

Modelling growth of *Ruppia cirrhosa*

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Received 30 November 1998; received in revised form 5 January 2000; accepted 13 April 2000

Abstract

The main objectives of this work were to synthesise information on the autoecology of *Ruppia cirrhosa* Petagna (Grande) in a mathematical model and to use the model to simulate its growth, production and harvest. Model parameters were allowed to vary as a result of acclimation, following experimental data reported in the literature. Biomass data from Santo André lagoon (SW Portugal) were used to calibrate the model. Validation was carried out with independent data sets from Santo André lagoon and from Tancada lagoon (NE Spain). Model simulations show a reasonable agreement with observed data with a similar biomass temporal dynamics and peaks. Self-shading appears to be an important self-regulating mechanism of biomass growth and production. The results obtained predict an annual net primary production of 361 g DW m⁻² well within the estimates based on harvesting techniques (295–589 g DW m⁻²). Model results suggest that controlled harvesting of macrophyte biomass may be carried out without affecting macrophyte real net production, through the reduction of light limitation under the plant canopy. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Macrophyte production; Coastal lagoon; Modelling; *Ruppia cirrhosa*

1. Introduction

Aquatic macrophytes normally represent an important part of primary productivity in shallow waters, particularly in land-locked systems, such as some coastal lagoons (Wetzel, 1975). Some species are able to form dense stands covering wide areas in the lagoons, being very important primary contributors to many food webs, that may include resources used

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by man. Mann (1972) suggests that macrophyte production in shallow waters can be ten times higher than phytoplankton production.

Ruppia cirrhosa Petagna (Grande) is an aquatic angiosperm inhabiting European coastal brackish waters, never found in places with a permanent tidal regime. It is common in large permanent water bodies and in these environments it is the only macrophyte to survive and show healthy growth in salinities above 20 ppt (Verhoeven, 1979). It has an annual life cycle, hibernating as short quiescent leaf-bearing stolons. In spring, it starts a fast vegetative growth, with budding of rhizomes and strongly branching stems colonising the bottom and the water. A few weeks later flowers are induced and fruits are produced. In late autumn vertical stems begin to lose contact with the vegetation mat near the bottom and are gradually decomposed and washed ashore (Verhoeven, 1979; Menéndez and Peñuelas, 1993).

Santo André lagoon is a shallow land-locked coastal system located in the Portuguese Southwest coast (38°05'N; 8°47'W). It receives inflows from six small rivers forming a drainage basin of about 96 km². Its average annual depth is about 1 m, with a maximum of 5 m reached in autumn in certain zones due to freshwater inflows. Marine colonisation develops during about one month when a man-made channel connects the lagoon with the sea in the spring. Low salinity water and sediments are exported through this inlet. After the lagoon is closed by the accumulation of sand, salinity progressively decreases, except in summer, and organic matter accumulates leading to eutrophy and summer dystrophic processes (Cancela da Fonseca et al., 1989). Salinity values oscillate from ca. 35 ppt after the opening to the sea to almost zero at the end of winter.

Macrophyte production can represent an important part of primary production in coastal lagoons. High macrophyte biomasses may contribute to night anoxia during summer, especially in shallow waters during calm weather, when water column stratification is most likely to occur. These biomasses are also an important reservoir of nutrients and their harvest may help to prevent eutrophication and dystrophic crisis.

Lagoon eutrophication and dystrophic crisis could probably be reduced by harvesting macrophytes to remove nutrients and organic matter. This would improve its recreational usage. Macrophyte harvesting for fertiliser has been a traditional activity in Portugal since at least the Middle Ages (Veiga de Oliveira et al., 1975) and may prevent eutrophication in semi-enclosed water bodies (Thornton et al., 1995).

Santo André lagoon is used not only for recreation but also as a fishing ground, and the removal of macrophytes could lead to a reduction in secondary production. One way to evaluate this effect is to develop a mathematical model capable of simulating *R. cirrhosa* biomass dynamics and productivity, as well as macrophyte harvest. Biomass removal may help to decrease intraspecific competition for light, nutrients or space, and thus increase the growth of the remaining biomass.

Macrophyte production can be evaluated by means of harvesting techniques and incubation experiments. The former, based on biomass differences, are a function of time and have important errors proportional to the time lag between two consecutive samplings (Murthy et al., 1986). These methods allow only the estimation of net production. The latter are based on the production and consumption of oxygen or inorganic carbon and are limited to short-time experiments (Vollenweider, 1974). These methods allow the estimation of net and gross production. Once demographic and physiological processes are well known, modelling can be a useful method for estimating primary production as a function of

environmental forcing (Duarte and Ferreira, 1993). Demographic processes (mortality and recruitment) can be studied by sampling and tagging experiments. Physiological processes (photosynthesis and respiration) can be measured in situ or in the laboratory. Modelling can therefore be used as a way to synthesise the results of both the harvest and the incubation techniques.

