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# Modelling macroalgae (*Ulva rigida*) in the Venice lagoon: Model structure identification and first parameters estimation

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## Abstract

The paper describes the definition and a first parametrization of a dynamic model of macroalgae (*Ulva rigida*) population. Based on specific literature, a two-step kinetic scheme is selected for modelling growth and uptake of nitrogen and, therefore, the intratissual concentration of nitrogen has been considered as a state variable of the model. Accordingly, *Ulva r.* growth rate depends on the concentration of phosphorus in the external medium and on the intratissual nitrogen concentration, which influences, in turn, the uptake rates of reduced and oxidized nitrogen. The influences of temperature and light intensity on *Ulva r.* photosynthetic activity are also discussed. The dynamics of dissolved oxygen has also been modelled and a specific mortality rate, depending on dissolved oxygen, has been adopted. The model has proved to be qualitatively consistent with the available literature, while a first parametrization yields results in quantitative agreement with short term laboratory experiments, regarding samples collected in the lagoon of Venice. The model has been applied to data sets collected in the lagoon of Venice and is capable of reproducing the main features of the seasonal dynamic of *Ulva r.* These results prompted its inclusion in a comprehensive 3D transport-water quality model of the Venice lagoon ecosystem. © 1997 Elsevier Science B.V. All rights reserved

## 1. Introduction and objective of the work

Macroalgae communities occupy an important ecological niche in coastal ecosystems, as they appreciably affect the free energy transformation processes and the biogeochemical cycles (Mann, 1973; Hanisak, 1983), especially of nitrogen (Lapointe and Tenore, 1981; Parker, 1981; Rosemberg and Ramus, 1982a; Rosemberg and Ramus, 1982b; Hanisak, 1983; Fujita, 1985; Fujita et al., 1989; Sfriso et al., 1989). During the eighties, macroalgae communities

have progressively invaded a large portion of the Venice lagoon, with levels of primary productivity ranging from 1 to 8.3 mg C/(g dw) for *Ulva rigida*, the dominant species (Sfriso, 1987; CRSCT, 1990). Production is high from early spring to late autumn, and the biomass density reaches peaks of up to about 20 kg/m<sup>2</sup>, (Sfriso et al., 1987). Anoxic crises, followed by a consistent release of hydrogen sulphide, are likely to occur, especially during the summer, under particular hydrodynamic and climatic conditions (Sfriso, 1994).

For this reason, we have attempted to include the dynamics of this population in an already existing eutrophication–diffusion model of the Venice lagoon, in which phytoplankton was considered as the

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only primary producer (Dejak et al., 1987; Bertonati et al., 1987).

The main physiological and ecological characteristics of *Ulva r.*, indicated by the general literature, have provided a rational basis for selecting the state variables, the structure of the model and a first set of values for the parameters.

## 2. Physiological and ecological features of *Ulva rigida*

*Ulva rigida*, the most common macroalgae species in the Venice lagoon, can successfully survive in shallow water environments and it can cope with nitrogen shortage and low irradiance. (Littler, 1980; Lapointe and Tenore, 1981; Rosemberg and Ramus, 1982a; Rosemberg and Ramus, 1982b; Fujita et al., 1989; Murthy and Sharma, 1989; Henley et al., 1992). Its thallus often reaches a considerable size, and it can survive for more than a year. Even though this species does not seem to be able to assume nutrients from the sediment (Hanisak, 1983), the high surface to volume ratio of *Ulva r.*'s leaves favours a fast uptake of various forms of dissolved nitrogen (Rosemberg and Ramus, 1984; Duke et al., 1989a; Duke et al., 1989b), which is partially metabolized and partially stored, both under inorganic forms (Mohsen et al., 1974), and as organic compounds (Rosemberg and Ramus, 1982b; Wheeler, 1983), such as proteins or nucleic acids. Thus, this species can survive for as long as a fortnight, at low nitrogen concentrations, and even in the absence of this nutrient (Mohsen et al., 1974; Lapointe and Tenore, 1981; Rosemberg and Ramus, 1982b; Fujita, 1985; Fujita et al., 1989). According to Hanisak (1983), a fraction  $Q_{\min}$  of the internal nitrogen per unit weight, thereafter called quota ( $Q$ ), becomes part of the structure of the organism. Above  $Q_{\min}$  the growth rate increases approximately linearly with the availability of nutrient ( $Q - Q_{\min}$ ), because the nitrogen is immediately used for synthesizing new tissues. At a critical level,  $Q_c$ , the growth reaches its maximum efficiency, which is then maintained, while the surplus of nitrogen can be stored up to a value  $Q_{\max}$ .

On the contrary, the growth rate of *Ulva r.* does not seem to be limited by the phosphorus at the levels of concentration usually found in colonized

areas (Berland et al., 1980). In fact, the internal concentration of this element is low and does not show such a great variability (Faganeli et al., 1986; Pugnetti et al., 1987; Sfriso et al., 1987; Bjornaster and Wheeler, 1990; Lavery and McComb, 1991; Sfriso, 1994).

The hydrodynamic regime also affects *Ulva r.* productivity, but there is no general agreement as to whether the global influence is positive or negative. An intense mixing favours nutrient transport and therefore enhances *Ulva r.* uptake (Parker, 1981; Wheeler, 1983; Fujita et al., 1988), but, on the other hand, a statistical analysis of experimental data shows that high *Ulva r.* standing crops are correlated with areas of low turbulence (Sfriso et al., 1989). This might be because, in these conditions, the dispersion of *Ulva r.* biomass due to tidal agitation is limited, but a real analysis of the influence of the transport phenomena requires the coupling of the present model with an improved version of a reaction-eddy diffusion model of the central part of the lagoon of Venice (Dejak et al., 1987; Pastres et al., 1995).

## 3. Choice of state variables

A careful survey of the current literature, together with general information on trophic conditions in the lagoon of Venice, indicates nitrogen as the main limiting macronutrient. Since its uptake rate depends on its oxidation state (Lapointe and Ryther, 1979; Lapointe and Tenore, 1981; Mac Farlan and Smith, 1982; Hanisak, 1983; Fujita et al., 1989), it is not possible to pool the oxidized and reduced forms. As already said, *Ulva rigida* can store the surplus of nitrogen; therefore, the processes of growth and nitrogen uptake from the environment are separated and the global kinetics can be correctly modelled only by taking into account the tissue concentration  $Q$  of this element.

The effect of the concentration of phosphorus on the growth rate is not relevant in most environments, including the lagoon of Venice (Sfriso et al., 1989), but it has been included in the model to maintain a general formulation, which might prove useful in investigating the competition between macroalgae and phytoplankton.

Low levels of dissolved oxygen have been recognized as one of the factors which enhance the mortality of *Ulva r.*. This non-linear feedback, which might be one of the causes of the anoxic crisis, leads to the inclusion in the model of the dynamic of dissolved oxygen. Further, at non-critical levels, the dynamic of dissolved oxygen can be used for an indirect comparison of the model with sets of experimental data, in which the photosynthetic production is measured in oxygen units.

