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A model of the seasonal dynamics of biomass and production of the seagrass *Posidonia oceanica* in the Bay of Calvi (Northwestern Mediterranean)

Khalid Elkalay [a,*], Constantin Frangoulis [a], Nikos Skliris [b], Anne Goffart [a], Sylvie Gobert [c], Gilles Lepoint [c], Jean-Henri Hecq [a]

[a] *Ecohydrodynamics, University of Liège, Institute of Physics (B5), Sart Tilman, B4000 Liège, Belgium*
[b] *Department of Meterology, Oceanography Group, University of Athens, Athens, Greece*
[c] *Oceanology, University of Liège, Sart Tilman (B6), B4000 Liège, Belgium*

Abstract

Modelling of seagrasses can be an effective tool to assess factors regulating their growth. Growth and production model of *Posidonia oceanica*, the dominant submerged aquatic macrophyte occurring in the Bay of Calvi (Corsica, Ligurian Sea, Northwestern (NW) Mediterranean) was developed. The state variables are the above- and below-ground biomass of *P. oceanica*, the epiphyte biomass, and the internal nitrogen concentration of the whole plant. Light intensity and water temperature are the forcing variables. The model reproduces successfully seasonal growth and production for each variable at various depths (10, 20 and 30 m). The model can simulate also a number of consecutive years. Sensitivity analysis of model's parameters showed that the maximum nitrogen quota n_{max} rate is the most sensitive parameter in this model. The results simulations imply that light intensity is one of the most important abiotic factors, the diminution of which can cause an important reduction in seagrass density.
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1. Introduction

Seagrass meadows are found in many coastal areas around the world. They help the stabilisation of sediments, provide nursery habitats for fish (Orth and Van Montfrans, 1984), contribute significantly to the primary production, and play an important role in the nutrient budget of the coastal marine ecosystems (Oshima et al., 1999). They can take nutrients both through below- and above-ground biomass, and can

grow under low nutrient concentrations (Iizumi and Hattori, 1982). The presence of large amounts of seagrass influences nutrient cycling.

Posidonia oceanica meadows extend from near the surface down to 40 m depth (Bay, 1984). Knowledge of the *P. oceanica* life cycle observed in the Bay of Calvi (Bay, 1984; Gobert et al., 1995) including several aspects of their physiology is well studied (e.g. Alcoverro et al., 1995, 2000; Zupo et al., 1997). As in most marine phanerogams, the leaves of *P. oceanica* support many plant and animal epiphytes, which can reach up 20–30% of the biomass of the leaves (Gobert et al., 1995). The epiphytic community probably plays an important role in the productivity and growth

* Corresponding author. Tel.: +32-4-366-3647;
fax: +32-4-366-2355.
E-mail address: khalid.elkalay@wanadoo.be (K. Elkalay).

patterns of the host plant in terms of competition for available light, energy and nutrients (Mazzella and Ott, 1984; Libes and Boudouresque, 1987; Mazzella et al., 1989, 1992; Pergent et al., 1994; Alcoverro et al., 1997a).

Light and nutrients represent the input of energy and matter for growths, and determine the annual production (Dennison et al., 1987; Duarte, 1990, 1991; Lorenti et al., 1995; Gallegos and Kenworthy, 1996). Therefore, the total annual production is mainly influenced by light and nutrients (Pirc, 1985a,b; Williams and Ruckelshaus, 1983), while the seasonal production pattern is affected by temperature (Zupo et al., 1997). This represents a modulating factor which varies in different bodies of water, and influences the seasonal growth pattern (Buia and Mazzella, 1991; Zupo et al., 1997).

Several works have produced simulation models for seagrass dynamics (Short, 1980; Zimmerman et al., 1987; Bach, 1993; Madden and Kemp, 1996; Bach et al., 1997; Bocci et al., 1997; Coffaro and Sfriso, 1997; Zupo et al., 1997; Elkalay et al., 2000). The majority of the models integrating seagrass are made in lakes (e.g. Asada and Van Bon, 1999), and most are based on carbon, few are based on nitrogen, they do not make the distinction between nitrate and ammonium, and in general the models are established for *Zostera marina* (e.g. Bach, 1993), and do not take into account the biomass of the rhizomes. To our knowledge for *P. oceanica*, there are only two models: one concerning growth of only above-ground biomass of *Posidonia* based only on the temperature (Zupo et al., 1997) and the other concerning the architecture of this plant (Molinaar et al., 2000). The models available on the seagrasses did not completely meet our needs. In addition to this lack of modelling on the *Posidonia*, it is necessary to note that this plant is different from the other seagrass about growth and physiology. This difference makes difficult the application of a model made on other species and other areas. Consequently, we considered it necessary to develop our model. The model of *P. oceanica* presented here fills a gap in existing models in that it is a whole-plant approach; for example, changes in below-ground biomass are explicitly included.

The major aims of this research are to test preliminary models for *P. oceanica* and epiphytes growth, and to consider the influence of change in forcing functions such as light. The sensitivity of the model to altered light regimes was evaluated by varying the water depth and the average annual water column light attenuation. Effects of water depth were simulated by fixing the depth at 10, 20 and 30 m. Therefore, the attenuation coefficient was varied through fixed values.

The principal aim of the present study was to quantify the development of *P. oceanica* by modelling its growth and biomass. The mathematical model is based on the analysis of the growth process in the Bay of Calvi. This study represents part of larger model to quantify the dynamic relationships between the different compartments of the bay ecosystem, in which a model considering the physiology of the whole plant was required. Development of the model will also help to identify avenues of research important to further development of seagrass models.

2. Model description

The components of the ecosystem are represented by compartments, and interactions are described by linking compartments (Fig. 1). The state variables are: leaf biomass (L) (g DW m^{-2}); below-ground biomass (R) (g DW m^{-2}); nitrogen concentration in seagrass (Q_n) (mg N mg^{-1} DW); and epiphyte biomass (E) (g DW m^{-2}). The major nitrogen sources for seagrasses are NH_{4w}^+ and NO_{3w}^- in the water column for leaves and NH_{4w}^+ in sediment pore water for below-ground biomass (Touchette and Burkholder, 2000).

P. oceanica is exposed to a broad range of physical factors, e.g. temperature and light. The adaptation of the plant to these different environmental conditions should rely on the ability to respond to external constraints, as well as on inner regulating mechanisms (Ott, 1979). The balance between the intrinsic and extrinsic factors is crucial for the success of growth and the stability of the meadow.

Epiphytes were modelled as an autotrophic community dominated by microflora (Wetzel and Neckles, 1986) although, in the Bay of Calvi, epiphyte fauna constitute between 10 and 30% of the total epiphytes biomass (Lepoint et al., 1999). Epiphytes growth is influenced by the same abiotic factors, which influence the seagrass host (e.g. Borum, 1985; Mazzella et al., 1989).
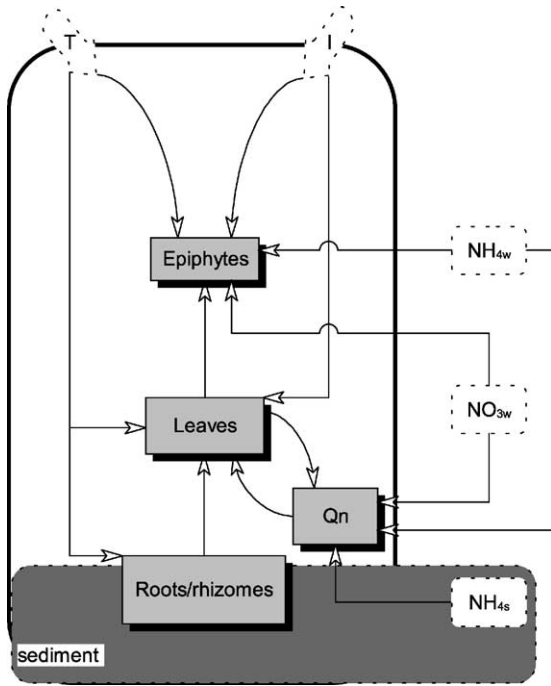
Fig. 1. Diagrammatic representation of interactions between main ecological state variables. (*T*) temperature, (*I*) irradiance, (Q_n) nitrogen concentration in seagrass, (NH_{4w}) ammonium water column, (NO_{3w}) nitrate water column, (NH_{4s}) ammonium in sediment pore water.