A central question in ecology, is in regard to the mechanisms which regulate population size (Krebs, 1994). It is common to observe that species develop biomasses until certain asymptotic values that are a result of some negative feedback mechanisms. These mechanisms stabilise species biomass and therefore community structure and function. Environmental factors, whether biotic or abiotic and self-regulating factors have all been proposed as controlling mechanisms in different populations (Krebs, 1994). In the case of *R. cirrhosa* one such mechanism is its annual life cycle. However, the limitation imposed by the life cycle itself is not enough to explain why biomass is not greater than that observed during the growing season. Self-regulating mechanisms have been described for plant species including the self-thinning rule (Westoby, 1984).

For a mathematical model to have stability, feedback mechanisms are also needed. In fact, mathematical models may be used to test the effect of alternative feedbacks in species biomass regulation. If the correct mechanisms are included in the model, it is expected that the model results will mimic reasonably well the observed dynamics. It needs to be recognised however, that a model may predict the right dynamics even if the processes are incorrectly formulated. However, modelling may be a useful way to test the validity of hypotheses regarding the natural regulation of population size.

The objectives of this work are:

- to develop a mathematical model to simulate biomass dynamics and productivity of *R. cirrhosa*;
- to use the model to test the importance of some factors in regulating population size in the studied species;
- to quantify *R. cirrhosa* production;
- to quantify the impact of *R. cirrhosa* harvest on secondary production;
- to evaluate the usefulness of the model with data from other ecosystems.

2. Methods

2.1. Field work

In order to follow biomass dynamics during the years 1996–97 four sampling regimes were carried out in Santo André lagoon (Fig. 1) between August 1996 and February 1997. Five replicate samples were collected at nine different sites in the main water body. A 16 cm diameter cylindrical sampler ‘core’ (Menéndez and Comín, 1989) was sunk up to 20 cm into the sediment in monospecific stands of *R. cirrhosa*. Plants and sediment were sorted from the core through a 5 mm mesh bag and sieved in the water. Samples were frozen (–18°C) until subsequent analysis. Plant material was then separated and dried to constant weight at 105°C. Aliquots were incinerated at 550°C for 3 h to obtain the ash content (Verhoeven, 1980; Menéndez and Comín, 1989). Ash content remained fairly constant during the sampling period (20% DW).

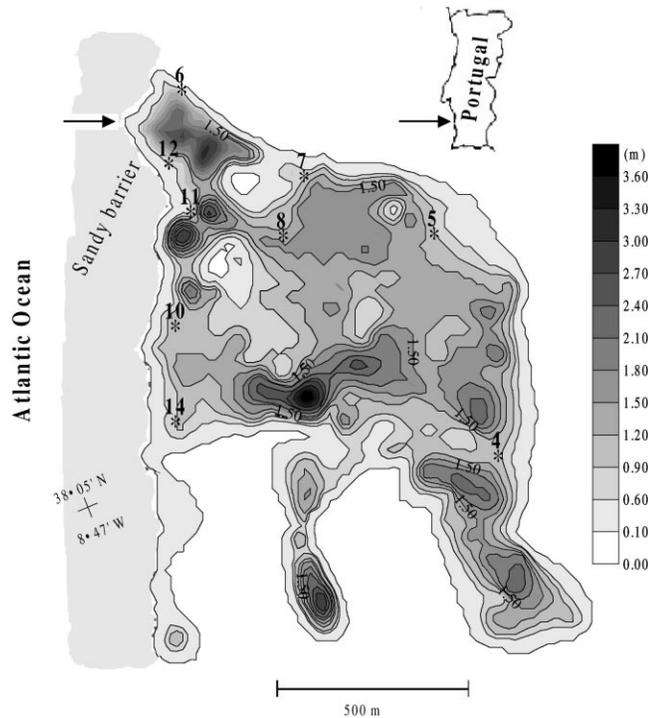


Fig. 1. Santo André lagoon: Bathymetric chart with the location of the nine sampling stations marked with an asterik (*). The arrow on the upper left corner shows the place where the lagoon is artificially opened to the sea every spring.

Net production was estimated from biomass data, using two different methods described by Murthy et al. (1986). Method 1 is based on the sum of the positive biomass variations, assuming that a negative variation in a period between two samplings, corresponds to a biomass loss that was not produced within the considered period. Method 2 is based on summing the absolute values of all biomass variations. It is assumed that a negative variation corresponds to a loss of biomass that was produced within the period of observation. Method 1 tends to underestimate production, without any compensation for the biomass lost between two samplings. Method 2 tends to overestimate production by assuming that the biomass lost between two samplings was produced within that time interval. One way to overcome the disadvantages of these harvesting methods is to quantify mortality. However, in the case of *R. cirrhosa* it is practically impossible to quantify the dead parts. Even if they remain at the bottom, it is very difficult to separate them from other types of organic debris.