The state equations of the model are

$$\frac{dB}{dt} = (\mu(I, T, Q, [P]) - f_{\text{death}}(\text{DO}))B \quad (1)$$

$$\begin{aligned} \frac{dQ}{dt} = & (V_{\text{NH}}([\text{NH}_4^+], Q) + V_{\text{NO}}([\text{NO}_x^-], Q) \\ & - \mu(I, T, Q, [P]) \cdot Q \end{aligned} \quad (2)$$

$$\frac{d\text{DO}}{dt} = (\varphi(I, T, Q, [P]) - f_{\text{resp}}(T))B \quad (3)$$

where  $B$  stands for *Ulva r.* biomass,  $I$  for irradiance intensity,  $T$  for temperature and  $Q$  for the internal nitrogen concentration, whereas the generic functions  $\mu$ ,  $V$  and  $\varphi$  identify specific growth, specific uptake rates (for ammonium and nitrate) and gross oxygen production, respectively.  $f_{\text{death}}(\text{DO})$  is the term referring to *Ulva r.* mortality,  $f_{\text{resp}}(T)$  the one referring to respiration of *Ulva r.*. Orthophosphate is labelled as  $P$ .

#### 4. Modelling *Ulva r.* growth

The influence of the limiting factors on the primary production rate has been described with a multiplicative formulation:

$$\mu(I, T, Q, [P]) = \mu_{\text{max}} g_1(Q) g_2([P]) g_3(I) g_4(T) \quad (4)$$

and, since in normal conditions, gross oxygen production is proportional to growth, one can write:

$$\varphi(I, T, Q, [P]) = \varphi_{\text{max}} g_1(Q) g_2([P]) g_3(I) g_4(T) \quad (5)$$

Although other formulations are often employed in phytoplankton models, such as Liebig's minimum

model or the harmonic model, the multiplicative one leads to an easier interpretation of the results and it has been also used in all other attempts at modelling *Ulva r.* growth, presently known to the authors (Menesguen and Salamon, 1987; Bendoricchio et al., 1994).

##### 4.1. Dependence of growth on internal nitrogen

Phytoplanktonic models for growth and uptake processes can be roughly divided into two types. One, the more widely used, assumes that growth and uptake rates are equal and, therefore, depend on the external concentration of the nutrient. In the other, uptake kinetic is independent from growth, which is a function of the nutrient content of the cell,  $Q$  (Droop, 1970; Lehman et al., 1975; Nyholm, 1978; Jorgensen, 1976; Straskraba and Gnauk, 1985). In general, single step kinetics fails to explain the behaviour of *Ulva r.* and of macroalgae (Parker, 1981; Rosemberg and Ramus, 1982b; Hanisak, 1983; Wheeler, 1983; Figueroa and Rudiger, 1991), as demonstrated by the wide range of ammonia uptake rates observed at comparable concentrations in the medium (Fujita et al., 1988; Fujita et al., 1989), and by the fact that the growth can be measured also in the absence of external nutrients. As a consequence, the half saturation constants and the maximum growth rates reported in the literature depend on the nutritional state of the samples and are site specific. For this reason, they show a great variability (Table 1), that can be consistently reduced by interpreting the same data with a two-step consecutive reaction. This formulation gives a Monod kinetic when a steady state condition is reached, and therefore uptake and growth rate are equal (Dugdale, 1967), but it is more flexible, and offers the possibility of modelling transient situations.

As proposed by Hanisak (1983) and confirmed by the experimental results of Fujita et al. (1989) and of Lavery and McComb (1991), when other factors are not limiting, the growth rate is an hyperbolic function of  $Q$ . The original Droop formulation  $g_1(Q) = (Q - Q_{\text{min}})/Q$  cannot provide a good quantitative interpretation of the data, because the concept of the critical level of nitrogen, see Fig. 1, is not taken into consideration. As it has already been done in phytoplanktonic models (Nyholm, 1978), it seemed rea-

sonable to use as a variable the difference  $q = Q - Q_{\min}$  and to approximate the behaviour shown in Fig. 1 with a Monod kinetic:  $g_1(Q) = q/(q + k)$ . Substituting back  $q$  and defining a new parameter  $k_c = Q_{\min} - k$ , the hyperbolic expression may be rewritten as

$$g_1(Q) = \frac{Q - Q_{\min}}{Q - Q_{\min} + k} = \frac{Q - Q_{\min}}{Q - k_c} \quad (6)$$

Eq. (6) is more flexible than the Droop basic formulation, which represents a limit case for  $k_c = 0$ , i.e. for  $k = Q_{\min}$ .

#### 4.2. Dependence of growth on phosphorus availability

The internal concentration of phosphorus is low compared with  $Q$ , and, more important, its variability is restricted within a narrower range, between 1 and 5 mg P/(g dw) (grams dry weight) (Faganeli et

al., 1986; Pugnetti et al., 1987; Sfriso, 1987; Bjornaster and Wheeler, 1990; Lavery and McComb, 1991). In this case, the identification of a two-steps kinetic would be very difficult, because steady state conditions are reached quickly. Further, the growth rate would be practically unaffected by phosphorus cell concentration, because, as shown in Lavery and McComb (1991), the critical concentration level for internal phosphorus is close to the minimum quota value. For this reason, we prefer to relate *Ulva r.* growth with the external phosphorus concentration through the Monod kinetic:

$$g_2([P]) = \frac{[P]}{k_p + [P]} \quad (7)$$

This choice is also sustained by the opinion of some researchers (Wheeler and Bjornaster, 1992), who claim that phosphorus is not stored, but is taken from the environment when needed.

Table 1  
Uptake parameter values

$V_{NH}$ (mg N (g dw) <sup>-1</sup> h <sup>-1</sup> )	$k_{NH}$ (mg N/l)	Notes	References
0.7	0.07	independent from I enriched plant	Cohen and Neori, 1991
1.4	0.37	enriched	
5.2		starved	
1.9	0.2	enriched	Fujita, 1985
3.5	0.6	starved	
5.1	0.7	starved	
3.6		model	Fujita et al., 1989
not saturable kinetics: linear relationship proposed		in agreement with our model	Lavery and McComb, 1991
5	0.5	model	Menesguen and Salamon, 1987
3.5	0.2	model	Rosemberg and Ramus, 1982a; Rosemberg and Ramus, 1982b
$V_{NH}$ (mg N (g dw) <sup>-1</sup> h <sup>-1</sup> )	$k_{NO}$ (mg N/l)	Notes	References
0.4			Bjornaster and Wheeler, 1990
1.8			
0.82	0.25		Lavery and McComb, 1991
1.2	0.5		
0.2	< 0.02		Lapointe and Tenore, 1981
0.4			

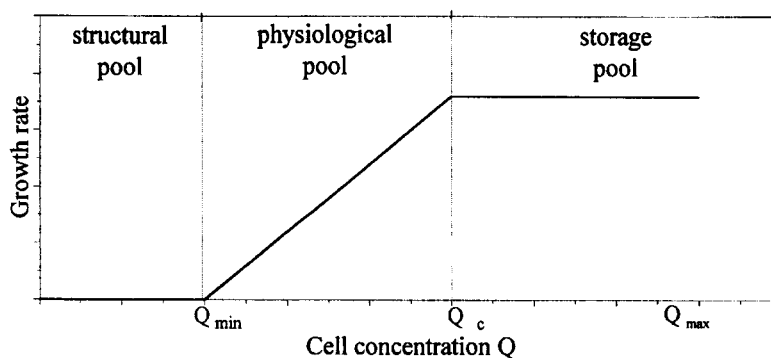


Fig. 1. Schematic qualitative description of the growth rate as a function of the tissue nitrogen concentration.