In primary producers, the net growth is a result of the balance between productive processes, which incorporate biomass, and degradative processes, which consume biomass. The variation of the above-ground (Eq. (1)), below-ground (Eq. (2)) and epiphytes (Eq. (3)) biomass can be described by the differential equations:

$$\frac{dL}{dt} = (Grol - transl - Resl) \times L + transr \times R \quad (1)$$

$$\frac{dR}{dt} = (Gror - transr - Resr) \times R \quad (2)$$

$$\frac{dE}{dt} = (Groe - Rese) \times E + transl \times L \quad (3)$$

where Grol, Gror and Groe are the specific growth rate coefficients (day^{-1}) for leaves, below-ground biomass and epiphytes, respectively. Resl, Resr and Rese are the specific respiration rate coefficients (day^{-1}) for leaves, below-ground biomass and epiphytes, respec-

tively. transl is the translocation rate from leaves to epiphytes and transr is the translocation rate from below- to above-ground biomass.

The strong seasonality of seagrass growth has been demonstrated to be coupled to seasonal variations in light (e.g. Zimmerman et al., 1994) and temperature (Buia and Mazzella, 1991; Zupo et al., 1997), nutrient availability (Harlin and Thorne-Miller, 1981; Orth, 1977), and space limitation. The leaf, below-ground biomass and epiphyte growth rate coefficients were calculated, respectively, as a fraction of the maximum rate (Eq. (4)):

$$Grol = Groml \times f(I_z) \times f(T) \times f(N) \times f(S) \quad (4)$$

where Groml is the leaf maximum specific gross growth rate coefficient (day^{-1}); and f(·) are the dimensionless functions describing the effects of light (I_z), temperature (*T*), nutrient (*N*) and space (*S*) on growth. The same equation was used for below-ground biomass and epiphytes, with Gromr and Grome the root and epiphyte maximum specific gross growth rate coefficients, respectively. The influence of limiting factors is taken into account in a multiplicative formulation for both communities. The assumption of the multiplicative factors is that light, temperature, nutrients and space act independently on the growth. In models that in principal are similar to the model presented here, the law of multiplicative factors has been successfully applied (e.g. Bach, 1993).

Light availability is the most important factor regulating the depth distribution, abundance and productivity of submerged aquatic macrophytes (Zimmerman et al., 1994). The basic attenuation equation, including extinction due to turbidity and water colour is represented as an exponential decrease in light intensity with depth. The equation of water column light attenuation is given by Beer's Law:

$$I_z = I_0 e^{-k_z \times z} \quad (5)$$

where k_z is water column light attenuation coefficient, I_z is the irradiance at depth *z* (10, 20 and 30 m) within the water column and I_0 is the surface irradiance. The response to light intensity is formulated as:

$$f(I_z) = \frac{I_z}{kel + I_z} \quad (6)$$

where kel is the irradiance half-saturation constant. According to this formulation, growth is a linear

function of light at low intensities, then saturates and asymptotically approaches their maximum at higher intensities. The same equation was used for below-ground biomass and epiphytes, with kee the irradiance half-saturation constant of epiphytes.

Temperature (T) can significantly affect the rates of physiological processes such as photosynthesis and respiration. Effects on the leaf, root and epiphyte growth have been described using:

$$f(T) = \exp\left[-\left(\frac{T - \text{Toptl}}{\text{stl}}\right)^2\right] \tag{7}$$

where Toptl is the leaf optimal growth temperature, and stl is the leaf growth dependence on temperature. The same equation was used for below-ground biomass and epiphytes with Toptr and Topte the optimal growth temperature, and str and ste are the associated growth dependence on temperature, respectively.

The ability of *P. oceanica* to assimilate inorganic *N* varies in response to internal (tissue age and type) and external (environmental) factors (Kraemer et al., 1997). Internal nitrogen content is simulated by considering uptake from water and sediment and the consumption for growth (controlled with a feedback effect). Kinetics nutrient uptake by *P. oceanica*, was assessed using a linear dependence of growth from average nitrogen concentration (N) of the whole plant:

$$f(N) = \frac{N - n_{\min}}{n_{\text{crit}} - n_{\min}} \tag{8}$$

where $n_{\min}$ is the minimum internal nitrogen quota, and n_{crit} is the critical internal nitrogen quota. $f(N)$ is unity when the nitrogen concentration of the *P. oceanica* equals its critical value and decreases linearly to zero as N decreases to the minimum nitrogen concentration.

The shading effect is not introduced in this version of the model. But this factor can be related to space limitation mechanism (S) to control the carrying capacity of the system. Epiphytes reduce the surface available for photosynthesis in *P. oceanica* leaves, and are thus responsible for direct shading. The increase in space limitation parallels an increase in leaf shading by epiphytes. Similarly, self-shading increases as a consequent of the increase in space limitation for leaves. This effect also indirectly controls the rhizome and root compartments that is related to the above-ground

biomass though the translocation process. A space limitation effect has been proposed in other models for above- and below-ground biomass (Verhagen and Nienhuis, 1983). The present model assumes a spatial limitation for epiphytes also.

$$f(S) = 1 - \exp\left[-\left(\frac{L - \text{sl}}{\text{ksl}}\right)^2\right] \tag{9}$$

where sl is the maximum leaf biomass, and ksl is the leaf growth dependence on the space availability. The same equation was used for the below-ground biomass and the epiphytes. sr and se were the maximum biomass with the associated ksr and kse growth dependence on the space availability for roots and epiphytes, respectively.

Libes and Boudouresque (1987) reported the ability of *P. oceanica* to transfer organic compounds between leaves, roots and rhizomes. In the model used here, only transport from below- to above-ground material is considered. The formulation used assumes that transport is proportional to below-ground biomass uptake rate by means of translocation coefficient k_{trans} estimated by model calibration.

$$\text{transr} = k_{\text{trans}} \times \text{Gror} \tag{10}$$

For the translocation from leaves to epiphytes we made a major simplification, considering that part of the nutrients released by leaves are immediately consumed by epiphytes.

The mechanism causing senescence in seagrass, and the factor or factors-controlling dehiscence of old leaves are processes of major importance. The loss of leaf biomass can occur by the action of herbivory and hydrodynamism causing leaf breakage, however, these two factors can prevent retranslocation of nutrients (internal recycling) (Romero et al., 1998). From differences found in nitrogen concentrations between living and dead tissue. Mateo and Romero (1997) suggested that important nutrient recycling (50–70%) may be due either to reclamation or to leaching after plant death (Hemminga et al., 1991; Kraemer et al., 1997). According to this important nitrogen economy developed by *P. oceanica*, which decreases the loss of nutrients, we considered respiration as the only permanent mechanism of loss, which is modelled as temperature dependent. The general forms of the

respiration terms used for leaf, root and epiphytes were as follow:

$$\text{Resl} = \text{resl} \times f(T) \qquad (11)$$

where resl is the maximum leaf respiration rate. The same equation was used for below-ground biomass and epiphytes, with resr and rese the below-ground biomass and epiphytes maximum respiration rate, respectively.