2.2. Model development

Biomass change is the main process described by the model. In primary producers, this is a result of the balance between productive processes, which incorporate biomass,

and degradative processes, which consume biomass. The variation of the biomass can be described by the differential Eq. (1)

$$\frac{dB}{dt} = P - R - M - G - H \quad (1)$$

where B is the biomass of *R. cirrhosa*, P the photosynthetic production, R the respiration, M the natural (non-predatory) mortality, G the grazing by macroinvertebrates and H is the harvesting when simulated (see later).

Exudation and photorespiration were not included since no data were available for this species. In the literature, estimates of dissolved organic carbon (DOC) losses through exudation are highly variable. Values ranging from almost zero to 90% of carbon fixed are given by different authors (see Khailov and Burlakova (1969) and Jørgensen et al. (1991)). There is also variability in the literature concerning the factors affecting DOC loss. In the case of phytoplankton, some authors refer increased losses with poor growth conditions (e.g. Ittekkot et al., 1981), and others have found greater DOC exudation at high productivity rates.

A depth integrated Michaelis–Menten type Eq. (2) was used to describe production as a function of light. Irradiance at surface was simulated according to Brock (1981) and Portela and Neves (1994). Photosynthetically active radiation (PAR) was assumed to represent 42% of global radiation (Parsons et al., 1984). The variation of light with depth was calculated according to the Lambert–Beer law.

$$P = \frac{B}{Z_b - Z_c} \int_{Z_b}^{Z_T} P_{\max} \frac{I_c e^{-k_c z}}{I_k + I_c e^{-k_c z}} dz = \frac{BP_{\max}}{(Z_b - Z_c)k_c} \ln \frac{[I_k + I_c e^{-k_w Z_c}]}{[I_k + I_c e^{-k_c Z_b}]} \quad (2)$$

where Z_T is the depth at the top of the macrophyte stand, Z_b the depth at the bottom of the macrophyte stand, k_w the light extinction coefficient in the water, k_c the light extinction coefficient within the canopy, P_{\max} the maximal photosynthetic growth rate, I_k the half saturation irradiance and I_T the irradiance at the top of the macrophyte stand (calculated with the Lambert–Beer law, from irradiance at the surface and k_w , the light extinction coefficient in the water above the macrophyte stand).

The integration of P over time allows the calculation of gross production and the integration of R allows the calculation of total respiration. The difference between the results of both integrations gives net production. All these calculations were included in the model in order to calculate total gross and net production for any time interval.

In Eq. (2), gross production is a function of P_{\max} and I_k . It was assumed that *R. cirrhosa* is not nutrient limited, since rooted aquatic macrophytes usually uptake nutrients both from the bottom and from the water column (Short and McRoy, 1984; Thursby and Harlin, 1984; Harlin, 1995), transferring them through different parts of the plant (Brix and Lyngby, 1985). Thus, P_{\max} may be assumed to depend mainly on temperature and physiologic adaptation, (Menendez and Peñuelas, 1993) as has been observed in algae (Davison, 1991; Falkowski and LaRoche, 1991). I_k is a measure of efficiency in light utilisation. The smaller the value of I_k the larger the initial slope of the P – I relationship and therefore the quantum yield of photosynthesis. In the present model, adaptation was taken into account by changing P_{\max} and I_k has a function of water temperature, season and ambient irradiance. P_{\max} values measured in Tancada lagoon (NE Spain) (Menéndez and Peñuelas, 1993) at different

temperatures similar to those of Santo André lagoon were chosen to use in the model. Linear interpolations were used to recalculate those parameters over time as a function of temperature and season. The same procedure was used to obtain values for respiration, also measured by Menéndez and Peñuelas (1993) in Tancada lagoon.

I_k is considered a measure of photoadaptation (Parsons et al., 1984; Menéndez and Peñuelas, 1993). This parameter must be related to turbidity, self-shading and depth. In the model I_k is calculated as a function of the daily average irradiance within the macrophyte canopy, that is calculated by integrating vertically irradiance between the canopy top and bottom over a day (Eq. (3)). Then, Eq. (4) is used to calculate I_k . The rationale behind this equation is that plants exposed to higher average light intensities tend to have a higher I_k and a lower quantum yield than plants exposed to low light. This has been observed in algae (e.g. Falkowski and LaRoche, 1991) and is presumably true for other plants due to the common physiological basis of photosynthesis. When the biomass standing stock is very high, k_c will increase (see below) and I_d will decrease, leading to a decrease in I_k .

$$I_d = \frac{1}{(Z_b - Z_T)k_c} \cdot \int_{t=0}^{t=24} I_s [e^{-k_w Z_T} - e^{-k_c Z_b}] dI_s \quad (3)$$

where I_s is the surface irradiance, I_d the daily average irradiance within the macrophyte canopy.

$$I_k = \max(22 \times I_d k_1) \quad (4)$$

where k_1 is a dimensionless calibration factor with a value of 1.5.

