f_{13}(LG) = 1 - \left(\frac{\frac{LGR}{LB}}{\frac{LGR}{LB} + K_{LGR}}\right)$	tent.
Epiphytes nitrogen uptake			
$EABS_{NH4}$	ammonium upake by epiphytes (mmolN.mmolC^{-1}.d^{-1})	$EABS_{NH4} = \frac{EGR}{E_{C:N}} \times \frac{NH_4}{NH_4 + NO_3}$	tent.
$EABS_{NO3}$	nitrates upake by epiphytes (mmolN.mmolC^{-1}.d^{-1})	$EABS_{NO3} = \frac{EGR}{E_{C:N}} \times \frac{NO_3}{NH_4 + NO_3}$	tent.
Epiphytes mortality			
EM	epiphytes mortality rate (d^{-1})	$EM = LM$	tent.
Epiphytes photosynthesis and respiration			
EP	epiphytes production (gO$_2$.mmolC^{-1}.d^{-1})	$EP = EGR \times \frac{\omega \times 32}{1000}$	tent.
ER	epiphytes respiration (gO$_2$.mmolC^{-1}.d^{-1})	$ER = ER_{20°C} \times f_{11}(t)$	tent.

- = dimensionless

Table 5 : List and values of parameters linked to photosynthesis and respiration processes. References: 1, Auby (personal communication) ; 2, Plus et al. (2001) ; 3, Pérez-Lloréns and Niell (1993) ; 4, Chapelle et al. (2000) ; 5, Fong and Harwell (1994) ; 6, Varlet-Granchet et al. (1993) ; 7, Clavier et al. (1994) ; cal, estimated by calibration.

	Parameter	**Value**	**Unit**	*References*
Θ_{Pmax}	production increasing rate with temperature	2.65×10^{-2}	$gO_2.mmolC^{-1}.°C^{-1}.d^{-1}$	1, cal
$P_{max}^{0°C}$	theorical maximum production at 0°C	-4.67×10^{-2}	$gO_2.mmolC^{-1}.d^{-1}$	1, cal
K_{LAI}	$\frac{LAI}{LB}$ ratio	8.64×10^{-4}	$m^2.mmolC^{-1}$	2, 3
K_1	light extinction coefficient due to water	0.4	m^{-1}	4
D	Water column depth	1.4	m	fixed
K_2	light extinction coefficient due to epiphytes	4.8	sd	5
K_3	absorption coefficient linked to canopy optical and geometrical properties	0.6	sd	6, 3
I_{kmax}	maximal saturation light intensity	80	$W.m^{-2}$	1
I_{kmin}	minimal saturation light intensity	35	$W.m^{-2}$	1
d	day in the year	variable	-	
Θ_{LR}	leaf respiration increasing rate with temperature	4.5×10^{-5}	$gO_2.mmolC^{-1}.°C^{-1}.d^{-1}$	1, cal
$LR_{0°C}$	theorical leaf respiration rate at 0°C	5.9×10^{-4}	$gO_2.mmolC^{-1}.d^{-1}$	1, cal
Θ_{RR}	rhizomes and roots respiration increasing rate with temperature	1.4×10^{-5}	$gO_2.mmolC^{-1}.°C^{-1}.d^{-1}$	1, cal
$RR_{0°C}$	theorical rhizomes and roots respiration rate at 0°C	1.47×10^{-4}	$gO_2.mmolC^{-1}.d^{-1}$	1, cal
$ER_{20°C}$	theorical epiphytes respiration rate at 20°C	1.76×10^{-3}	$gO_2.mmolC^{-1}.d^{-1}$	4, cal
ω	photosynthetic quotient	1.1	$molO_2.molC^{-1}$	7

Table 6 : List and values of parameters linked to growth and nitrogen dynamics processes. References: 1, Van Lent (1995) ; 2, Laugier (1998) ; 3, Plus et al. (2001) ; 4, Bach (1993) ; 5, Thursby and Harlin (1982) ; 6, Pedersen and Borum (1993) ; 7, Lin et al. (1996) ; 8, Verhagen and Nienhuis (1983) ; 9, Fong and Harwell (1994) ; 10, Chapelle et al. (2000) ; cal, estimated by calibration.