The previous studies suggest that both below-ground biomass and leaves play a role in the N nutrition of seagrasses (Alcoverro et al., 2000). We consider one compartment for leaves and below-ground biomass internal nitrogen quota.

$$\frac{dN}{dt} = \text{Upt} - \text{Grol} \times N - \text{Gror} \times N \qquad (12)$$

Its balance is controlled by the uptake (Upt) from water and sediments, and by assimilation in new tissues.

$$\text{Upt} = (\text{uptL} + \text{uptR}) \times \text{fb} \qquad (13)$$

$$\text{uptL} = \text{uptL}_{\text{NH}_4} + \text{uptL}_{\text{NO}_3} \qquad (14)$$

Uptake of water ammonium ($\text{uptL}_{\text{NH}_4}$) and nitrate ($\text{uptL}_{\text{NO}_3}$) by leaves, and the uptake of sediment ammonium by below-ground biomass (uptR) will be assumed to occur in a Michaelis–Menten fashion:

$$\text{uptL}_{\text{NH}_4} = \text{Vml}_{\text{NH}_4} \times \frac{\text{NH}_{4w}}{\text{NH}_{4w} + \text{kl}_{\text{NH}_4}} \qquad (15)$$

$$\text{uptL}_{\text{NO}_3} = \text{Vml}_{\text{NO}_3} \times \frac{\text{NO}_{3w}}{\text{NO}_{3w} + \text{kl}_{\text{NO}_3}} \qquad (16)$$

$$\text{uptR} = \text{Vmr}_{\text{NH}_4} \times \frac{\text{NH}_{4s}}{\text{NH}_{4s} + \text{kr}_{\text{NH}_4}} \qquad (17)$$

Vml_{NH_4}, Vml_{NO_3} and Vmr_{NH_4} represent a maximum mass-specific uptake rate for NH_{4w} and NO_{3w} by leaves, and NH_{4s} for below-ground biomass, respectively with the associated Michaelis constants kl_{NH_4}, kl_{NO_3} and kr_{NH_4}.

As usual in phytoplankton and macroalgae, to control the range of internal nitrogen, a feedback effect (fb) is applied to the uptake function.

$$\text{fb}(N) = \frac{n_{\max} - N}{n_{\max} - n_{\min}} \qquad (18)$$

where $n_{\max}$ and $n_{\min}$ are the maximum and the minimum nitrogen quota.

The nutrient limitation used in epiphyte growth defined by Michaelis–Menten function:

$$f(\text{Ne}) = \frac{\text{NH}_{4w} + \text{NO}_{3w}}{\text{NH}_{4w} + \text{NO}_{3w} + \text{kn}} \qquad (19)$$

$f(\text{Ne})$ is the epiphyte limitation coefficient by nitrogen and kn is the epiphyte half nitrogen saturation constant.

The values of the parameters have been set in the ranges reported in the literature. Some values are found from local laboratory or in situ experiments, and when no information was available the values were fixed by calibration within the literature range. The selected values of parameters used in this model are reported in Table 1. The system of differential equations has been implemented in Fortran and integrated with a Runge–Kutta fourth order routine with a daily time step.

3. Results and discussion

The versatility of the model allows to perform different simulation experiments. In this paper, part of the results are presented as an example of how insights can be derived from this model.

3.1. Temperature and irradiance

Fig. 2a shows the simulated and observed temperature values, considered the same at all depths. Fig. 2b gives the simulated and observed irradiance at the surface and at 10 m in the water column. The model also calculates the irradiance value at 20 and 30 m (not shown). Comparison of the model predictions with in situ measurements shows a good accordance.

3.2. Leaves and epiphytes biomass

Baseline leaf and epiphyte biomasses in the model were set to the approximate conditions in the Bay of Calvi during 1993 (Gobert et al., 1995). The maximum standing stocks for leaf biomass occurred in summer with 700, 550 and 200 g DW m^{-2} for 10, 20 and 30 m, respectively (Fig. 3a). Maximum simulated epiphyte biomass was 160, 95 and 40 g DW m^{-2} for 10, 20 and 30 m, respectively (Fig. 3b). At 10 m leaf and epiphyte growth typically begins in April, peaks in

Table 1
The parameters used in the *P. oceanica* growth model

Name	Symbol	Value	Unit	Reference
Leaf maximum specific growth rate	Groml	0.012	day^{-1}	1
Root maximum specific growth rate	Gromr	0.0115	day^{-1}	1
Epiphyte maximum specific growth rate	Grome	0.065	day^{-1}	1
Translocation rate from leaves to epiphytes	transl	0.005	day^{-1}	1
Water column light attenuation coefficient	k_z	0.058	m^{-1}	2
Irradiance half-saturation constant for leaf	kel	225	$\mu E\, m^{-2}\, s^{-1}$	3
Irradiance half-saturation constant for epiphyte	Kee	90	$\mu E\, m^{-2}\, s^{-1}$	3
Leaf optimal growth temperature	Toptl	20	°C	4
Root optimal growth temperature	Toptr	20	°C	4
Epiphyte optimal growth temperature	Topte	15.5	°C	1
Leaf growth dependence on temperature	stl	3.6	°C	5
Root growth dependence on temperature	str	3.6	°C	5
Epiphytes growth dependence on temperature	ste	2.6	°C	1
Posidonia minimum internal nitrogen quota	n_{min}	4.28	$mg\,N\,g^{-1}\,DW$	1
Posidonia critical internal nitrogen quota	n_{crit}	7.5	$mg\,N\,g^{-1}\,DW$	1
Maximum leaf biomass	sl	750	$g\,DW\,m^{-2}$	6
Maximum root biomass	sr	3038	$g\,DW\,m^{-2}$	7
Maximum epiphyte biomass	se	225	$g\,DW\,m^{-2}$	6
Leaf growth dependence on the space	ksl	5	$g\,DW\,m^{-2}$	5
Root growth dependence on the space	ksr	3	$g\,DW\,m^{-2}$	1
Epiphyte growth dependence on the space	kse	2	$g\,DW\,m^{-2}$	1
Means of translocation coefficient	k_{trans}	0.2	day^{-1}	1
Leaf respiration rate	Resl	0.0038	day^{-1}	8
Root respiration rate	Resr	0.0041	day^{-1}	8
Epiphyte respiration rate	Rese	0.0047	day^{-1}	1
Leaf maximum specific uptake rate for NH$_4$	Vml_{NH_4}	0.2×10^{-3}	$g\,N\,g^{-1}\,N\,h^{-1}$	7
Leaf Michaelis constants for NH$_4$	kl_{NH_4}	0.021×10^{-3}	$g\,N\,l^{-1}$	7
Leaf maximum mass-specific uptake rate for NO$_3$	Vml_{NO_3}	0.2×10^{-3}	$g\,N\,g^{-1}\,N\,h^{-1}$	7
Leaf Michaelis constants for NO$_3$	kl_{NO_3}	0.0301×10^{-3}	$g\,N\,l^{-1}$	7
Root maximum mass-specific uptake rate for NH$_4$	Vmr_{NH_4}	1.3×10^{-3}	$g\,N\,g^{-1}\,N\,h^{-1}$	7
Root Michaelis constants for NH$_4$	kr_{NH_4}	0.149×10^{-3}	$g\,N\,l^{-1}$	7
Leaf maximum nitrogen quota	n_{max}	11.003	$mg\,N\,g^{-1}\,DW$	1
Epiphyte Michaelis constants for nitrogen	kn	6.1	μM	1

(1) Calibration; (2) Dauby (1985); (3) Madden and Kemp (1996); (4) Bulthuis (1987); (5) Bocci et al. (1997); (6) Gobert (1993); (7) Lepoint (2001); (8) Marsh et al. (1986).