The range of values obtained from Eq. (4) ($22.0\text{--}102.5 \mu\text{mol m}^{-2} \text{s}^{-1}$) is lower to those reported in Menéndez and Peñuelas (1993). Z_T from Eq. (2) will depend on the average depth of the lagoon in the *R. cirrhosa* stand, and average height of its canopy (H_c), while Z_b will only depend on the average depth of the lagoon in the *R. cirrhosa* stand. The more the plants grow, the more the canopy will be closer to the water surface, being exposed to higher irradiance. At the same time, self-shading increases reducing the light in near-bottom zones. At the beginning of the annual vegetative growth, k_w is identical to k_c when plant stems are just a few centimetres long. When the canopy becomes higher self-shading will increase k_c .

For k_w transparency (Secchi disc) values measured monthly in Santo André lagoon during the years 1984 and 1985 (Cancela da Fonseca, 1989) were used according to the empirical expression

$$k_w = \frac{1.7}{\text{Sd}} \quad (5)$$

where Sd is the transparency measured with a Secchi disc (Parsons et al., 1984).

k_c results not only from water turbidity but also from the self-shading effect of the macrophyte canopy. It was calculated with a Michaelis–Menten like expression relating biomass (g DW m^{-2}) with self-shading (Eq. (6)). This expression was calibrated with PAR values measured in Santo André lagoon in autumn 1997, using a underwater quantum sensor (LI-COR mod. 193SA) when vegetative growth was near maximum ($k_c=8 \text{ m}^{-1}$). For values of biomass (B_i) obtained at the beginning of vegetative growth (late spring), k_c takes the

same values of $k_w=1.5$, whereas values of 10 correspond to asymptotic biomass values (B_{\max}) — 360 g DW m^{-2} , assuming 20% ash content for *R. cirrhosa* (Verhoeven, 1980):

$$k_c = \frac{\text{Biomass}}{k_2 + \text{Biomass}} k_3 \quad (6)$$

where k_2 is the biomass value that forces the ratio $B_i/(k_2+B_i)$ to be 1.5 and the ratio $B_{\max}/(k_2+B_{\max})$ to be 10, while k_3 converts it in k_c units (m^{-1}). The rationale beyond this is that k_c will grow almost linearly until an asymptotic value of $10 m^{-1}$. The increase in k_c is potentially an important negative feedback regulating biomass growth.

A similar method was used to relate canopy height (H_c) with biomass, according with average values obtained in Santo André lagoon (7 cm in late spring; 40 cm as maximal height in August), as described in Eq. (7):

$$H_c = \frac{\text{Biomass}}{k_4 + \text{Biomass}} k_5 \quad (7)$$

where k_4 is the biomass value that forces the ratio $B_i/(k_4+B_i)$ to be 7 and the ratio $B_{\text{Aug}}/(k_4+B_{\text{Aug}})$ to be 40, while k_5 converts it to H_c units (cm).

For values of biomass greater than B_{Aug} , canopy is maintained at 40 cm, as it was observed during field surveys in Santo André lagoon.

The dynamic formulations described above in Eqs. (4), (6) and (7) were chosen in order to synthesise current knowledge regarding the autoecology of the studied species and also as a result of preliminary model simulations, in order to achieve a population dynamics similar to that observed in nature.

At Santo André lagoon *R. cirrhosa* is consumed by macroinvertebrates, mainly *Gammarus* sp. and *Sphaeroma* sp. Grazing was treated as a forcing function. Biomass data for these two species obtained in Santo André between 1984 and 1985 (Cancela da Fonseca, 1989), together with consumption rates measured in Tancada lagoon for *Gammarus aequicauda* and *Sphaeroma hookeri* (Menéndez and Comín, 1990) were used to calculate the grazing pressure on *R. cirrhosa*.

A situation of harvesting (H in Eq. (1)) was simulated with an outflow of biomass of 50% in 1 day (15 August), representing a summer situation, just before the biomass reached its maximum, when dystrophic phenomena are more likely to occur in the lagoon. Since no data were available on natural (non-predatory) mortality, a constant rate was assumed and used to calibrate the model.

A time step of 0.1 day was used in all model runs. Each simulation started on Day 146 (26 May) corresponding to the first field survey, approximately at the beginning of vegetative growth. Table 1 synthesises the parameters used in the model. The model was implemented in Stella II 3.0.

