Long term simulations of population dynamics of *Ulva r.* in the lagoon of Venice

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**Abstract**

The dynamic of macroalgae is implemented in a 3D transport-water-quality model of the central part of the lagoon of Venice. Ulva biomass density and nitrogen concentration in Ulva tissue have been added to the set of state variables previously considered, that is to phytoplankton and zooplankton densities, concentrations of nutrients in water, detritus and dissolved oxygen. The model shows that Ulva succeeds in the competition with the phytoplanktonic community in the shallower areas, where water temperature and irradiance levels reaching the bottom are sufficient to sustain growth. Long term evolutions of Ulva colonies, under different scenarios of forcing functions, show that adverse metoeclimatic conditions can be more effective in reducing Ulva biomass than a consistent decrease in the loads of Nitrogen. © 1997 Elsevier Science B.V.

**Keywords:** Water quality; Macroalgae; Competition; 3D model; Venice

1. Introduction

In the early eighties, the macroalgae community became an important component of the ecosystem in the Venice lagoon, reaching standing crops at an order of magnitude higher than those of the phytoplanktonic pool in 1987 and 1989. High levels of biomass production have been main-
reasons for such a change and at forecasting the long-term evolution of the system.

A few models of the dynamic of *Ulva* r have already been proposed, both zero dimensional (Bendoricchio et al., 1994; Pecenik et al., 1991) and one dimensional (Solidoro et al., 1997b), but a full understanding of the seasonal cycle of macroalgae and of the mechanisms underlying the behaviour of the ecosystem requires the development of a 3D model. In fact, only in this way one can describe the transport phenomena and the interactions between biotic and abiotic components, as well as the competition with other communities, such as that of phytoplankton. This paper presents the implementation of *Ulva* r. dynamic (Solidoro et al., 1997b) in a 3D model (Dejak and Pecenik, 1987), whose major features are briefly outlined below.

2. General features of the 3D model

The 3D finite-difference model covers the central part of the lagoon of Venice and includes the most important industrial area and the city of Venice. This area is divided on a mesh of 100 m by 100 m, with a vertical step of 1 m, in order to reproduce the bathymetry in sufficient detail (Fig. 1). The model, developed during the eighties, couples transport processes with the dynamics of the communities of primary producers and that of zooplankton (Dejak and Pecenik, 1987; Dejak et al., 1990), and succeeds in simulating the seasonal evolution of the lower trophic levels. The dynamic of the dissolved oxygen concentration is also included, as it is an important water quality index.

Advective terms are not considered (Dejak et al., 1987a), because of the marginal influence of the residual current in this water body. As a consequence, the average effect of tidal agitation has been embodied in the turbulent diffusion. Eddy diffusion coefficients are the same for all species, but they are not constant throughout the spatial domain. The horizontal diffusivities have been estimated on the basis of a statistical approach, as in Dejak et al. (1995). Along the vertical column, eddy diffusivities have been calibrated by comparing the model output with many temperature profiles observed in the deepest channels (Dejak et al., 1992). Open boundary conditions are discussed in (Dejak et al., 1987b).

After the inclusion of *Ulva* r. dynamics (Solidoro et al., 1995), the model follows the evolution of eleven state variables: zooplankton (Z), phytoplankton (P) and *Ulva* r. (U) density; internal nitrogen in *Ulva* r., quota, (Q), concentrations of NH$_4^+$, NO$_3^-$ and PO$_4^{3-}$ in the water, nitrogen as detritus, (DN), nitrogen in the sediment, (SN), and dissolved oxygen (DO).

Temperature, $T$, is considered as a state variable, because it varies within the spatial domain. Its seasonal evolution is forced by solar radiation and heat exchanges with the atmosphere (Dejak et al., 1992). Local perturbations, due to the presence of a power plant, are also taken into account. Heat diffusion within the water body is treated in the same way as the diffusion of the other state variables.

![Fig. 1. Area covered by the model and depth along the section A-A'. Gray intensity increases with depth. Superimposed pattern and encircled letters mark the areas a, b, c and d. Areas b and d are mostly 1 m deep, area a 2 m deep, while area c contains both 1 and 2 m deep regions. Areas b and c are physically separated by a 4 m deep channel.](image-url)
The nutrients loads are, together with energetic inputs, forcing functions for the model. The loads have been estimated on the basis of the available data (CVN, 1993); immission points are shown in Fig. 1.

The reaction–diffusion equation is solved by a fractional step method, that is by decomposing the 3D problem in three 1D ones. The integration is carried out by using an implicit method, (Dejak et al., 1987a,b), which guarantees stability and conservativity at high diffusion numbers. The method has been efficiently implemented, also in the exploitation of the potentialities of vector parallel supercomputer (Pastres et al., 1995), but, at present, the model can also be run on medium-size workstations.

3. Major features of the trophic submodel

The formulations here proposed, Table 1, take into account the characteristics of two communities of primary producers, phytoplankton and macroalgae. The governing equations for the two groups will be briefly discussed together, in order to highlight their similarities and differences. Formulations concerning the dynamics of Ulva and their experimental basis are discussed in detail in Solidoro et al. (1997b).