June, and declines from early July. The biomass at 20 and 30 m diminished compared to 10 m, and the peak for each variable occurred approximately 1 month and 1.5 months later, respectively than the peaking time at 10 m. This suggests that the relative importance of biomass changes not only temporally but also as a function of depth within the community. The decrease of biomass according to depth is correlated with the low Leaf Area Index (LAI) (Gobert, 1993; Zupo et al., 1997), the low light compensation point, and high ratio of above- to below-ground biomass in deep water. The magnitude and the timing of epiphyte (except in 1993 at 10 m) and leaf biomass peak in the model closely reproduced field measurements (Fig. 3a

and b). In baseline runs, simulated dynamics for leaves and epiphyte biomass corresponded well with the data from the three depths (10, 20 and 30 m).

The values of the leaves biomasses of 1993 are comparable with those of 1997, 1998 and 1999 (Lepoint, 2001). And the model reproduce well the leaves biomass in 1975 and 1976 (Bay, 1984) (Fig. 4). In general, the leaf biomass is comparable with the literature data of other Mediterranean areas (Duarte and Chiscano, 1999). However, it should be noted that it is the density rather than the biomass, which informs about the health of the bed.

The epiphyte biomasses are also comparable with those of 1997–1999 (Lepoint et al., 1999). This is
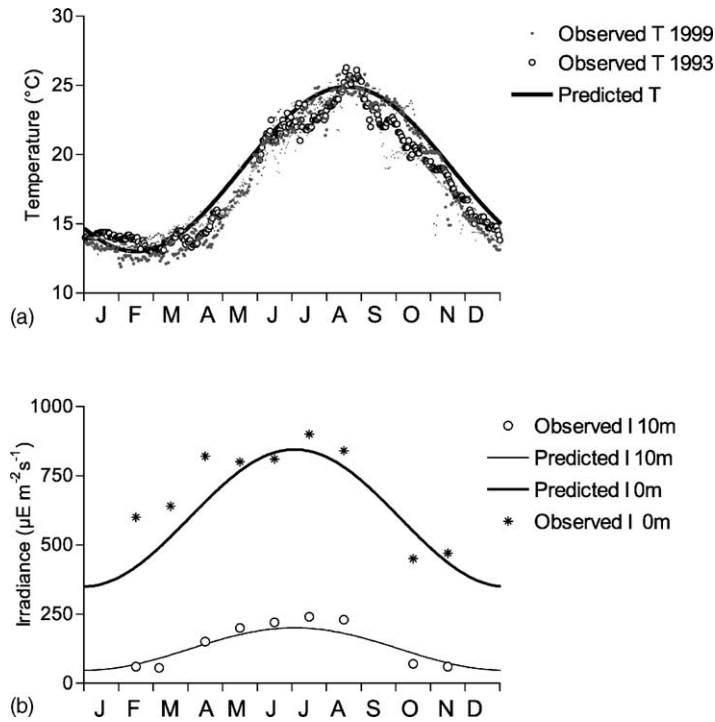
Fig. 2. Simulated and observed values of temperature (a) and irradiance (b).
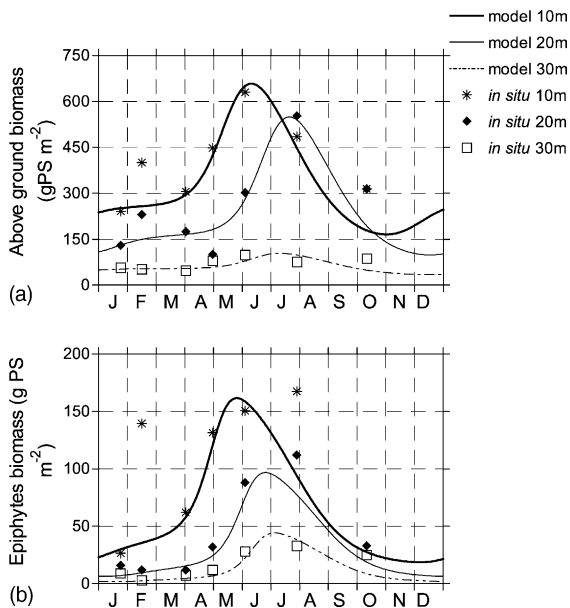

Fig. 3. Simulated (lines) and measured values of 1993 (points) for leaves (a), epiphytes (b) biomass at 10, 20 and 30 m, respectively.

consistent with measurements in other Mediterranean zones (Mazzella and Ott, 1984; Alcoverro et al., 1997a; Modigh et al., 1998), which is in agreement with the leaf biomasses.

The Fig. 5 presents the relationship between the observed and the simulated data. The correlation between the measured and simulated of leaf and epiphyte biomass values is in general good except for 30 m which is low and can be attributed to the influence of other so far unconsidered biological and environmental factors. This difference can also be explained by the fact that the model is more adapted for shallower depth, since the parameters are in general measured at low depths. Even if measurements are performed for each depth, the accuracy of the measured parameters would probably decrease with depth, due to the difficulty involved in sample collection and manipulation in deep water.

Fig. 6 presents the contribution of the epiphytes biomass to the total above-ground biomass. At 10, 20 and 30 m this contribution varies during the year with minima of 10, 5 and 5% and the maxima ones of
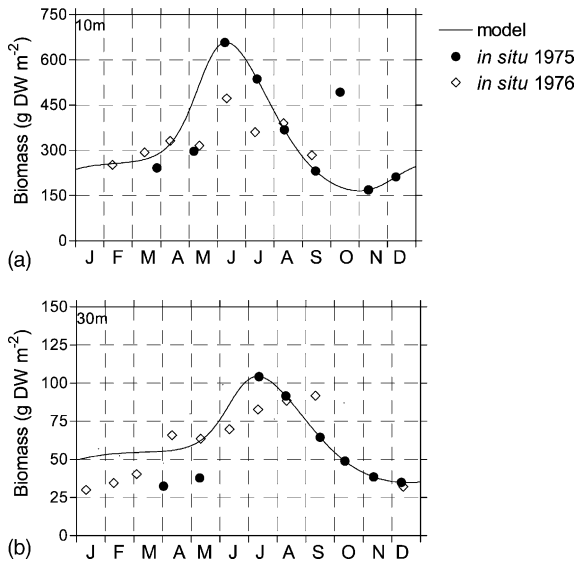
(a)

(b)

Fig. 4. Simulated (lines) and measured leaf biomass values of 1975 and 1976 (points) at 10 m (a) and 30 m (b).

25, 25 and 30%, respectively. Belkhiria (1992) reports that the epiphytes biomasses measured at 10 m in the Bay of Calvi contribute with 5% in winter to the total above-ground biomass and more than 25% in summer. Gobert (1993), in the same bed, indicated contributions of 10% in winter and 25% in summer which are in conformity with our simulations. These values indicate that the epiphytic community is characterised by an important contribution to the biomass of the *Posidonia* beds. In other areas, the estimated value of epiphytes contribution to above-ground biomass, is more variable, from 18 to 56% for the various seagrass bed (Mesureur, 1981).

Light is, of course an important factor for any plant, but this study demonstrated once again that *Posidonia* is such a stable and auto regulating plant that it is able to overcome the simple relationship between light and growth. The chloroplasts in *P. oceanica* leaves are densely packed in the monolayered epidermis and are able to collect light immediately at the leaf surface. This represents the adaptation of *P. oceanica* to the aquatic environment and low light conditions (Mariani-Colombo et al., 1983), as opposed to terrestrial plants. It stores the product of photosynthesis in a manner not allowing the immediate identification of the photosynthesis in terms of leaf elongation.

However, given the relationship between temperature and light, this type of model may be an alternative to the temperature one: while the real peaks of production cannot be seen, but the average yearly production may be calculated using an alternative system.