3. Results and discussion

3.1. Field work

In Fig. 2 *R. cirrhosa* biomass isolines corresponding to the four sampling periods are shown for the whole lagoon. *R. cirrhosa* is one of the most abundant macrophytes in this

Table 1
Values (or range of values) used in the model

Parameter	Value	Unit	Source
P_{\max}	5.50–21.04	mg O ₂ g DW ⁻¹ h ⁻¹	Menéndez and Peñuelas (1993) ^a
I_k	22.0–36.0	μmol m ⁻² s ⁻¹	Calibrated ^b
Respiratory rate	0.56–4.80	mg O ₂ g DW ⁻¹ h ⁻¹	Menéndez and Peñuelas (1993) ^a
Consumption _{Gammarus}	0.30	per day	Menéndez and Comín (1990)
Consumption _{Sphaeroma}	0.11	per day	Menéndez and Comín (1990)
Natural mortality	0.005	per day	Calibrated
Depth	0.95–3.10	m	Measured
Biomass _{Sphaeroma}	0.003–1.440	g DW m ⁻²	Cancela da Fonseca (1989)
Biomass _{Gammarus}	0.003–1.740	g DW m ⁻²	Cancela da Fonseca (1989)
Turbidity (Secchi)	0.70–1.25	m	Cancela da Fonseca (1989)
Initial biomass	24.0	g DW m ⁻²	

^a Values extracted from graphs.

^b Calculated as explained in the text.

ecosystem, with stands covering up to 60% of the total area. By the end of May only small plants could be observed (<10 cm in height). Within 2 months, *R. cirrhosa* stands had an approximate height of 40 cm and covered almost all areas with depths between 0.5 and 1 m. Peak biomass values of upto 400–500 g DW m⁻² were observed in October. These biomass values are amongst the highest reported in the literature according to Verhoeven (1980), Pérez and Camp (1986) and Menéndez and Comín (1984).

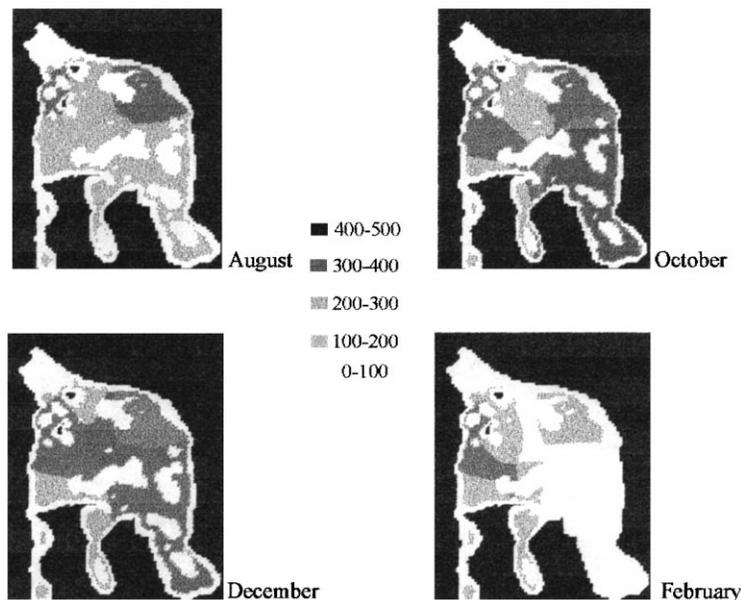


Fig. 2. Biomass isolines obtained from samples collected between August 1996 and February 1997.

Table 2
Range of biomass values reported in the literature for *Ruppia cirrhosa*

Biomass values (g DW m ⁻²)	Locality	Source
10.8–13.2 ^a	Askö, Sweden	Ankar and Emegreen (1977) in Verhoeven (1980)
4.8–18.0 ^a	Askö, Sweden	Jerling and Linde (1977) in Verhoeven (1980)
10–111	Murcia, Spain	Ballester (1985) in Menéndez and Comín (1984)
110.6–176.3 ^a	Twärminne, Finland	Verhoeven (1980)
59.6–188.5 ^a	Camargue, France	Verhoeven (1980)
68.3–226.1 ^a	Coastal ponds, Netherlands	Verhoeven (1980)
150–330 ^a	Bahía del Fangar, Spain	Pérez and Camp (1986)
90.1–485.3	Santo André lagoon, Portugal	This study
61.2–656.1 ^a	Tancada lagoon, Spain	Ménendez and Comín (1984)

^a Original values in g AFDW m⁻², converted to g DW m⁻² assuming 20% ash content.

According to Verhoeven (1979), the maximal depth for *R. cirrhosa* growth is 1.5 m, although it may be found as deep as 7 m in Finland. This is probably related to light availability. If it is assumed that the photic depth corresponds to the limit where irradiance is 1% of surface light and, assuming a extinction coefficient of 1.5 m⁻¹ for the Santo André lagoon, photic depth calculated from the Lambert–Beer law, would be approximately 3 m. This is the depth of the *R. cirrhosa* stand when the lagoon is at its maximum depth. At depths lower than 0.5 m desiccation may limit *R. cirrhosa*.