	Parameter	**Value**	**Unit**	**References**
Seagrass growth				
ε_1	leaf nitrogen content limitation coefficient	0.4	-	1, cal
$LN_{quotmin}$	minimum leaf nitrogen content	0.03	$molN.molC^{-1}$	3, cal
$LN_{quotmax}$	maximum leaf nitrogen content	0.07	$molN.molC^{-1}$	3, cal
K	part of carbon translocated to the rhizomes	0.4	-	1, 4, cal
ε_2	below ground nitrogen content limitation coefficient	1	-	1, cal
$RN_{quotmin}$	minimum below-ground nitrogen content	0.01	$molN.molC^{-1}$	3, cal
$RN_{quotmax}$	maximum below-ground nitrogen content	0.05	$molN.molC^{-1}$	3, cal
Nitrogen dynamics				
LV_m	maximum leaf nitrogen uptake rate	0.007	$molN.molC^{-1}.d^{-1}$	5
K_L	half-saturation coefficient for leaf uptake	9.2	$mmolN.m^{-3}$	5
δ_1	limitation coefficient for leaf nitrogen uptake	0.6	-	cal
RV_m	maximum nitrogen root uptake rate	0.0035	$molN.molC^{-1}.d^{-1}$	5
K_R	half-saturation coefficient for root uptake	104	$mmolN.m^{-3}$	5
δ_2	limitation coefficient for root nitrogen uptake	0.6	-	cal
τ	nitrogen transfer speed between leaves and rhizomes	0.1	$molN.molC^{-1}.d^{-1}$	cal
S_{rec}	internal reclamation threshold	0.9	-	cal
REC_{max}	maximum reclamation rate	0.7	-	6, cal
$E_{C:N}$	carbon : nitrogen molar ratio for epiphytes	9	$molC.molN^{-1}$	7
Mortality				
$LMR_{20°C}$	maximum leaf mortality rate at 20°C	0.025	d^{-1}	1, cal
Θ_{LM}	leaf mortality increasing rate with temperature	1.1	-	4, cal
LMR_v	leaf sloughing coefficient due to the wind	0.08	d^{-1}	1, cal
K_4	wind effect attenuation with depth	1.2	m^{-1}	1, 8
$RMR_{20°C}$	maximum rhizomes/roots mortality rate at	0.025	d^{-1}	1, cal

	20°C			
Recruitment				
REC_{max}	theorical maximum recruitment rate	0.039	d^{-1}	2, cal
Θ_{REC}	recruitment increasing rate with temperature	1.1	-	4
SB_0	initial biomass of a new shoot	0.05	mmolC	1, 8, cal
K_{rec1}	half-saturation coefficient for limitation by the light	8	$W.m^{-2}$	cal
K_{rec2}	half-saturation coefficient for limitation by the below-ground biomass	10	$gDW.m^{-2}$	cal
Epiphytes growth				
EGR_{max}	maximum epiphytes growth	0.34	d^{-1}	9, cal
I_{k2}	saturation light intensity	40	$W.m^{-2}$	10, cal
Θ_E	growth increasing rate with temperature	1.1	-	10
K_E	half-saturation coefficient for the nitrogen limitation	2	$mmolN.m^{-3}$	10
K_{LGR}	half-saturation coefficient for the limitation by the leaf growth rate	0.1	d^{-1}	cal

Table 7. State variables list, units and distribution in the box system.

State variable	abbreviation	State	Unit	Boxes[*]			
				1 wat.	2 sed.	3 sed.	4 sed.
ammonium	NH_4	dissolved	$mmolN.m^{-3}$	✓	✓	✓	✓
nitrates	NO_3	dissolved	$mmolN.m^{-3}$	✓	✓	✓	✓
organic particulate nitrogen (detritus)	Ndet	particulate	$mmolN.m^{-3}$	✓	✓	✓	✓
above-ground biomass	LB	particulate	$mmolC.m^{-2}$	✓			
above-ground nitrogen pool	LN	particulate	$mmolN.m^{-2}$	✓			
below-ground biomass	RB	particulate	$mmolC.m^{-2}$		✓	✓	✓
below-ground nitrogen pool	RN	particulate	$mmolN.m^{-2}$		✓	✓	✓
density of shoots	SD	particulate	m^{-2}	✓			
epiphytes biomass	EB	particulate	$mmolC.m^{-2}$	✓			
oxygen	O_2	dissolved	$g.m^{-3}$	✓	✓	✓	✓

[*] wat. = water box ; sed. = sediment box.

Table 8 : Comparaisons for $\frac{\text{above} - \text{ground}}{\text{below - ground}}$ biomasses ratios ($R_{\text{above/below}}$). Data have been averaged for each season (mean ± standard errors at 5 %, n : number of data). The probabilities given present the results for a mean comparison test (Kruskall - Wallis test).

$\mathbf{R}_{\textbf{above/below}}$	**Spring**	**Summer**	**Autumn**	**Winter**
years 1996 to 1998, observed data (Plus et al., in press)	0,72 ± 0,07 (n=12)	1,05 ± 0,09 (n=22)	1,86 ± 0,25 (n=6)	1,37 ± 0,23 (n=6)
year 1995, simulated data	1,66 ± 0,11 (n=94)	3,20 ± 0,06 (n=92)	1,95 ± 0,09 (n=90)	1,03 ± 0,02 (n=88)
	p < 0,0001	p < 0,0001	p = 0,51	p = 0,0001

Table 9 : Some ammonia and nitrate concentrations reported in the literature for the Thau lagoon and model results averaged for each season.