#### 4.3. Influence of temperature and light on growth

The studies of Brocca and Felicini (1981), Rosemberg and Ramus (1982a) and Hough and Fornwall (1988) appeared to be the most useful for giving a quantitative formulation of the relationship of the growth vs. incident light and water temperature. The first one, in particular, regards samples collected in the Southern Adriatic Sea, and investigates ranges of temperature and light intensity close to those experienced by *Ulva r.* in the Venice Lagoon. These data support the decision to use the multiplicative model, because the rate of oxygen production at different temperatures shows the same qualitative behaviour when the light intensity is varied. Within the range of these observations (from 10 to 27°C and from 0 to 26000 lx), *Ulva r.* growth is not inhibited and can be described by two asymptotic functions.

The temperature dependence has been expressed by using an S type formulation, adopted also by Menesguen and Salamon (1987):

$$g_3(T) = \{1 + \exp[-\zeta_p(T - \vartheta_p)]\}^{-1} \quad (8)$$

This formulation is consistent with the Arrhenius law, which governs biochemical processes at low temperatures.

The influence of the incident light has been expressed by (Cosby et al., 1984):

$$g_4(I) = 1 - \exp(-I/I_0) \quad (9)$$

This function is in agreement with the qualitative features of the data (Brocca and Felicini, 1981; Littler, 1980; Rosemberg and Ramus, 1982a; Rosemberg and Ramus, 1982b) within a wide range of light

intensity. Clearly, inhibition of photosynthetic activity should be expected, but it occurs at values ( $\approx 90000$  lx, Riccardi and Solidoro, 1996; Rosemberg and Ramus, 1982a; but see also Table 4) seldom reached in coastal shallow water environments, characterized by high levels of turbidity. A formulation which takes into account photoinhibition, (Bendoricchio et al., 1993), would require the estimation of more parameters, which is difficult to carry out, as the experimental data presently available refer mainly to conditions of low irradiance.

An S type formulation is adopted also for describing the respiration term (Brocca and Felicini, 1981; Bendoricchio et al., 1994):

$$f_{\text{resp}}(T) = \{1 + \exp[-\zeta_{\text{resp}}(T - \vartheta_{\text{resp}})]\}^{-1} \quad (10)$$

The rate of mortality is composed of two terms. The first represents the intrinsic mortality of *Ulva r.* when it is not stressed by lack of oxygen and has been estimated by a regression analysis of field data collected in the lagoon of Venice (Franco, 1990). The mortality increases proportionally to the difference between the oxygen demand exerted by respiration of *Ulva r.*,  $f_{\text{resp}}^* B$ , and the availability of dissolved oxygen, DO, normalized by the oxygen request. This represents the fraction of biomass that can not respire and is likely to be damaged.

$$f_{\text{death}}(\text{DO}) = K_d B^B + k_t \frac{\max[(f_{\text{resp}} B - \text{DO}), 0]}{f_{\text{resp}} B} \quad (11)$$

This formulation, which has been chosen after evaluating other ones (Solidoro, 1993), can be compared with that of Bendoricchio et al. (1993), which is, in our opinion, less intuitive.

## 5. Modelling nutrients uptake

The specific uptake rate  $V_{NX}([NX], Q)$  of nitrogen under a chemical form NX (in turn  $NH_4^+$  and  $NO_x^-$ ) depends on the nature of the species, on its concentration, as well as on the level  $Q$  of nitrogen tissue concentration (Fujita, 1985). Using the multiplicative model, a general equation for  $V_{NX}([NX], Q)$  can be written as

$$V_{NX}([NX], Q) = V_{mNX} f_1([NX]) f_2(Q) \quad (12)$$

where  $V_{mNX}$  is the maximal uptake rate for the nitrogen species NX. As far as the dependence on external concentration is concerned, a Monod kinetic seems reasonable and consistent with experimental observations that put in evidence the existence of a saturation threshold for the assimilation rate:

$$f_1([NX]) = \frac{[NX]}{k_{NX} + [NX]} \quad (13)$$

whereas a simple expression for  $f_2(Q)$  is

$$f_2(Q) = \frac{Q_{max} - Q}{Q_{max} - Q_{min}} \quad (14)$$

The above formulations, also adopted in the two-step phytoplanktonic models (Lehman et al., 1975, Jorgensen, 1976) have been modified by Menesguen and Salamon (1987), raising Eq. (14) to a power of 1/5 without explanation. However, the linear dependence appears adequate, since the scarcity of experimental data does not permit the identification of the parameters of more complex formulations. Eqs. (13) and (14) have been employed for describing both  $NH_4^+$  and  $NO_x^-$  assimilation. The different uptake rates of the two forms have been reproduced with a specific parameterization.

The total nitrogen uptake is given by the sum of the two uptake terms. Under this hypothesis, the mass balance for  $Q$  turns out to be

$$\begin{aligned} \frac{dQ}{dT} = & \left( V_{mNH} \frac{[NH_4^+]}{k_{NH} + [NH_4^+]} + V_{mNO} \frac{[NO_x^-]}{k_{NO} + [NO_x^-]} \right) \\ & \times \left( \frac{Q_{max} - Q}{Q_{max} - Q_{min}} \right) - \mu(I, T, [P]) \\ & \times \left( \frac{Q - Q_{min}}{Q - k_{cl}} \right) Q \end{aligned} \quad (15)$$

where  $V_{mNH}$  and  $V_{mNO}$  are the maximal uptake rates of  $NH_4^+$  and  $NO_x^-$ ,  $k_{NH}$  and  $k_{NO}$  the half saturation constants relative to them.

## 6. Estimation of Parameters

The maximum growth rate has been estimated by several authors, under different external conditions, and this explains the variability of the values reported in Table 2. According to the structure of the model, the maximum rate is a limit which can be experimentally approached if the following conditions are fulfilled:

$$Q \approx Q_{max} \quad P \gg K_P \quad I \gg I_0 \quad T \gg \vartheta \quad (16)$$

In order to assess this limit, each function should be calculated, but, unfortunately, the information available does not enable one to perform an accurate computation. For this reason, the highest measured growth rate ( $0.5 \text{ day}^{-1}$ ) has been tentatively chosen as maximum growth constant, because an underestimation of this parameter is likely to have occurred in experimental measurements.

As regards the maximum and minimum internal nitrogen concentration, it has been decided to compromise between the widest possible bounds suggested in the literature (see Table 3), and the range that is given for *Ulva r.* in the Venice lagoon, (Sfriso, 1994) by setting  $Q_{min} = 10 \text{ mg N/(g dw)}$  and  $Q_{max} = 45 \text{ mg N/(g dw)}$ .