The life cycle of *R. cirrhosa* with a hibernating phase may be viewed as a self regulating mechanism limiting biomass growth. The behaviour of *R. cirrhosa* in Santo André lagoon with its biomass reaching maximal annual values around 300–500 g DW m⁻² (Cancela da Fonseca et al., 1985, 1989; Bernardo, 1990; Cancela da Fonseca, 1989) suggests stable population dynamics. In other ecosystems, biomass values were generally lower or within the range observed in Santo André lagoon (Table 2).

According to Verhoeven (1979) *R. cirrhosa* vegetative growth starts when minimal temperatures are above 10°C and maximal temperatures above 15°C. These conditions are met in Santo André lagoon during March. However, at this time the tidal regime imposed by the opening of the lagoon to the sea may limit growth due to severe dehydration during the ebb (Adams and Bate, 1994). Except for this delay in the start of vegetative growth, the life cycle of *R. cirrhosa* follows the patterns described in the literature.

3.2. Model calibration and validation

Mean biomass values measured at Santo André from May 1996 to February 1997 were used to calibrate the model (Fig. 3). The positive inflection in March is probably an artefact due to sudden reduction of depth due to opening of the lagoon. The modelled biomass peak occurs in October, near the highest biomass point measured in the field. There is a good agreement between the observed and the simulated values.

Data from the years 1984/85 (Cancela da Fonseca, 1989) were compared to the model results (Fig. 4). Although these data reflect the total macrophyte biomass (mainly *Ruppia cirrhosa* and *Potamogeton pectinatus*) there is a reasonable agreement with the model

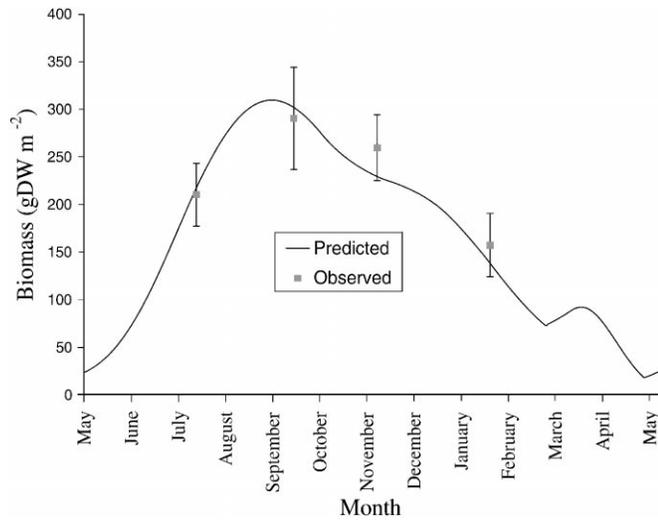


Fig. 3. Observed biomass values between May 1996 and February 1997 with 95% confidence limits (means of five replicates) and predicted by the model.

results, except for some winter months where the model overestimates the observed values. The biomass of *P. pectinatus* in St. André lagoon is small compared to that of *R. cirrhosa* and its life cycle shorter. Generally, the former begins to grow during autumn, when the latter is already declining. The opening of the lagoon to the sea stops its growth at the end of winter.

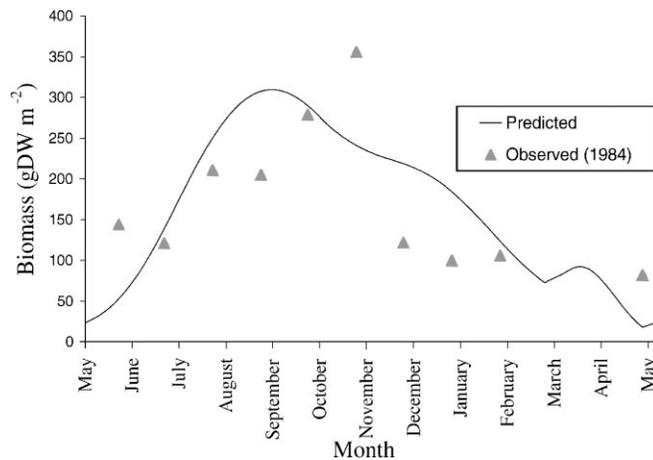


Fig. 4. Biomass values in Santo André lagoon (triangles) for the years 1984/85, taken from Cancela da Fonseca (1989) and model results (line).

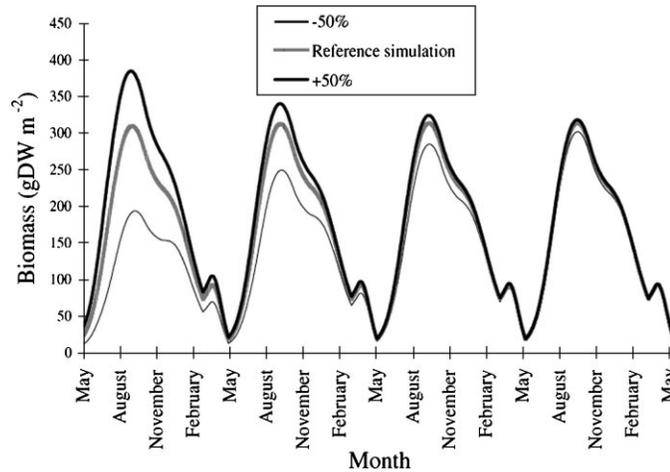


Fig. 5. Model results assuming three different initial biomass values as in the reference simulation of Fig. 3, 50% higher and 50% lower.