	Spring		**Summer**		**Autumn**		**Winter**	
	mean	(min-max)	mean	(min-max)	mean	(min-max)	mean	(min-max)
NH_4^+								
Casellas et al. (1990)[1]	1.02	(0.4-2)	0.91	(0.4-2.2)	10.3	(0.4-14.4)	3.22	(1-30.4)
Pichot et al. (1994)[1]	0.63		0.46		2.05		1.91	
Gasc (1997)[2]			annual mean : 0.99 (0.2-3.8)					
Souchu et al. (1998)[2]			0.47					
MEZO-1D simulations	0.20	(0.1-0.6)	0.04	(0-0.1)	0.27	(0.5-1.5)	1.5	(0.5-2.8)
NO_3^-								
Casellas et al. (1990)[1]	0.16	(0-1.2)	1.97	(0.2-7)	10.45	(2.7-21.9)	15.22	(2.3-69.7)
Pichot et al. (1994)[1]	1.71		0.52		0.72		2.16	
Gasc (1997)[2]			annual mean : 0.71 (0-4.2)					
MEZO-1D simulation	1.07	(0.5-2.1)	0.51	(0.4-0.7)	1.45	(0.6-3.7)	3.3	(1.6-4.8)

[1] measurements have been done outside from the shellfish cultivation areas.[2] measurements have been done at station TB (located in the middle of the lagoon and outside from the shellfish cultivation areas).

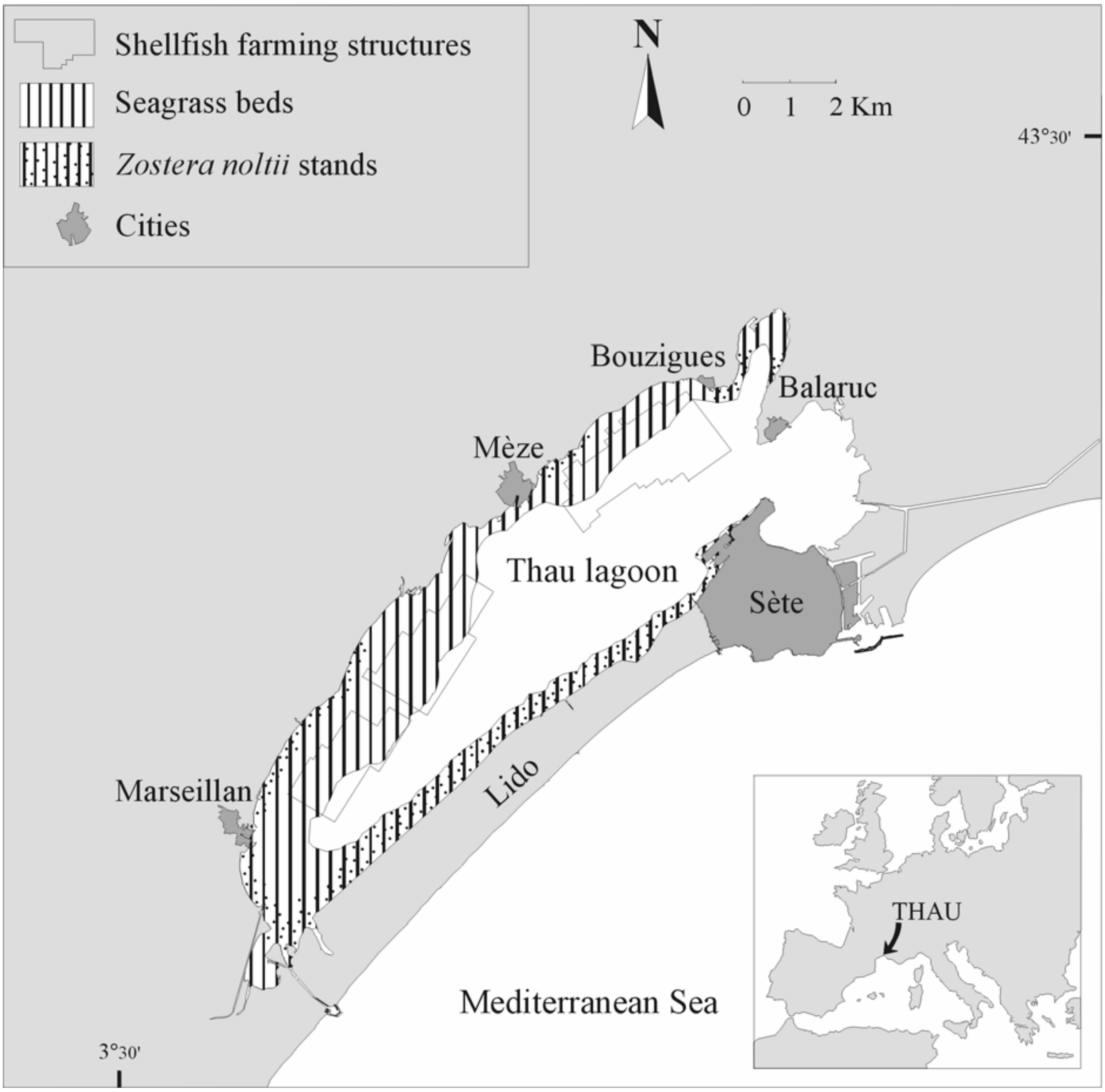


Figure 1. The Thau lagoon. Distribution of *Zostera noltii* beds (Gerbal and Verlaque, 1995, Verlaque, Belsher and Deslous-Paoli, personal communication).