3.3. Below-ground biomass

For the below ground biomass there are less measurements than the leave one. We, therefore, limited the simulation to the below ground biomass at 10 m because we haven't measurements at 20 and 30 m. The simulation at 10 m (Fig. 7) indicated that the below-ground biomass shows very small seasonal changes (around $3000\,g\,DW\,m^{-2}$), in contrast to the above-ground biomass, which is confirmed by Lepoint (2001). The below-ground biomass simulated in this work can constitute up to the double of those evoked for other areas (Duarte and Chiscano, 1999). The fact that the below-ground biomasses in this work are higher constitutes an essential ecological aspect of the *Posidonia* of the Bay of Calvi, because they play a paramount role in the incorporation of the nutrients necessary to the plant (Touchette and Burkholder, 2000). The weak nutrient concentration in the sediment pore water of the Bay of Calvi compared to the other areas (Lepoint, 2001), is correlated with the importance of the below-ground biomass. This importance constitutes an advantage in the oligotrophic zone making it possible to benefit from the sediments nutrients, inaccessible to the other producers (Hemminga, 1998).

P. oceanica, like the seagrasses species of the genera *Amphibolis* and *Phyllospadix*, tends to develop very high above-ground (about $500\,g\,DW\,m^{-2}$ or higher) biomass. On the other hand, below-ground biomass developed by *Posidonia* exceeds by far (about $1000\,g\,DW\,m^{-2}$ or higher) those developed by other seagrasses (Duarte and Chiscano, 1999). Other species of the genera *Zostera*, *Halophila* and *Halodle*, are particularly characterised by a high biomass of the above-ground relative to the below-ground biomass (Duarte and Chiscano, 1999).

The *P. oceanica* average simulated ratio of below- to above-ground biomass vary between 4.5 and 19.3. The minimal value correspond to the experimental one proposed by Lepoint et al. (in press), which
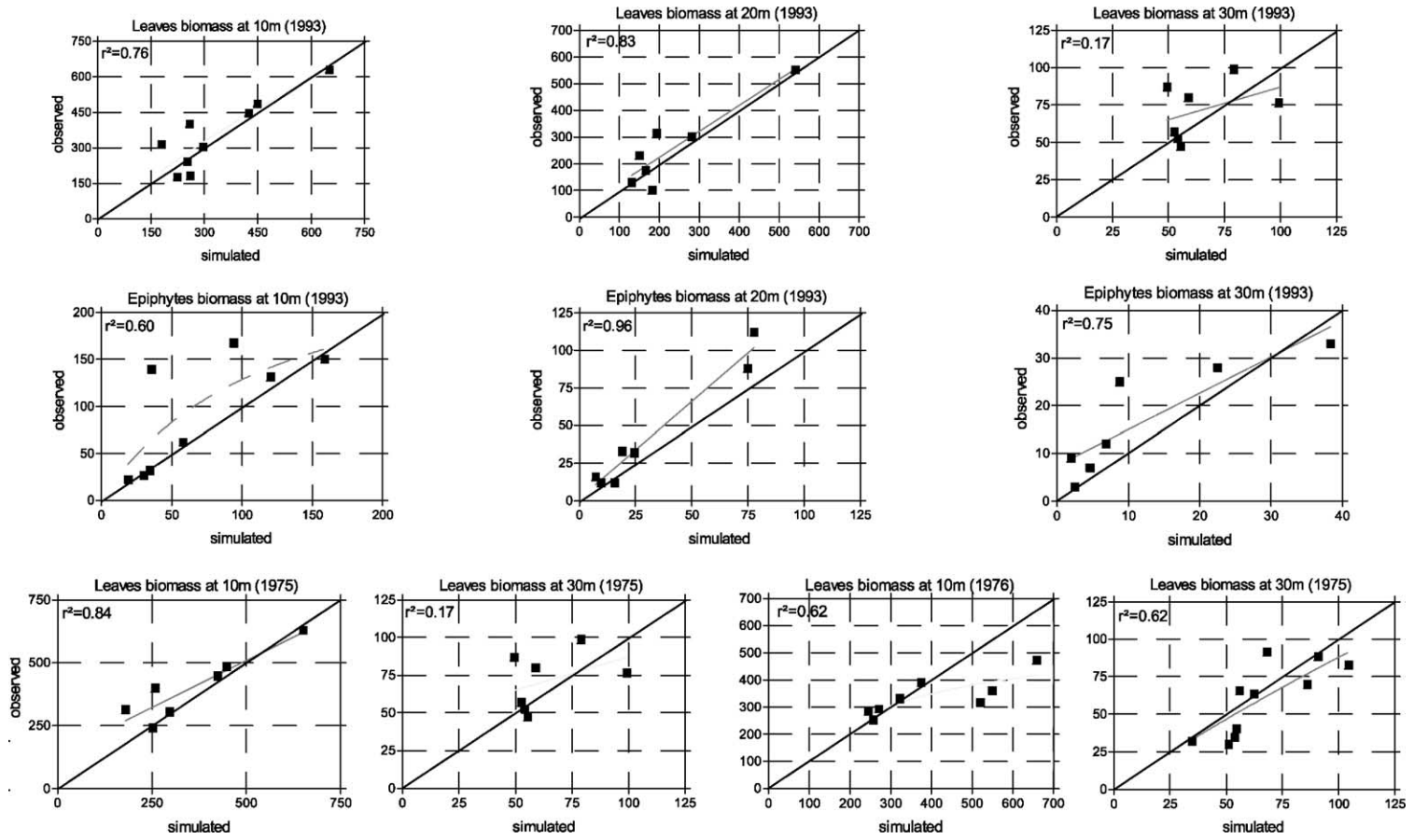
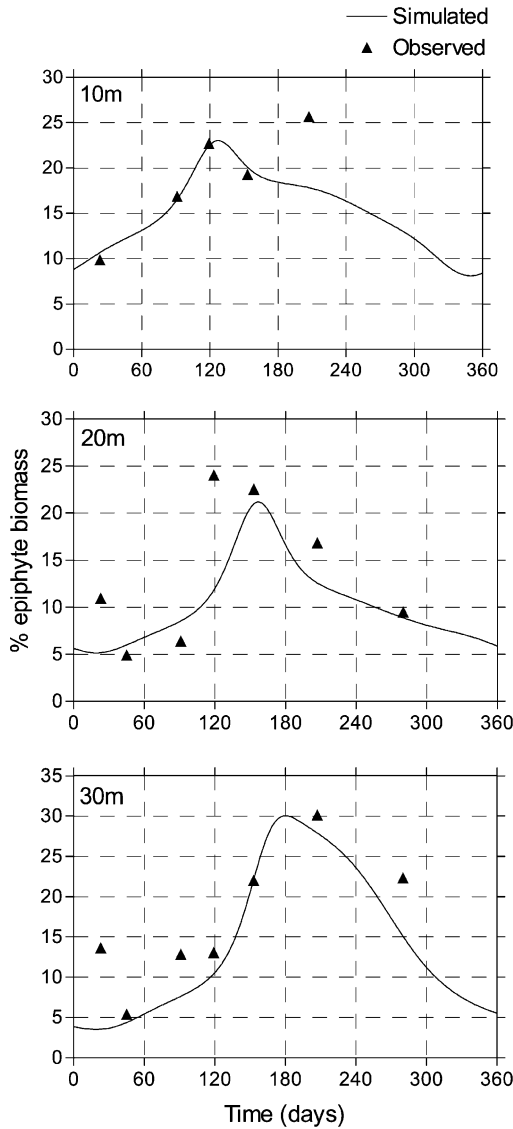Fig. 5. Leaves and epiphytes biomass ($g\,DW\,m^{-2}$) observed vs. simulated data.