The estimation of  $k_c$ , which is related to the physiological parameter  $Q_c$ , appears more uncertain,

Table 2  
Growth values

$\mu\text{m/day}$	Notes	Reference
0.35	13°C	Bjornaster and Wheeler, 1990
0.21		Coutinho and Zingmark, 1993
0.50		Duke et al., 1989a
0.30	13°C, different nutrients	Fujita et al., 1989
0.35	impulsed irradiance	Henley et al., 1991
0.36		Lapointe and Tenore, 1981
0.35	25°C	Lavery and McComb, 1991
0.40		Menesguen and Salamon, 1987
0.20		Neori et al., 1991
0.40		Parker, 1981

Table 3  
 $Q$  values range

$Q_{\min}$ (mg N/ (g dw))	$Q_{\max}$ (mg N/ (g dw))	Reference
13	54	Bjornaster and Wheeler, 1990
10	45	Cohen and Neori, 1991
7	27	Duke et al., 1989a
17	39	Faganeli et al., 1986
10	36	Fujita, 1985
24	42	Fujita et al., 1989
15	50	Menesguen and Salamon, 1987
9	45	Rosemberg and Ramus, 1982a; Rosemberg and Ramus, 1982b
13	43	Sfriso, 1994
20	52	Wheeler and Bjornaster, 1992

being based on studies of Fujita et al. (1989), who propose a  $Q_c$  of about 23 mg N/(g dw) when only  $\text{NO}_3^-$  is available and a  $Q_c$  of 30 mg N/(g dw) if only  $\text{NH}_4^+$  is used as a nitrogen source by *Ulva* r.. The acclimatization of the samples could explain this

discrepancy, because the two inorganic forms stimulate the synthesis of different aminoacids, which constitute the physiological pool and, as a consequence, a variation of the metabolic efficiency might occur (Nasr et al., 1968). Nevertheless, it seems that the plotted data reported by Fujita et al. (1989) can be fitted using the formulation here proposed, and a reasonable agreement is reached by setting  $k_c$  around 8 mg N/(g dw), which means postulating a  $Q_c$  around 20 mg N/(g dw). The choice is qualitatively consistent with other data showing an approximately linear dependence between growth and  $Q$  for values in the range from 10 to 20 mg N/(g dw), above which a constant growth rate is maintained (Lavery and McComb, 1991).

The estimation of  $V_{\text{NH}}$  and  $k_{\text{NH}}$ , has been difficult because their ratio covers a rather wide range, from 3 to 30 g dw<sup>-1</sup> h<sup>-1</sup> (Cohen and Neori, 1991; see also Table 1). Our assumption about  $f_1(N)$  and  $f_2(Q)$ , leads to the conclusion that  $k_{\text{NX}}$  and  $V_{\text{NX}}$  can be determined by fitting external concentration data against uptake for starved algae. The values pro-

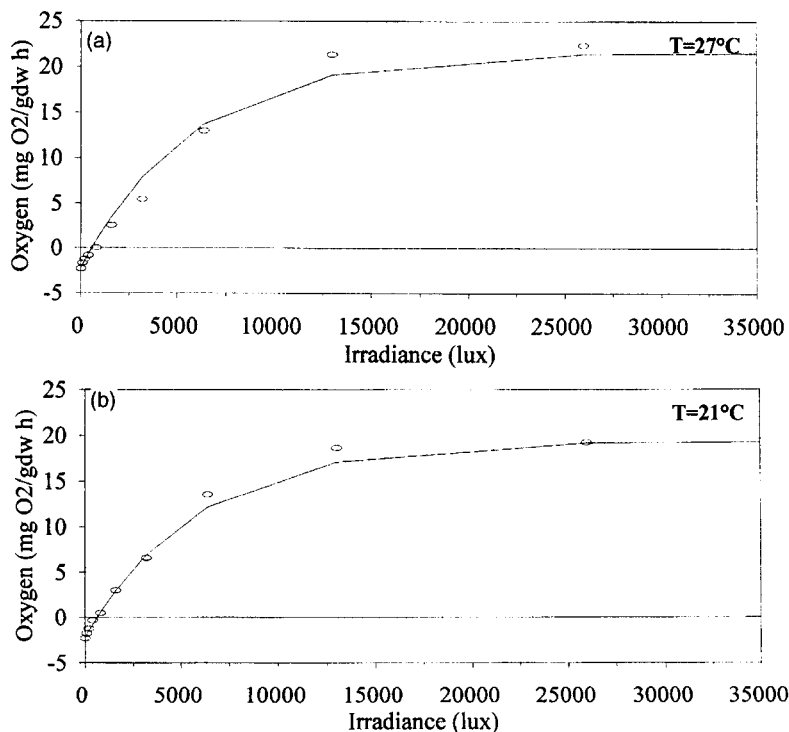


Fig. 2. Model fitting of the Brocca and Felicini (1981) data set, used for calibrating the dependence of *Ulva* growth rate from incident light intensity and temperature. Data refer to temperatures of 27°C (a) and 21°C (b).

posed by Fujita (1985),  $V_{NH} = 5.2$  mg N/(g dw · h),  $k_{NH} = 0.7$  mg N/l, have been chosen as a first guess, because the experimental conditions there described seemed to best approach a situation in which *Ulva* growth is not limited.

As regards the assimilation of oxidized forms of nitrogen, the experimental database is not as large, but it has been recognized that its uptake rate is about five times slower than that of the reduced form (Lapointe and Tenore, 1981). The uptake rate for this nutrient, as measured by Bjornaster and Wheeler (1990) varies approximately between 0.1 to 0.4 mg N/(g dw · h), whereas Lavery and McComb (1991), in different conditions found maximum uptake values of either 0.82 mg N/(gdw h), with a corresponding half saturation constant of 0.25 mg N/l, or 1.2 mg N/(gdw · h), with half saturation equal to 0.5 mg N/l. Lapointe's estimates indicate instead 0.2 and 0.4 as maximum uptakes and a half saturation constant smaller than 0.02. While waiting for further experimental findings, the same criterion adopted above has led to the choice of values proposed by Lavery and McComb (1991), that is, 1.2 mg N (g dw · h)<sup>-1</sup> for  $V_{NO}$  and 0.4 mg N/l for  $k_{NO}$ , among the ones listed in Table 1.

The choice of a very low half saturation constant for phosphorus, ( $k_p = 0.01$  mg P/l), is in agreement with findings that the growth of *Ulva r.* is not limited above 0.03 mg P/l.

The subset of parameters linked to the influence of temperature and light on *Ulva r.* growth and respiration have been estimated mainly relying on data reported by Brocca and Felicini (1981), regarding a series of measurements of dark respiration and

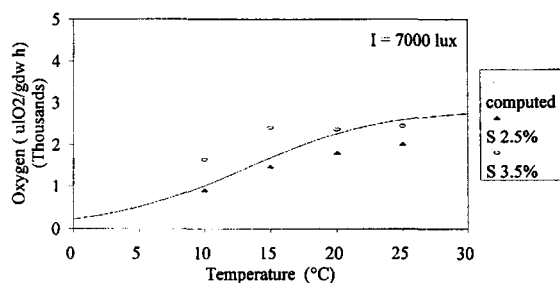


Fig. 3. *Ulva* growth rate as a function of incident light intensity; functional response of the model compared with the Zavodnik (1987) experimental data set.

gross oxygen production rate as a function of light intensity at four different temperatures.

After estimating a first set of parameters on a subset of the available data, the whole set has been used for testing the consistency of the model and improving the estimates, by varying  $I_0$ ,  $\zeta_p$ ,  $e$ ,  $\vartheta_p$  around the first approximation values and choosing the combination ( $I_0 = 5800$  lx,  $\zeta_p = 0.3^\circ\text{C}^{-1}$  and  $\vartheta_p = 10.0^\circ\text{C}$ ). This minimizes the distance between the model and the observations, the parameter regarding respiration being fixed at the best estimates ( $\zeta_{resp} = 0.2^\circ\text{C}^{-1}$  and  $\vartheta_{resp} = 12.5^\circ\text{C}$ ). Data and interpolation for two different temperatures are presented, as an example, in Fig. 2a and b.