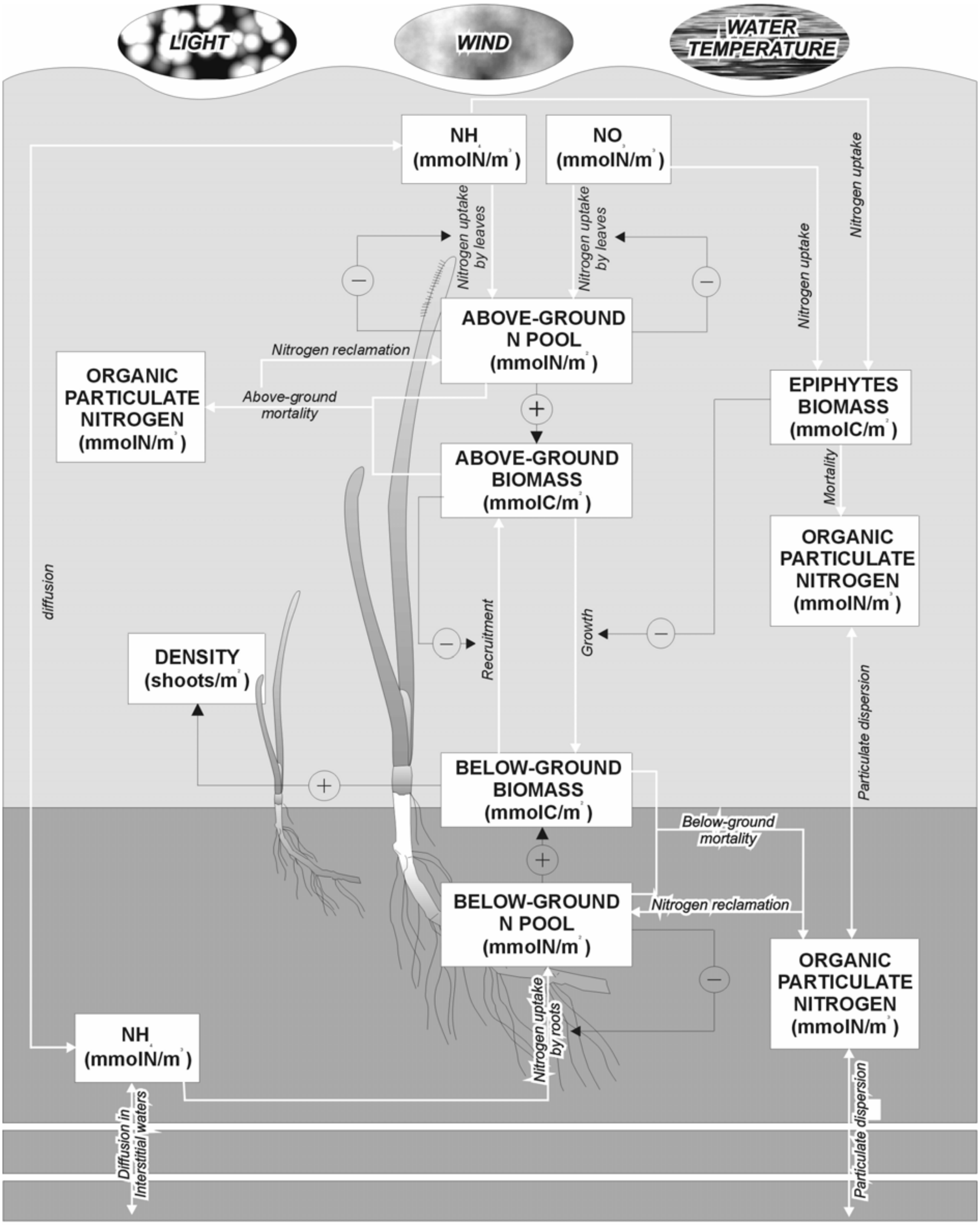
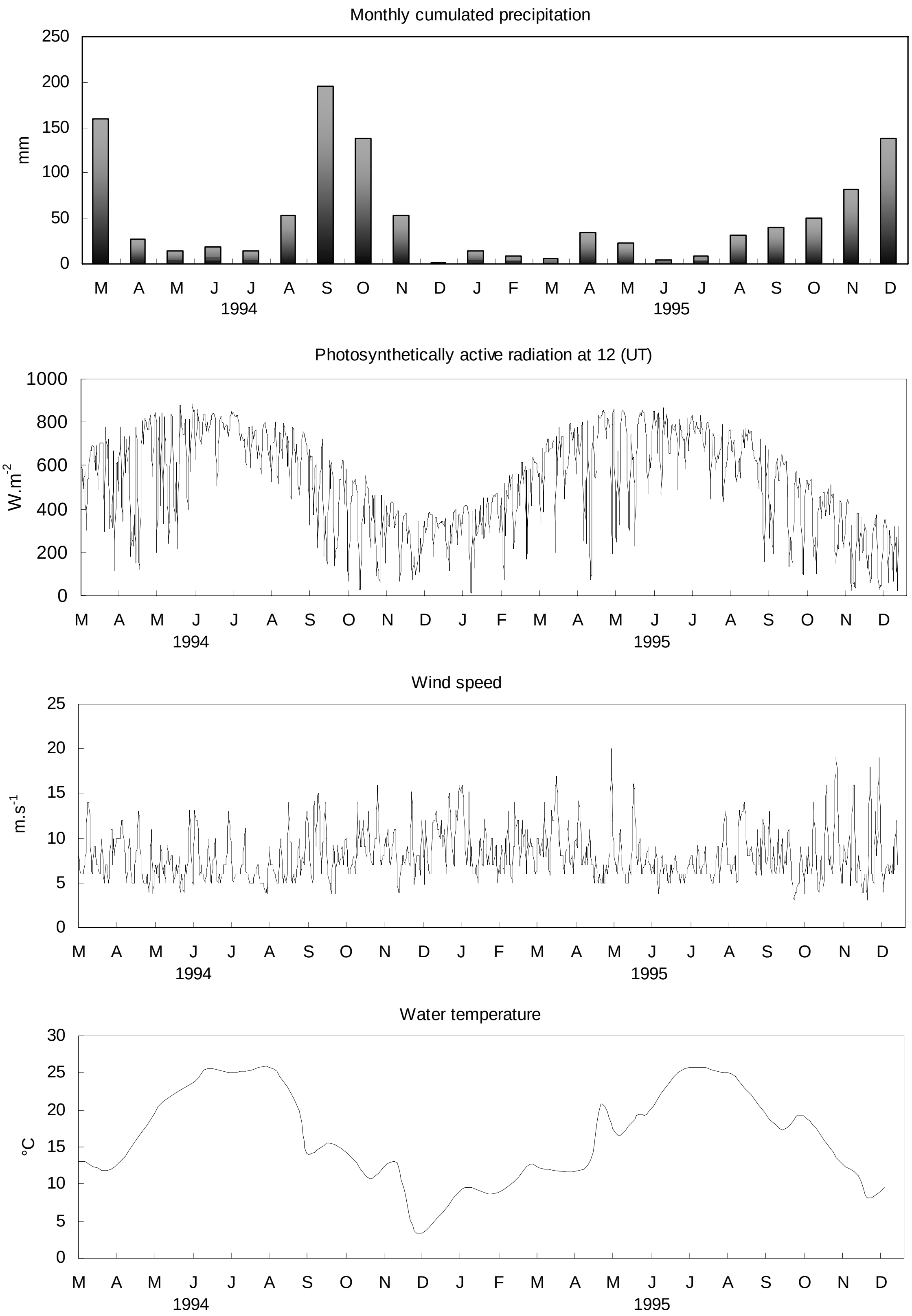