Fig. 6. Simulated (line) and measured values (points) of the percentage contributions of the contribution of the epiphytes biomass to the above-ground biomass.

was calculated with maximal value of above-ground biomass. The massive below-ground biomass can play a major role in nutrient economy by means of storage and retranslocation (Alcoverro et al., 1997b). The decrease of the below-ground biomass with depth is related to the decrease in that above-ground biomass. Therefore, there is a significant tendency for the ratio
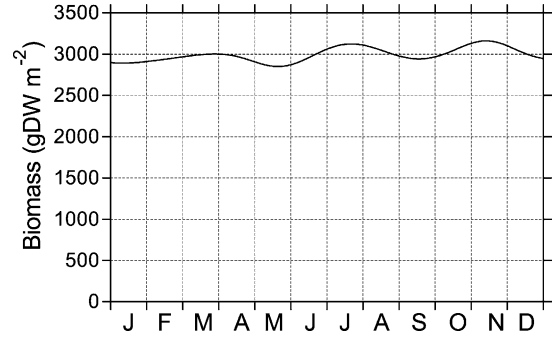
Fig. 7. Simulated values of the *Posidonia* below-ground biomass.

of above-ground to below-ground biomass to decline with increasing depth.

3.4. Internal nitrogen concentration

The simulation of the annual evolution of the internal nitrogen concentration presents (Fig. 8) a good fit with measurements of 1997 (Lepoint, 2001), which is characterised by a weak variation during the year. As far as the importance of the below-ground biomass is concerned more than 50% of internal nitrogen that is contained in the plant is in this compartment, therefore it is not surprising that the evolution of the internal nitrogen follows the below-ground biomass. It is important to indicate that the internal nitrogen concentration is characterised by a slow variation, which can be related to the capacity of the posidonie to use several strategies to satisfy his nutrients need (e.g. take the nutrients by different parts of the plant, nutrients reclamation from dead leaves . . .).
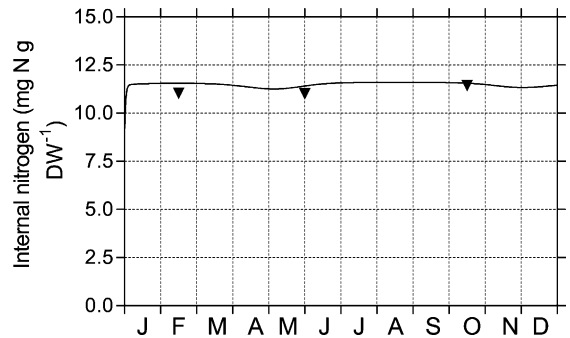

Fig. 8. Simulated (line) and measured value (points) of the *Posidonia* internal nitrogen quota.

3.5. Above- and below-ground production

In our knowledge for all seagrasses the above-and below-ground productions were estimated in a small fraction as the below-ground biomass. To determine the production of above-ground we used the relationships (Eq. (20)) between the production and biomass proposed by Duarte and Chiscano (1999). For below-ground production data were estimated using a relationship between above- and below-ground productions (Eq. (21))

Above-ground production

$$= 0.1 \times \text{above-ground biomass}^{(0.64 \pm 0.06)} \quad (20)$$

Above-ground production

$$= 2.81 \times \text{below-ground production}^{(0.5 \pm 0.07)} \quad (21)$$

In the relationships (20) and (21) the values used for the power is 0.64 and 0.5, respectively. These relationships were derived from 30 species of seagrass (including *P. oceanica*), which represent more than half of the global seagrass species.

In our model, we observed that the production reaches a maximum of 2.45, 1.54 and 0.41 g DW m^{-2} day^{-1} for above-ground, and 0.29, 0.28 and 0.268 g DW m^{-2} day^{-1} at 10, 20 and 30 m, respectively. The average production rate calculated over a 12-month period: 1.59, 0.90 and 0.29 g DW m^{-2} day^{-1} for above-ground and 0.28, 0.27 and 0.264 g DW m^{-2} day^{-1} for below-ground at 10, 20 and 30 m, respectively. Bay (1984) has found in the of Bay of Calvi average values of the leaves production of 1.632 and 0.261 g DW m^{-2} J^{-1}, respectively at 10 and 30 m, which are comparable with values found in this work. The model showed that 84% of the *P. oceanica* total production may be contributed by the above-ground biomass. The production of shoot levels of deep-water *P. oceanica* meadows is lower than values obtained in shallow-water (Dalla Via et al., 1998). In fact, the shallow-water meadows are receiving higher levels of irradiance compared to the deep-water meadows. A reduction in shoot density caused a reduction in self-shading by *P. oceanica* leaves at the deep site, and light conditions within the stand became, therefore, similar at both sites (Dalla Via et al., 1998).

The relatively high production of these seagrass meadows is ecologically significant. However, the average biomass and primary production of phytoplankton is 9.2 and 0.35 g DW m^{-2} day^{-1}, respectively (Duarte and Chiscano, 1999). In particular, in the study area where the local water column primary production rate is very low (Goffart, 1992; Dauby and Bouquegneau, submitted).

A previous study (Romero et al., 1998) demonstrated that the rank of leaves in the shoot is important
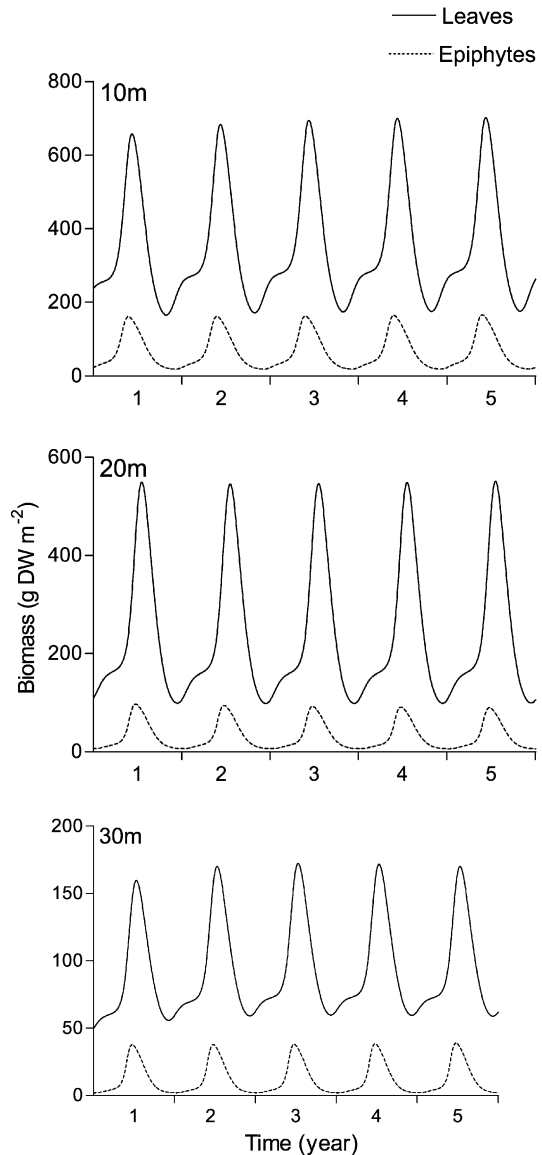

Fig. 9. Simulated epiphytes and leaves biomass for 5 years at 10, 20 and 30 m.

for growth evaluation of *P. oceanica*. In fact, the youngest leaves showed the highest growth rates and, in particular, the growth of leaves of second and third rank is correlated to the growth of the whole shoot, regardless of depth (Kraemer et al., 1997; Zupo et al., 1997; Dauby and Bouquegneau, submitted). The density and leaf assemblage of the shoot (number of leaves by shoot, age of each leaf, etc.) can influence the growth mechanism. Therefore, environmental factors influence *P. oceanica* growth dynamics, although internal mechanisms regulate growth as demonstrated previously (Ott, 1979).