The light saturation intensity obtained this way is around 30000 lx, in agreement with the data of Table 4. The temperature dependence here proposed agrees with in situ measurements reported by Zavodnik (1977), regarding the oxygen production of *Ulva r.* in a marine site on the North Adriatic Coast at fixed light intensity (7000 lx); as is shown in Fig. 3, the calculated gross oxygen production lies between the two series of data.

The effects of light and temperature on the growth of *Ulva r.* sampled in the the lagoon of Venice are still under investigation. A first analysis has shown that the formulations here adopted can describe these data (Riccardi and Solidoro, 1996).

## 7. Discussion of model results

The structure of the model is reported, as well as the parameter values in Table 5. Once again it should be pointed out that this structure can explain the

Table 4  
Irradiance saturation levels

$I_0$ (lx)	Notes	Reference
27000	no photoinhibition	Brocca and Felicini, 1981
27000		Fujita, 1985
39000	no photoinhibition	Hough and Fornwall, 1988
27000		King and Schramm, 1976
32000		Lapointe and Tenore, 1981
> 15000		Mac Farlan and Smith, 1982
50000	parameter of a model	Menesguen and Salamon, 1987
30000		Parker, 1981
36000	weak photoinhibition	Rosemberg and Ramus, 1982a;
above 90000		Rosemberg and Ramus, 1982b



great variability of the experimental results reported in Tables 1–4. Some short-term simulations were performed for testing the model by comparing its output with the results of short-term batch experiments.

In order to follow the dynamics of dissolved nutrients, mass balances are set up for these compounds:

$$\begin{aligned}\frac{d[\text{NH}_4^+]}{dT} &= -V_{\text{NH}}([\text{NH}_4^+], Q)B \\ &= -\left(V_{\text{mNH}} \frac{[\text{NH}_4^+]}{k_{\text{NH}} + [\text{NH}_4^+]}\right) \\ &\quad \times \left(\frac{Q_{\text{max}} - Q}{Q_{\text{max}} - Q_{\text{min}}}\right)B; \quad (17)\end{aligned}$$

$$\begin{aligned}\frac{d[\text{NO}_x^-]}{dT} &= -V_{\text{NO}}([\text{NO}_x^-], Q)B \\ &= -\left(V_{\text{mNO}} \frac{[\text{NO}_x^-]}{k_{\text{NO}} + [\text{NO}_x^-]}\right) \\ &\quad \times \left(\frac{Q_{\text{max}} - Q}{Q_{\text{max}} - Q_{\text{min}}}\right)B; \quad (18)\end{aligned}$$

$$\begin{aligned}\frac{d[P]}{dT} &= -\text{PCR} \mu(I, T, Q, [P])B \\ &= -\text{PCR} \mu_{\text{max}} g_1(Q) g_2([P]) \\ &\quad \times g_3(I) g_4(T). \quad (19)\end{aligned}$$

The choice of the subset of parameters regarding *Ulva r.* growth as a function of the uptake of reduced nitrogen has been tested by using the Eqs. (1), (2) and (17) of the model, to simulate the dependence of the assimilation rate of  $\text{NH}_4^+$  on the level of  $Q$  found by Fujita (1985) under optimal nitrate, phosphorus, temperature and light conditions. Time evolutions of quota, biomass and ammonium concentration are reported in Fig. 4(a–c) as a function of the initial value of quota,  $Q_0$ . The lower  $Q_0$ , the faster the assimilation of the nutrient and the increase in  $Q$ , as a comparison of Fig. 4a and b shows. For the highest  $Q_0$  (Fig. 4c) the decline of nutrients is less pronounced. The internal quota, opposite to the other cases, decreases from the beginning, because the biomass increase is faster. Uptake rates, determined by computing the time derivative of external nutrient

Table 5

Macroalgae growth model: Mass balances, functional expressions, parameters

Mass balances			
$dB/dt = (\mu - f_{\text{death}}) \cdot B$			
$dQ/dt = (V_{\text{NH}} + V_{\text{NO}}) - \mu \cdot Q$			
$d[\text{DO}]/dt = [\varphi - f_{\text{resp}}] \cdot B$			
$d[\text{NH}_4^+]/dt = -V_{\text{NH}} \cdot B$			
$d[\text{NO}_x^-]/dt = -V_{\text{NO}} \cdot B$			
$d[\text{PO}_4^{3-}]/dt = -\text{PCR} \cdot \mu \cdot B$			
Functional expressions			
$\mu = \mu_{\text{max}} \cdot g_1(Q) \cdot g_2(P) \cdot g_3(I) \cdot g_4(T)$			
$\varphi = \varphi_{\text{max}} \cdot g_1(Q) \cdot g_2(P) \cdot g_3(I) \cdot g_4(T)$			
$g_1(Q) = (Q - Q_{\text{min}})/(Q - k_c)$			
$g_2([P]) = [P]/(k_p + [P])$			
$g_3(T) = \{1 + \exp[-\zeta_p \cdot (T - \vartheta_p)]\}^{-1}$			
$g_4(I) = 1 - \exp(-I/I_0) \quad I = I_{\text{inc}} \cdot \exp[-\varepsilon_w - \varepsilon_B \cdot B]$			
$V_{\text{NX}} = V_{\text{mNX}} \cdot f_1([\text{NX}]) \cdot f_2(Q)$			
$f_1([\text{NO}_x^-]) = [\text{NO}_x^-]/(k_{\text{NO}} + [\text{NO}_x^-]) f_1([\text{NH}_4^+]) = [\text{NH}_4^+]/(k_{\text{NH}} + [\text{NH}_4^+])$			
$f_2(Q) = (Q_{\text{max}} - Q)/(Q_{\text{max}} - Q_{\text{min}})$			
$f_{\text{death}} = \alpha B^\beta + k_t \cdot \frac{\max[(f_{\text{resp}} \cdot B - \text{DO}), 0]}{f_{\text{resp}} \cdot B}$			
$f_{\text{resp}} = k_{\text{resp}} \{1 + \exp[-\zeta_{\text{resp}} \cdot (T - \vartheta_{\text{resp}})]\}^{-1}$			
Parameters			
$\mu_{\text{max}}$	0.45 day <sup>-1</sup>	$V_{\text{mNH}}$	5.2 mg N (g dw) <sup>-1</sup> h <sup>-1</sup>
$\varphi_{\text{max}}$	27.5 mg O (g dw) <sup>-1</sup> h <sup>-1</sup>	$V_{\text{mNO}}$	0.9 mg N (g dw) <sup>-1</sup> h <sup>-1</sup>
$Q_{\text{max}}$	45 mg N/(g dw)	$k_{\text{NH}}$	0.7 mg N/l
$Q_{\text{min}}$	10 mg N/(g dw)	$k_{\text{NO}}$	0.07 mg N/l
$k_c$	8 mg N/(g dw)	$k_d$	0.03 day <sup>-1</sup>
$k_p$	0.01 mg P/l	$\beta$	-0.16
$\zeta_p$	0.3°C <sup>-1</sup>	$k_t$	1
$\vartheta_p$	10°C	$k_{\text{resp}}$	2.5 mg O (g dw) <sup>-1</sup> h <sup>-1</sup>
$I_0$	5800 lx	$\zeta_{\text{resp}}$	0.2°C <sup>-1</sup>
$\varepsilon_B$	20 (g dw) <sup>-1</sup> l	$\vartheta_{\text{resp}}$	12.5°C
$\varepsilon_w$	0.04 m <sup>-1</sup>		