Figure 2. Conceptual diagram of the seagrass model. White rectangles are state variables, forcing variables are presented on the top of the diagram, white arrows mean fluxes between state variables (each one is controlled by a single process) and black arrows mean limitation factors for processes. In order to simplify the diagram, processes linked to oxygen state variable (photosynthesis, respiration and mineralization) are not reported here.



Monthly cumulated precipitation

Photosynthetically active radiation at 12 (UT)

Wind speed

Water temperature

Figure 3. Driving variables (precipitation, insolation, wind speed and water temperature) used in the model.

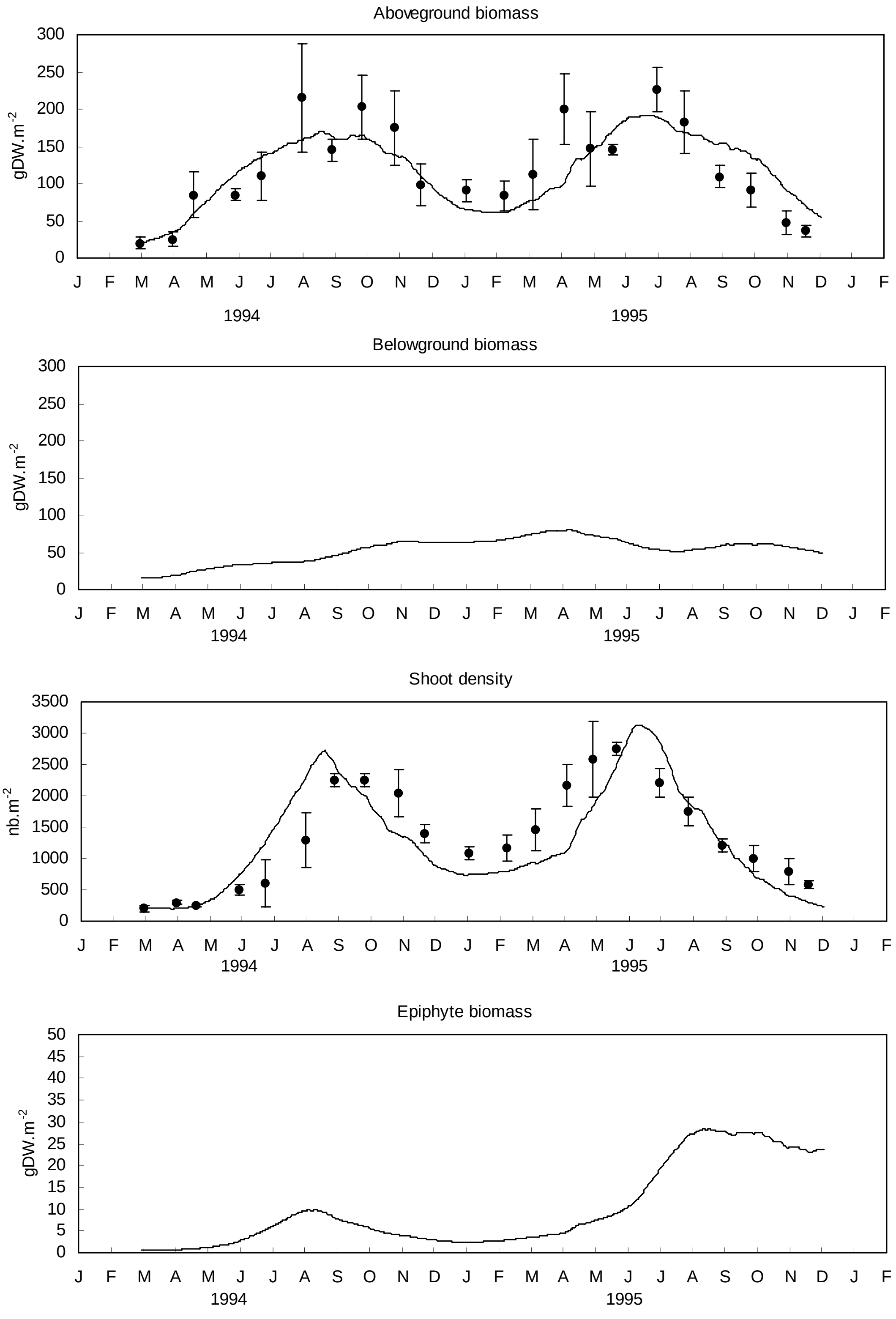


Figure 4. Simulated (black lines) and observed (black points) values for seagrasses and epiphytes during years 1994 and 1995. Biomasses have been converted to g dry weight using carbon content values from Plus et al. (2001). Measured data are means ± standard errors from Laugier (1998).