3.3. Stability and sensitivity analysis

In Fig. 5 the results of three simulations starting with three different initial biomasses — 24 g DW m^{-2} (reference value), 36 g DW m^{-2} (50% higher than reference) and 12 g DW m^{-2} (50% lower than reference) are shown. From the results obtained it is clear that the model remains stable after the third year of simulation independently of the starting biomass. This result demonstrates that the model simulates a stable equilibrium within a range of values of biomass, being resilient to variations in the initial values. One of the factors in the model contributing to this stabilising effect is the self-shading, reflected by the increasing value of k_c with biomass (Eq. (5)).

The sensitivity of the model to some of its parameters is synthesised in Table 3, where net and gross production as well as peak biomasses resultant from the sensitivity analysis are shown. The model exhibits high sensitivity to the parameter I_k without losing its in-

Table 3
Results of the sensitivity analysis (values in g DW m^{-2})

Simulations	Annual production		Maximum biomass
	Net	Gross	
Reference simulation	360.46	1636.08	311.06
$I_k + 10\%$	306.64	1386.38	259.10
$I_k - 10\%$	429.12	1950.03	377.39
Mortality + 10%	369.12	1579.35	298.50
Mortality - 10%	350.12	1695.88	324.32
$k_c + 10\%$	363.34	1648.95	313.23
$k_c - 10\%$	357.20	1621.48	308.57

terannual stability. A 10% increase in this parameter reduces annual gross production by approximately 20%, whereas a 10% decrease has the opposite effect. The sensitivity of the model to this parameter reveals its importance in the results obtained. This is a good evidence of its real importance as a biomass regulating mechanism.

It is important to note that an increase in mortality results in an increase of net production and a decrease of gross production. This is because the flows ‘production’ and ‘respiration’ depend on the biomass pool. As ‘production’ is only active during daylight hours, while ‘respiration’ is always active, a decrease in biomass (caused by mortality) in each time step will have more impact on production than on respiration.

Net production calculated with the model ($360.5 \text{ g DW m}^{-2}$) is slightly higher than values obtained by Verhoeven (1980) from biomass differences, of $150\text{--}360 \text{ g DW m}^{-2}$ for lentic ecosystems in Northern and Central Europe. When compared with other aquatic phanerogams the calculated value for net production is lower than that measured for *Zostera* in Denmark (Petersen (1913) in Mann (1972)) — 870 g DW m^{-2} . Net production calculated with the model ($360.5 \text{ g DW m}^{-2}$) is between the values estimated from biomass harvest data — $294.6 \text{ g DW m}^{-2}$ with Method 1 and $589.2 \text{ g DW m}^{-2}$ with Method 2 (see Section 2).

Consumption of *R. cirrhosa* by the grazers *Gammarus* sp. and *Sphaeroma* sp. calculated from the model is 86.4 g DW m^{-2} per year. It represents 24% of annual net production. Thus, grazing seems to have an important role on biomass consumption, which contrasts with the results obtained in Tancada Lagoon, NE Spain (Menéndez and Comín, 1990).

3.4. Harvesting

Fig. 6 represents a harvesting simulation on 15 August, with the extraction of 25% of the total biomass, every year and in alternate years. The model is only sustainable with crops in alternate years, with biomass maxima lower than those observed in the field and predicted by the reference simulation (Fig. 3).

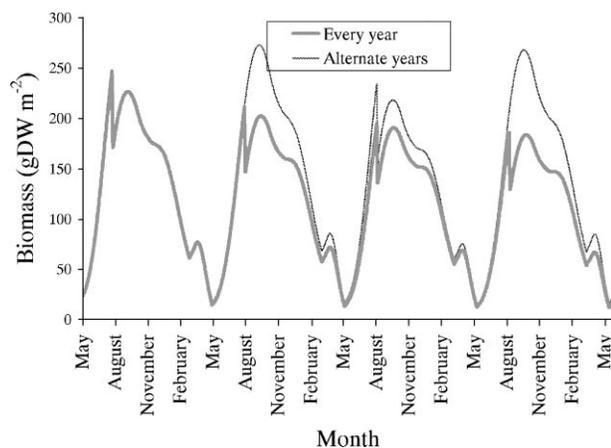


Fig. 6. Model results with a 25% harvest of total biomass in 15 August, every year and in alternate years.