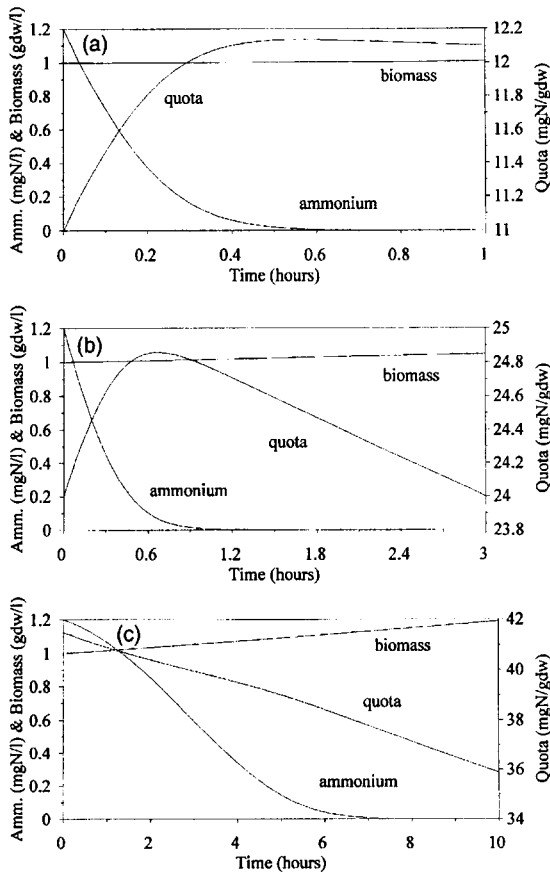


Fig. 4. Time evolution of biomass, quota and external ammonium concentration for initial values of quota set to 10 (a), 20 (b) and 40 (c).

concentrations, are plotted versus the external concentration at which they were computed in Fig. 5. The assimilation rate is strongly dependent on  $Q_0$ , which affects the shape of the kinetic. For low  $Q_0$ , the specific rate of assimilation is high and approximately linearly related to the external concentration. The rate decreases as the value of  $Q_0$  increases, and the shape of the kinetic resembles a Monod one until, at a very high  $Q_0$ , inhibition effects occur. These features are in agreement with the experimental findings of Fujita (1985) on starved and enriched cultures studied under controlled conditions.

The formulations and the parametrization here proposed, are consistent also with the results of another investigation (Cohen and Neori, 1991). The empirical function used by these authors for fitting their data (empty squares in Fig. 6) compares well

with the value assumed by  $Q$  at steady state as a function of the external ammonia concentration (dotted line in Fig. 6). The relationship between these two variables can be analytically expressed by solving the quota mass balance at steady state conditions. A closer agreement can be reached by tuning uptake parameters, for example by decreasing the half saturation constant at 0.4 mg N/l (continuous line in Fig. 6).

Despite the apparent contradiction with  $g_1$  in Eq. (7), the structure of the model is also in agreement with the experimental findings (Duke et al., 1989a; Duke et al., 1989b), which show a negative correlation between growth and  $Q$ . In fact, growth rate at steady state conditions,  $dQ/dt = 0$ , can be derived only from Eq. (15):

$$\begin{aligned}\tilde{\mu} &= \mu(I, T, Q, [P]) = \mu(I, T, [P]) g_1(Q) \\ &= \frac{V_{NH}([NH_4^+], Q) + V_{NO}([NO_3^-], Q)}{Q} \\ &= \frac{V_N([N], Q)}{Q}\end{aligned}\quad (20)$$

and, since  $V([N], Q)$  decreases by increasing  $Q$  (see Eqs. (12) and (14)),  $\tilde{\mu}$  is negatively correlated with  $Q$ ; see also Table 5.

The model has been applied for the simulation of a series of short term experiments, aimed at studying the rate of assimilation of  $NH_4^+$  and  $NO_3^-$  under controlled conditions (Ravera, 1994). Functional measurements can be very useful for a first estimate of the rate of each single process, even if, being carried out in the laboratory for quite a short time, their extension to the behaviour in situ is not straightforward. After preconditioning, *Ulva r. sam-*

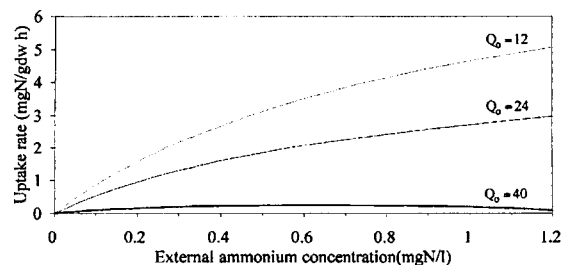


Fig. 5. Simulated uptake rate as a function of the initial value of quota  $Q_0$ ; the features are in agreement with the experimental findings of Fujita (1985).

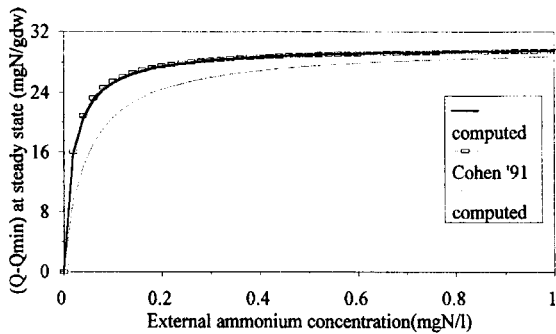


Fig. 6. Non-structural steady state nitrogen levels as a function of external Nitrogen concentration; comparison between the model and the curve interpolating the Cohen and Neori (1991) experimental data.

ples collected in the Venice lagoon were grown at constant light intensity and temperature in a circulating medium for 30 h, during which the solution was sampled in order to determine the concentration of nutrients. Initial and final biomass amounts were also measured. In both simulations, initial conditions for  $Q$  (not measured) were set to 35 mg N/(g dw), a value considered representative for these samples (Ravera, private communication).

In Fig. 7 and Fig. 8a, model simulations are compared with the results of two of these experiments, differing for nitrogen and biomass initial values. The higher level of biomass in the first case, Fig. 7, causes a rapid decrease in the concentration of nutrients, which is correctly reproduced by the

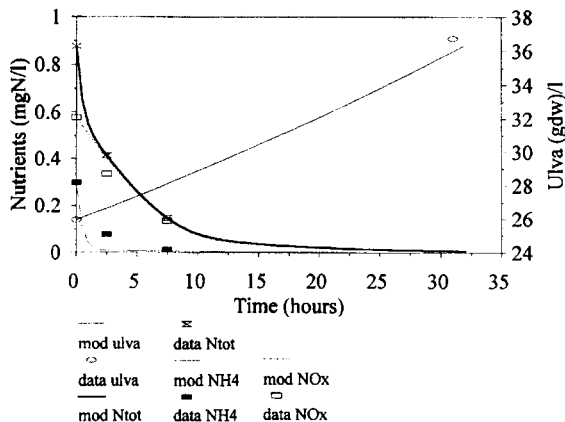


Fig. 7. Comparison between model output and a first set of experimental data aimed at studying the uptake rate of nitrogen under controlled conditions (Ravera, 1994).