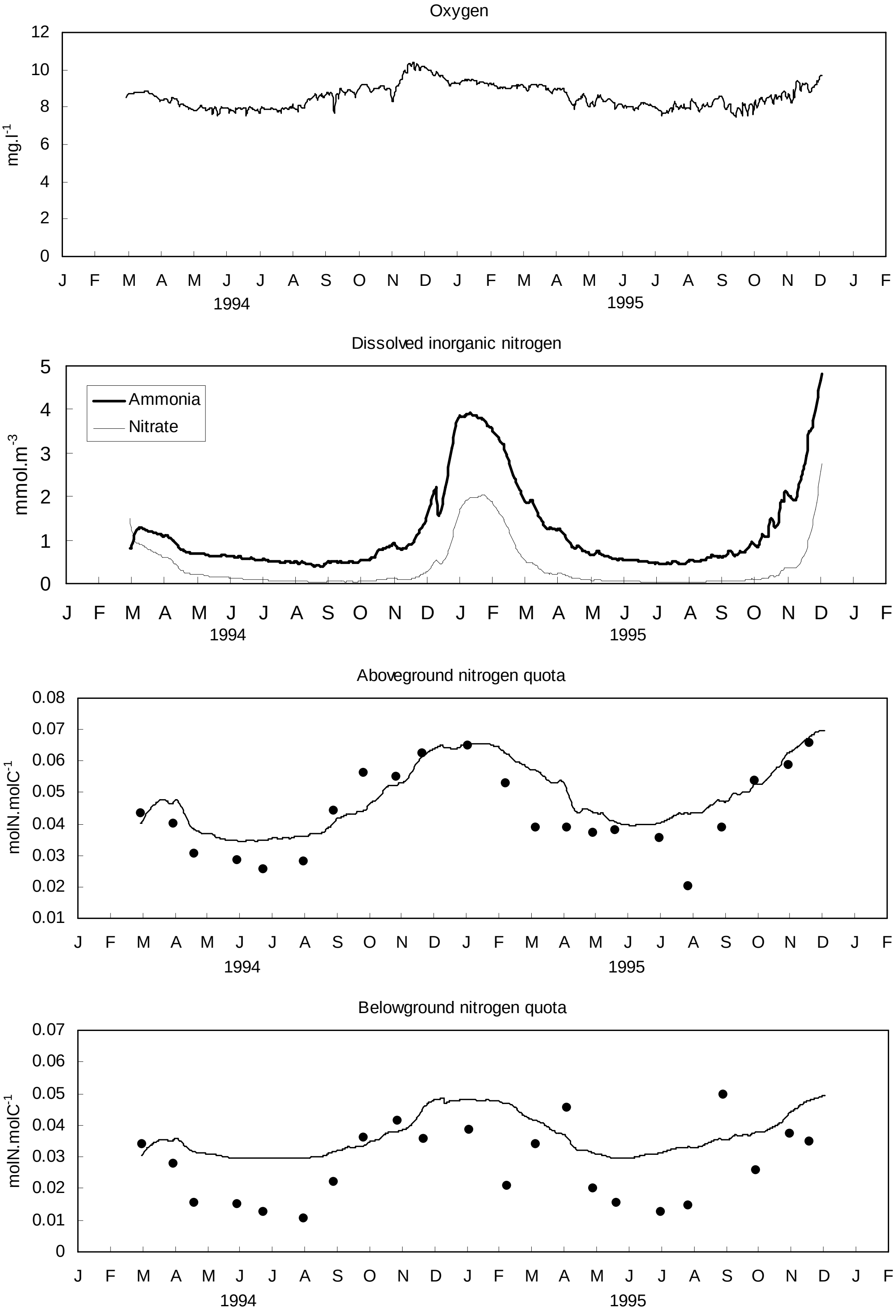


Figure 5. Simulated (black lines) and observed (black points) values for oxygen (water box), dissolved inorganic nitrogen (water box) and seagrass nitrogen quotas during years 1994 and 1995. Measured data are from Laugier (1998), standard errors were not available.