When expressed as relative growth rate (by dividing production by biomass), the value of growth rate was $47 \times 10^{-4}\,\mathrm{day}^{-1}$ for above ground and $1.21 \times 10^{-4}\,\mathrm{day}^{-1}$ for below ground. Thus, the growth rate is more important for leaf than for below ground.

In *P. oceanica* the turn-over of above-ground tissue is faster than that of below-ground tissue. The rela-

tively slower turnover of the below-ground organs of seagrasses indicates a greater capacity for the long-term accumulation of material. At the greater depths, lower irradiance levels are likely to result in lower production levels, hence a slower turn-over. This capacity can be explained by the long-lived seagrass *P. oceanica* compared to other species (Romero et al., 1994). The much slower turn-over of *P. oceanica* in comparison to other species is indicative of the climax species (Erftemeijer and Stapel, 1999), while the higher turn-over is indicative of the opportunistic species.

3.6. Long-term simulation

Since annual predictions agreed with available data, analyses of long-term stability can be done with temporal discrepancy. Using the same values of parameters, initial conditions and forcing functions as the first model, a long-term simulation (over 5 years) was
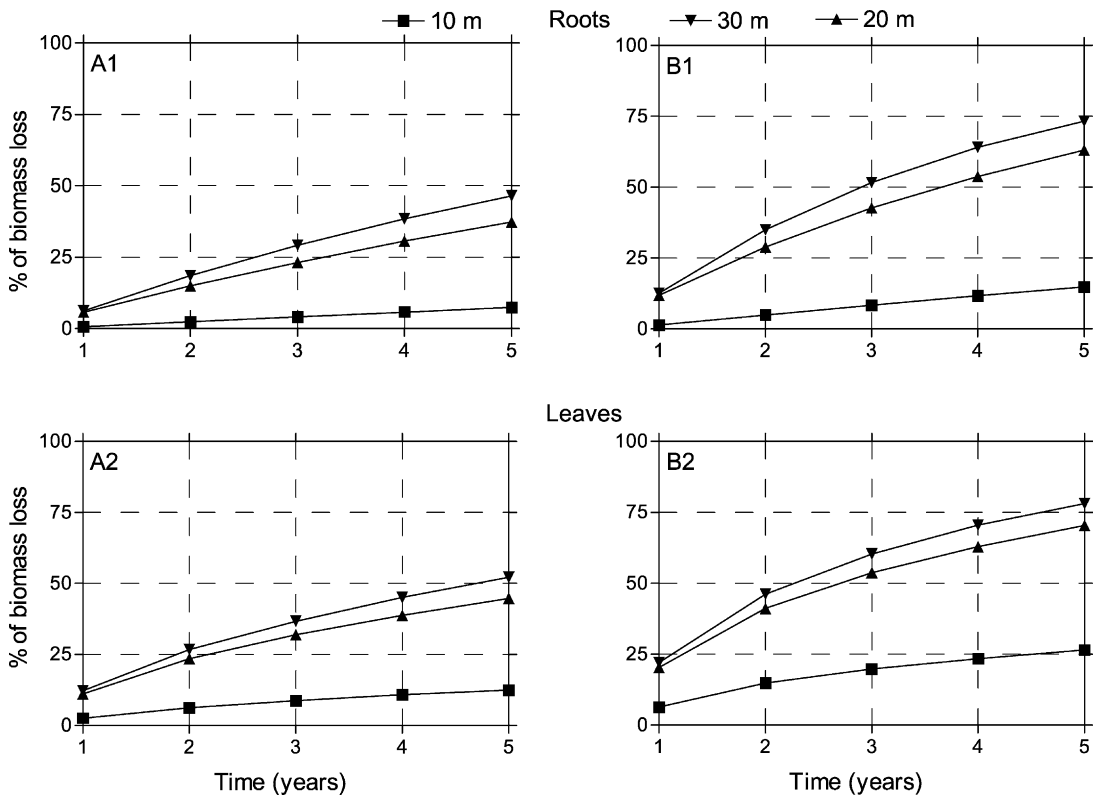

Fig. 10. Calculated percent of biomass loss as a function of water depth and time for 10% (A) and 20% (B) augmentation of extinction coefficient.

performed. The analysis of these results (Fig. 9) shows a conservation of the leaves, and epiphytes biomass at each depth for the 5 years, though in reality, biomass varies between years. The invariability in the model can be explained by the fact that temperature, light and initial conditions were the same for all years. Therefore, to study the evolution of the different variables over a long period, it is necessary to have a good representation of the variability of the forcing variables and of the initial conditions.

3.7. Change in the water irradiance

Several studies confirmed the evident long-term decrease of seagrass biomass in general (Short and Neckles, 1999) and of *P. oceanica* in particular (Pergent et al., 1994; Marba et al., 1996; Ruiz and Romero, 2001). The reduction in the light which reaches the bottom may be one of the main factors responsible for the biomass decrease (Hemminga, 1998). Submarine irradiance (as photosynthetically active radiation or PAR) is attenuated with depth in the water column due to absorption, and scattering by water itself, dissolved organic compounds, and suspended particles. The suspended particles concentration is by far the most important factor and variable parameter affecting irradiance attenuation of light in several bays in the coastal NW Mediterranean (Dauby et al., 1995; Duarte et al., 1998). The shading effect is a combination of the actual concentration of suspended particles and of the variation of this concentration in time.

We performed several simulations in order to evaluate the influence of light intensity changes which can be related to one or some of the factors indicated before. To this aim, we created an artificial disturbance by increasing the attenuation coefficient by 10 and 20%. Then, we evaluated at each depth the percentage of mean annual biomass, losses for above- and below-ground biomass which is compared to the reference state. The percentage of the biomass loss increases with time and depth, according to the disturbance augmentation and according to the variables. Below-ground biomass loss varied between 1% (Fig. 10A1) in the first year for the 10% disturbance and 73% for the 20% disturbance (Fig. 10B1) in the fifth year. Leaf biomass loss varied between 3% (Fig. 10A2) in the first year for the 10% disturbance and the loss reached 78% (Fig. 10B2) for the

20% disturbance for the fifth year. We noticed that the loss of leaf biomass is higher than losses in the below-ground biomass. The impact of light perturbation is less important in the below-ground biomasses. However, few studies have examined the cascade effects of light reduction involved in the below-ground organs of seagrasses (Hemminga, 1998).
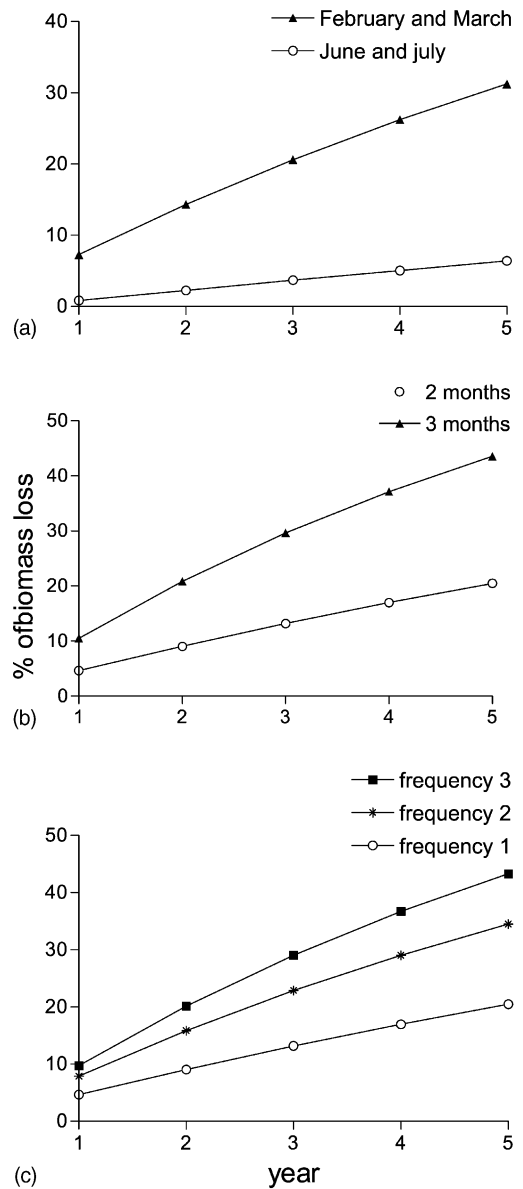

Fig. 11. Percent of epiphytes biomass loss for different scenario period (a), duration (b) and frequency (c) of the perturbation.