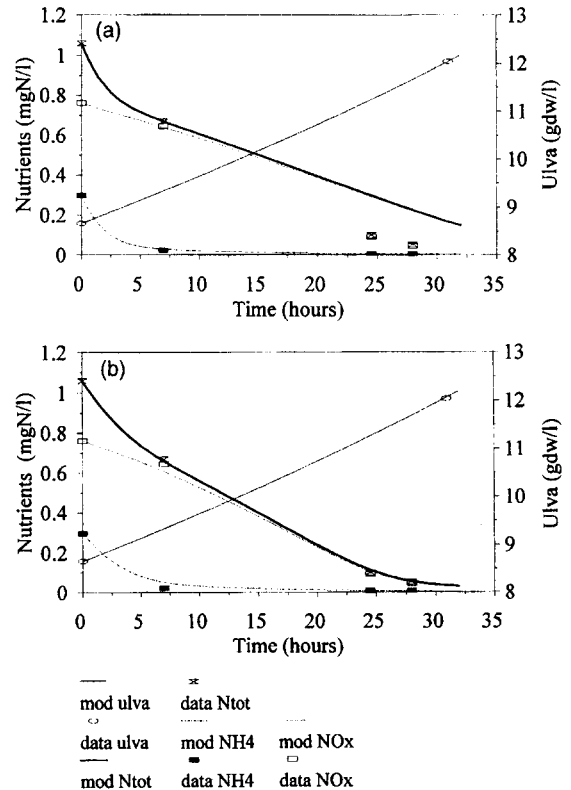


Fig. 8. Comparison between model output and another set of experimental data aimed at studying the uptake rate of nitrogen under controlled conditions (Ravera, 1994). Figure (b), obtained with a modified uptake parameter, shows a better agreement in nitrogen evolution.

model if the total nitrogen is considered, whereas the agreement, though fairly good, is not as close for the two different nitrogen forms. In the second experi-

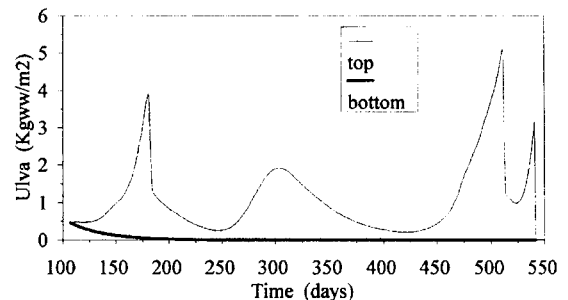


Fig. 9. Biomass evolution at the top (thin line) and bottom (bold line) layers of the grass bed. Simulation relies on data recorded during 1990–1991 in a sampling station located in the lagoon of Venice (S. Giuliano).

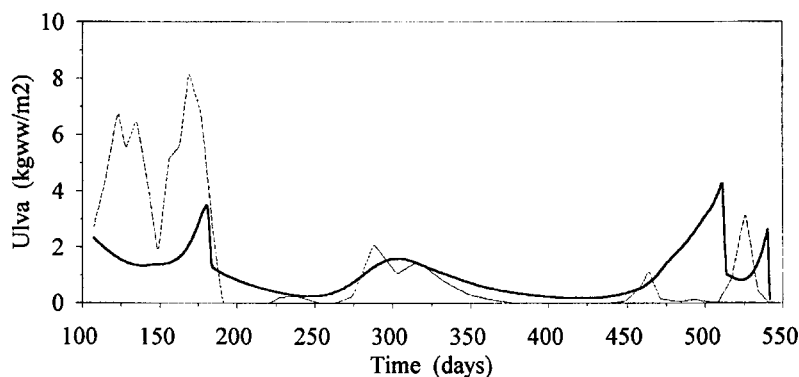


Fig. 10. Comparison between observed biomass evolution during years 1990–1991 at S. Giuliano (thin, dotted line) and model simulation (bold line). Total biomass in the water column is obtained by summing the values of each layer.

ment, Fig. 8a, nutrient depletion is less pronounced and the discrepancy as regards the  $\text{NO}_x^-$  concentration emphasizes the need for a recalibration of its uptake parameters. A formal approach would need the support of a larger set of experiments, and therefore the space between the parameters has been explored in a non-systematic way. However, a better agreement between the simulation and the experimental data can be obtained, as shown in Fig. 8b (to be compared with Fig. 8a), in which the simulation has been run by setting  $V_{\text{NO}} = 0.9 \text{ mg N (g dw)}^{-1} \text{ h}^{-1}$ ,  $k_{\text{NO}} = 0.07 \text{ mg N/l}$  and  $38 \text{ mg N/(g dw)}$  for  $Q_0$ . In every case biomass growth is appropriately described.

Even though a simple zerodimensional model can not reproduce the complexity of a real ecosystem, the comparison between model simulation and field

data is of great importance for calibrating and validating the model against an appropriate goal function, as the distance between observed and computed densities of biomass. In order to capture the major features of the seasonal evolution of the system, Eq. (3) has been modified by adding the effects of the reareation, phytoplankton activity and mineralization of detritus (Solidoro et al., 1995, Pastres et al., 1995). Therefore, a first mass balance for detritus has been considered, since the dead organic matter is a source of nutrients and also increases the shading of *Ulva* *r.*, but not that of phytoplankton. Shading by phytoplankton and self-shading have also been considered. Eqs. (1–3) has been solved, together with the detritus equation, introducing nutrients, phytoplankton and temperature records as forcing functions (Sfriso, 1994), while an average yearly pattern

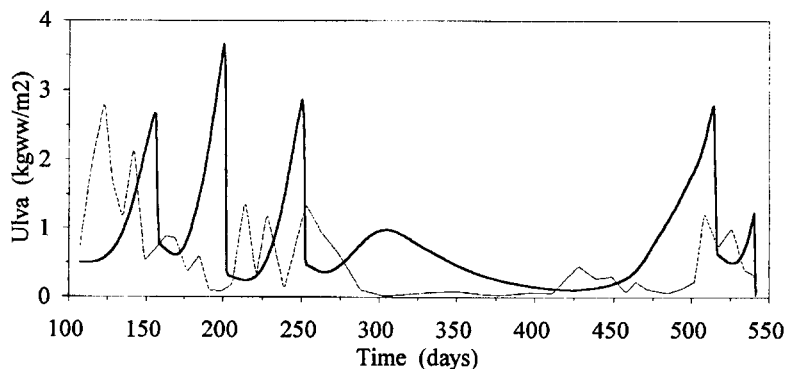


Fig. 11. Comparison between observed biomass evolution during the years 1990–1991 at Alberoni (thin, dotted line) and model simulation (bold line). Total biomass in the water column is obtained by summing the values of each layer.

of light intensity has been estimated from a record of meteorological data. In this way *Ulva r.* dynamics are forced by realistic levels of nutrients and the results

can be compared with the observations, without complicating the model. A set of preliminary simulations showed the necessity of a vertical discretization