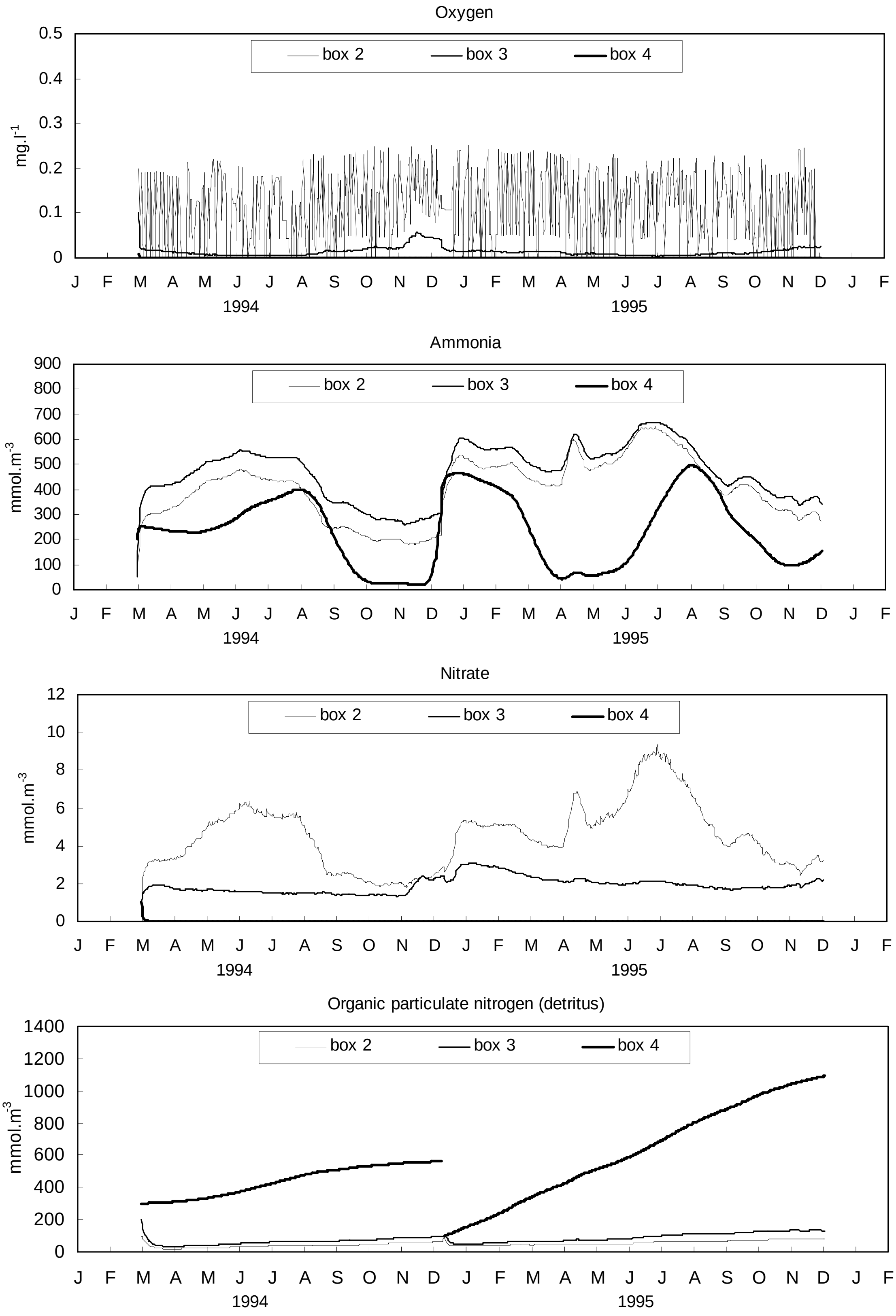


Figure 6. Simulated values for oxygen, dissolved inorganic nitrogen and detritus during year 1994 and 1995. Results are presented for the three sediment boxes: box 2 (0-0.5 cm); box 3 (0.5-2 cm); box 4 (2-40 cm).