Table 4

Results of the harvesting simulations (25 and 50% extractions) and reference simulation (values in g DW m⁻²)

Simulations	Annual production		Maximum biomass
	Net	Gross	
Reference simulation	360.46	1636.08	311.06
25% extraction	381.84	1444.53	248.60
50% extraction	387.29	1289.30	248.60

Harvesting may cause an additional input of nutrients to the water by disturbing the sediments, when roots and subterranean stems are pulled from the surface. Furthermore, re-suspended organic matter could induce a rapid reduction in dissolved oxygen concentration. These effects may be reduced by harvesting with a cutting device and removing only the branching stems above the bottom. Besides that, the time for harvesting could be adjusted in order to avoid periods of water stratification and therefore minimising any deleterious secondary effects.

Table 4 summarises the results obtained with the harvesting simulations (25% and 50% extractions of total biomass in August). Because of harvest, net production increases and gross production decreases. The variation of net production does not follow the biomass decrease, due to the reduction in selfshading. This reduction allows the remaining biomass to receive more light and grow faster. Thus harvesting does not seem to imply a reduction in secondary production. However, it is important to evaluate the harvest impact on benthic fauna to prevent potential losses on the second and third levels of the food chain.

3.5. The model in other ecosystems

In order to evaluate the capacity of the model to represent the life cycle of *R. cirrhosa* in other ecosystems, a simulation of the biomass dynamics was carried out for Tancada

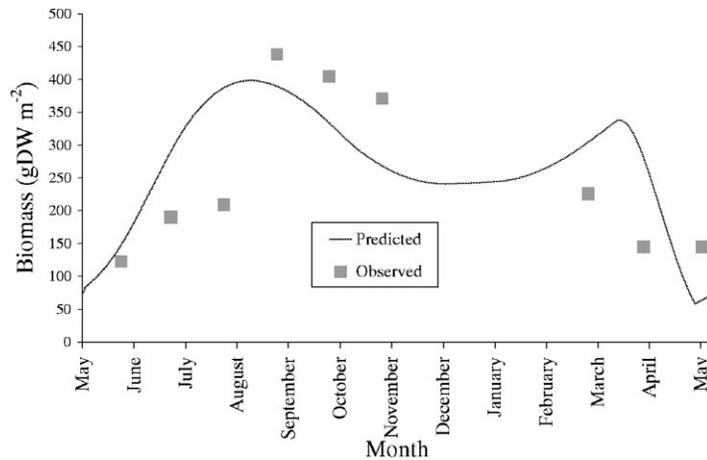


Fig. 7. Biomass values in the Tancada lagoon (squares) taken from Ménéndez and Comín (1984) and model results (line).

lagoon. It is a small (1.8 km²) and shallow (ca. 37 cm) coastal lagoon in Ebro Delta (NE Spain) (Menéndez and Peñuelas, 1993). Its hydrology is artificially controlled by inputs of freshwater irrigation from rice fields, with low salinity in spring and summer (Comín, 1984). Model parameters were the same as for Santo André lagoon. Lagoon depth and biomasses of *Gammarus aequicauda* and *Sphaeroma hookeri* were obtained from the literature (Menéndez and Comín, 1989, 1990). Since no data on turbidity and self-shading were available in the literature, the Santo André values were assumed.

The results obtained with the model are shown in Fig. 7 together with biomass data from Menéndez and Comín, (1989). The model simulates reasonably well the biomass dynamics of Tancada lagoon, except for the August value, which was considerably lower than predicted.

4. Conclusions

Considering the information reported in the literature and the results of the present work, some conclusions arise regarding the autoecology of *Ruppia cirrhosa*. Some biotic and abiotic external factors such as light availability, desiccation probability (near the margins of the lagoon), the tidal regime imposed by the artificial opening of the lagoon and grazing pressure play a role in the distribution, biomass standing stocks and production of the studied species. Its annual life cycle may be viewed as an internal limiting factor. Peak biomass may be reached well before the end of the vegetative cycle. Therefore, some other control mechanisms must work to halt further increases in biomass. Self-shading of the canopy seems to be another important internal limiting factor in controlling peak biomasses and production. It is also important to note that the model did not accurately simulate the biomass dynamics until acclimation of its parameters was taken into account. Parameter dynamics became an important topic in ecological modelling during the last decade with several authors describing acclimation patterns and stressing the importance of their inclusion in mathematical models (e.g. Jørgensen, 1992; Duarte and Ferreira, 1995, 1997).

The model showed a reasonable adjustment to independent datasets. Its predictions regarding primary production for Santo André lagoon suggest that harvest of upto 25% of macrophyte biomass may be carried out in summer in alternate years, without affecting macrophyte net production and therefore secondary production.

Acknowledgements

This work was supported by Fundação para a Ciência e Tecnologia (Project PBICT/MAR/2245/95 and Grant JNICT/FMRH/BM 4860). The authors acknowledge the editor and two anonymous referees, whose comments and criticism helped to improve the current version of the paper.

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