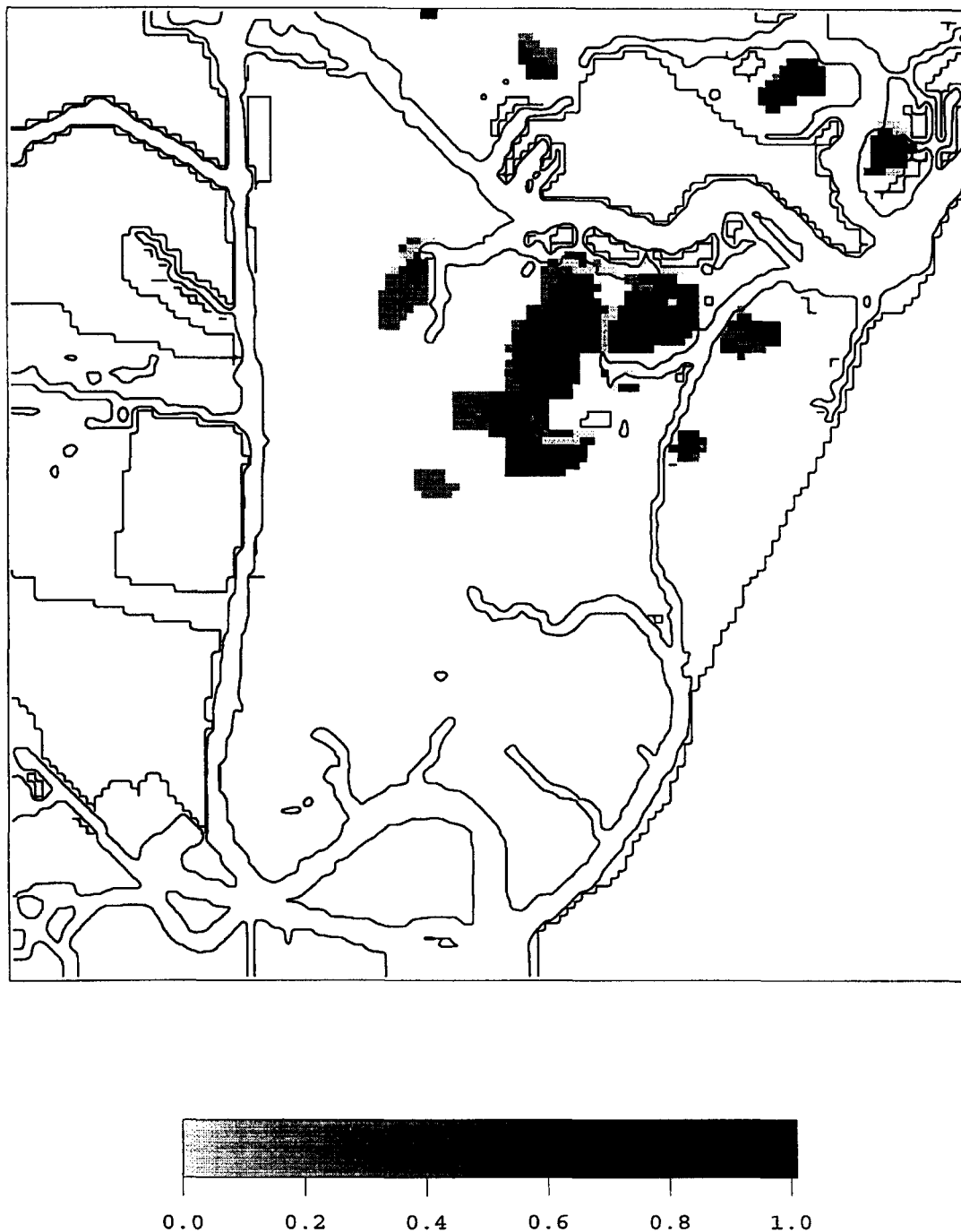


Fig. 12. Distribution of *ulva* biomass in a 3D simulation. Values vary from 0 (white) to 1 kg dw/m<sup>2</sup> (dark grey).

for reaching levels of biomass close to the observations. This requires the solution of a reaction–diffusion equation for the dissolved oxygen. In fact, the grass bed is not homogeneous, since its upper layers receive most of the incident radiation and are also well aerated. On the contrary, the bottom layers are heavily shaded and therefore their photosynthetic activity is reduced, as can be seen in Fig. 9. The vertical discretization of the water column emphasizes also the role of reaeration and diffusion in determining the oxygen profile, since the model becomes sensitive to the transport coefficients within the water column and at the interface with the atmosphere.

The model output is capable of capturing the main features of the seasonal evolution at S Giuliano (Fig. 10), and Alberoni (Fig. 11), two sampling stations located in the lagoon of Venice. In these figures the experimental data of standing crop (dotted line) are compared with the simulated total biomass in the water column (continuous bold line). Total biomass is obtained by summing the biomasses for each layer, i.e. the continuous line in Fig. 9 is the sum of values reported in Fig. 8. It should be pointed out that the most important forcing function, the actual incident light, was not recorded, and this could partially explain the difference between observed and computed biomass. For this reason, a formal calibration of the parameters in  $f(I)$  was not attempted, even though the model output is extremely sensitive to the variation of shading coefficients.

In a similar attempt with a zerodimensional model (Bendoricchio et al., 1994), the observed concentrations of dissolved oxygen were interpolated and used as a forcing function in the mortality term, which turned out to be the major factor in regulating *Ulva r.* dynamics. These results are confirmed and improved by the present study, where oxygen evolution is simulated on the basis of its mass balance, and therefore acts as a real feedback of the system.

Finally, a few attempts have been made to test the behaviour of the structure in a truly 3D model of the central part of the Lagoon of Venice, which solve the reaction diffusion–equation for ten state variables: temperature, concentration of  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ , detritus and OD, densities of phytoplankton, zooplankton and *Ulva r.*, and quota level. In a first model run, the initial conditions for all state variables were not

space-dependent. Further, *Ulva r.* density and the related internal nitrogen were not transported as passive solutes, like the other state variables. Despite these rough approximations, the model yielded a well defined spatial pattern, which indicates the areas where *Ulva r.* is likely to survive. A more realistic distribution, Fig. 12, as been obtained by using initial values for *Ulva r.* deduced from a qualitative analysis of remote sensing data.

## 8. Concluding remarks

A model has been identified, based on the physiological and ecological features of *Ulva rigida*. A one-step formulation does not enable the description of both nitrogen uptake and growth rate, because *Ulva r.* growth is observed also when the concentration of this element is very low in the external medium. These difficulties are overcome by adopting a two-step kinetic, which takes into account the luxury uptake. The results are globally satisfactory, also considering the great variability of the kinetic parameters. The model is consistent with the observations reported in specific literature, and its output is in satisfactory quantitative agreement with short term laboratory experiments, aimed at estimating uptake and growth rates for *Ulva r.* sampled in the lagoon of Venice.

After introducing a vertical discretization, the model has been applied for describing two sets of field data collected in the lagoon of Venice, and has succeeded in reproducing the main features of the seasonal evolution of *Ulva r.*. The vertical discretization greatly affects the quality of the simulation by allowing a better modelling of the self-shading effect and describing more appropriately the space-time evolution of DO within the water column. These results could be further improved by using the actual temperature and irradiance instead of an average yearly pattern of these two important forcing functions.

A first implementation in a 3D reaction–diffusion model gave encouraging results, prospecting the possibility of analysing the long term dynamics of *Ulva r.* and its competition with the phytoplanktonic community. Such an analysis will need the support of remote sensing data, both for setting the initial condi-

tions and for calibrating and validating the model. Nevertheless, the results so far obtained indicate that the model could become a useful tool for explaining the spatial distribution of these communities in the lagoon of Venice.

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