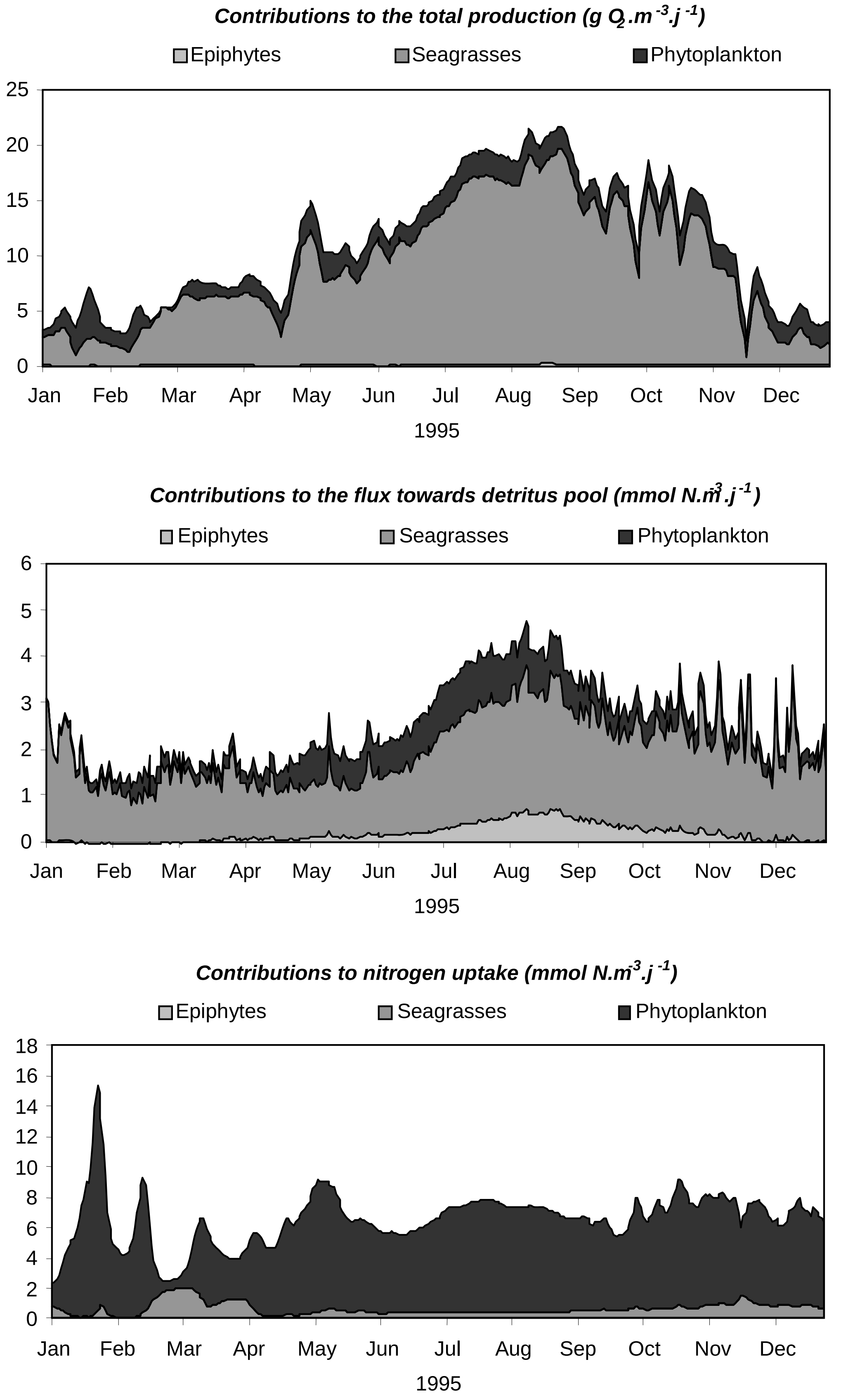


Figure 7. Simulated contributions (year 1995) of epiphytes, seagrasses and phytoplankton to total production, fluxes towards the detritus pool and nitrogen uptake in the water column.