To show the relative importance of period, frequency and duration of the attenuation of light we analysed the biomass of epiphytes at 10 m. To test the importance related to the period of the disturbance, we have applied the same increase (20%) in the attenuation coefficient at different periods. First at the beginning of the year (February and March) and subsequently during June and July. Fig. 10A shows that the mean annual biomass loss during the first period of disturbance is about 31% in the fifth year, which is higher than the loss in the second case (6%). This can be explained by the fact that at the beginning of the year *P. oceanica* assimilates nitrogen necessary for growth. Alcoverro et al. (1995) indicated that the *P. oceanica* tissue have high nutrient concentrations in winter which decline subsequently with increasing plant growth towards summer.

We tested two different durations of the disturbance, namely 2 and 3 months at the beginning of the year with the same increase (20%). We noticed that the biomass loss increased with increased duration with a loss of about 20 and 44%, respectively, for the first and second durations (Fig. 11b). In a plant such as *P. oceanica*, with an economic complex growth mechanism a short-term perturbation does not suffice to induce a significant loss.

We have also tested the importance of the frequency of the disturbance, using one, two and three times the same perturbation (20%). The losses are about 20, 35 and 43%, respectively (Fig. 11c). Thus, the simulation model indicates that losses in biomass positively correlate with frequency. Our results are consistent with those of Bach et al. (1997) which have already shown experimentally and by model in a *Z. marina* bed the importance of time, duration, intensity and frequency of the augmentation of the attenuation coefficients. The simulations indicated extreme sensitivity to changes in the average water column light attenuation. We can conclude that it is possible that gradual changes in these factors over the past decades be partially or totally responsible for the recent reduction in the *P. oceanica* in the Bay of Calvi and in other Mediterranean zones.

3.8. Sensitivity analysis

A sensitivity analysis of most parameters was done to investigate their influence on the state variables of the model. Sensitivity has been computed as (Chapelle et al., 2000):

$$\text{Sens} = \frac{1}{n} \sum_{i=1}^{n} \frac{|Y - Yx|}{Y} \tag{22}$$

where Y is the state variable at the standard run, Yx is the new variable value corresponding to the new parameter value, n is the simulated number of days (365).

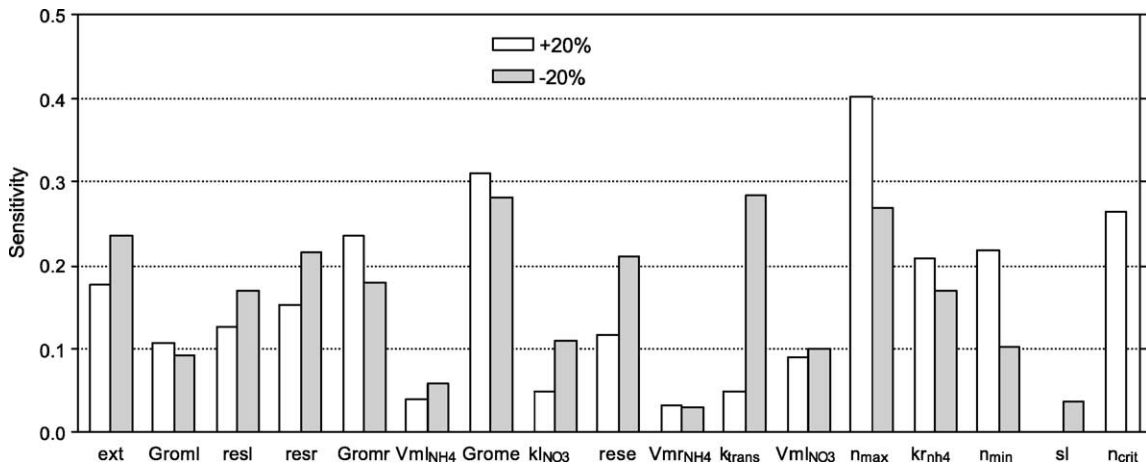To obtain an indication of the sensitivity of the model results to the parameters, setting we

Fig. 12. Sensitivity analysis results of parameters.

subsequently increased and decreased each of the main model parameters by 20%. Only important sensitivity of the above-ground, below-ground and epiphyte biomass for each parameter is represented in the Fig. 12. The model results are considerably sensitive (Sens greater than 0.25) to variation in the following parameters: ext, Grome, k_{trans}, n_{max} and n_{crit}. Other parameters such as Vml_{NH_4}, kl_{NO_3}, Vmr_{NH_4} and sl have only minor effects on the results.

This sensitivity can be explained by the major hypothesis assumed in this model for constant values for biological parameters. Normally, in ecosystems, rates of biological processes are not constant in time and with depth. However, the modeller has, in general only the possibility of choosing some mean values for the parameters. It may be a better approach to make a model with a flexible set of parameters, or at least have a specific parameter for each range of depth (10, 20 and 30 m). In this ecological model, it is not possible to reflect every detail of the system, and it is only desirable to simulate whole system characteristics. Experimental data restricting parameter uncertainty would give an important quality improvement to this simulation. Thus, particular care must be taken when selecting these coefficients.

4. Conclusion

In this study, the first steps to model *P. oceanica* growth and production in the Bay of Calvi have been developed. These processes are governed by environmental factors such as temperature and irradiance. For the investigated Bay of Calvi area it seems reasonable to conclude that the model includes the most important factors controlling seagrass growth.

The available field data showed that this model provides a reasonable representation of the seasonal cycle, at least during the period when samples are available. The completion of a seasonal sampling program will allow a more complete analysis. The model indicated successfully the long-term evolution and the effect of shading on the growth. The artificial shading experiments with seagrass clearly demonstrated the importance of reduced light conditions on the density decrease. In the Bay of Calvi, we calculated that minimum light requirements of *P. oceanica*

growth, is 15.7%, of surface irradiance, value which in accordance with the values (between 10 and 16%) proposed by Ruiz and Romero (2001).

This model confirm that *P. oceanica* reacts rapidly to external perturbation in the Mediterranean Sea, which are driven by climatic change (Goffart et al., in press). Due to their sensitivity to shading, seagrasses can be selected as key organisms for feedback monitoring systems. Leaf, below-ground biomass and epiphyte biomass can be chosen as response variables. This work supports the view that simulations can be a powerful tool to develop theoretical frameworks for understanding *P. oceanica* dynamics.

The model indicated also where data were lacking, thereby suggesting directions for future research. For example, better understanding of the internal nitrogen quota of the whole plant and of the nutrient translocation process between leaves and roots will lead to an increased understanding of *P. oceanica* dynamics.

This model considers a whole-plant approach. The dominance of below-ground tissues with respect to total seagrass biomass now is well recognised but seldom considered in physiological or ecological studies. Since below-ground biomass appears to play critical roles in the biogeochemical processes that occur in the sediments, as well as it regulate processes in the overlying water column, it is important to include this component in seagrass models.

This model will be further coupled with a phytoplankton model and other primary producers in order to simulate the competition between benthic and pelagic primary producers. It can be applied as a tool for simulating the effects of various changes in physical, chemical and biological interactions.

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