Phytoplanktonic species are pooled, and the composition of the pool in terms of major chemicals is kept constant (Redfield, 1934). This implies that the cells are in a steady-state condition and, therefore, the processes of growth and assimilation of nutrients from the water column are described by a single step kinetic. On the contrary, experimental evidence (Cohen and Neori, 1991; Fujita, 1985) indicates as more appropriate a distinction between assimilation and growth for Ulva r., because macroalgae store the excess of Nitrogen and use it for maintaining their metabolic efficiency when the concentration of Nitrogen in the water body is low. Internal storage plays a key role in regulating both growth rate, that does not depend on the external concentration of nitrogen, Eq. (14), and uptake rates, which are inversely related to storage, and proportional to external concentration, Eq. (12), Eq. (13).

The influence of limiting factors is accounted for in a multiplicative formulation for both communities, Eqs. (14) and (24), (Joergensen, 1988). A Monod-type kinetic describes the limitation of phytoplankton growth and macroalgae uptake, due to the lack of nitrogen Eqs. (28), (12) and (13), and phosphorus, Eqs. (29) and (18). The two groups assimilate nutrients in accordance with their own kinetic, as there is no a priori definition of a competitive efficiency. In this way, rates of uptake vary with local conditions, and macroalgae and Ulva r. compete for nutrients when their concentrations are low.

The dependence of phytoplankton growth on water temperature is modelled by a Lassiter–Kearns function, Eq. (27), whereas a sigmoidal function has been chosen for macroalgae, Eq. (20). The influence of light is described by a Steel function for phytoplankton, Eq. (25), while an asymptotic formulation has been adopted for the other community, Eq. (15). Other formulations, which consider inhibition phenomena at high irradiance values, can be found in literature (Bendorichio et al., 1993), but they require the estimation of a greater number of parameters. However, they would be in close agreement with the formulations here proposed, within the range of irradiance commonly found in the lagoon of Venice.

Incident light at the surface is interpolated from averaged monthly values, and its attenuation along the water column is computed according to a discretization of the Lambert–Beer law. Phytoplankton is affected only by self-shading, Eq. (26), as its presence is greater in the upper layers, while Ulva r., being in the deepest layers, is shaded by phytoplankton and by itself, Eq. (19).

Oxygen availability is another factor in competition. For both phytoplankton and macroalgae, the respiration rate is a linear function of the density, but the temperature dependence is different, being exponential for phytoplankton, Eq. (2), and asymptotical for Ulva, Eq. (20). In the model here proposed, a negative feedback relates the mortality rate of Ulva r. with the concentration of DO. The increase in mortality rate is proportional to the difference between the oxygen demand exerted by respiration, and the availability of DO, Eq. (3), that is, to the fraction of biomass that can not respire and is likely to be damaged.
Table 1
State variables and state equations of the model and functional forms used in the model

Global model

<table>
<thead>
<tr>
<th>State variables</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Z</td>
<td>density of zooplankton</td>
<td>mgC/l</td>
</tr>
<tr>
<td>P</td>
<td>density of phytoplankton</td>
<td>mgC/l</td>
</tr>
<tr>
<td>U</td>
<td>density of Ulva</td>
<td>gdw/l</td>
</tr>
<tr>
<td>Q</td>
<td>quota (nitrogen concentration in Ulva tissue)</td>
<td>mgN/gdw</td>
</tr>
<tr>
<td>(NH_4^+)</td>
<td>water concentration of reduced inorganic nitrogen</td>
<td>mgN/l</td>
</tr>
<tr>
<td>(NO_3^-)</td>
<td>water concentration of oxidized inorganic nitrogen</td>
<td>mgN/l</td>
</tr>
<tr>
<td>(PO_4^{3-})</td>
<td>water concentration of reactive phosphorous</td>
<td>mgP/l</td>
</tr>
<tr>
<td>DN</td>
<td>nitrogen in the detritus</td>
<td>mgN/l</td>
</tr>
<tr>
<td>SN</td>
<td>nitrogen in the sediment</td>
<td>mgN/l</td>
</tr>
<tr>
<td>DO</td>
<td>water concentration of dissolved oxygen</td>
<td>mgO/l</td>
</tr>
</tbody>
</table>

Equations

\[
dZ/dt = [k_{gzf}(P)Z \cdot E_{oi} - K_{az} - k_{ez}] \cdot a(T) \cdot Z \]

\[
dP/dt = \phi \cdot P \cdot (k_{a} \cdot a(T) + k_{a0} + k_{aP} \cdot a(T)) \cdot P
- k_{gzf}(T) \cdot (P) \cdot Z
\]

\[
dU/dt = \mu \cdot U - K_{at} \cdot U \cdot \max[\{f_{na}(T) \cdot (U - DO)\}, 0]
\]

\[
dQ/dt = T_{SU} - \mu \cdot Q
\]

\[
dNH_4^+/dt = -T_{SUNH} \cdot U - T_{SPNH} \cdot P
+ k_{a} \cdot a(T) \cdot NH_4^+
+ R_{NC} \cdot \{k_{aP} + k_{aaz} \cdot Z\} \cdot a(T)
\]

\[
dNO_3^-/dt = -T_{SUNO} \cdot U - T_{SPNO} \cdot P
- k_{a} \cdot a(T) \cdot NO_3^-
\]

\[
dPO_4^{3-}/dt = -T_{SUSO} \cdot U - T_{SPSO} \cdot P
+ R_{PC} \cdot \{k_{aP} + k_{aaz} \cdot Z\} \cdot a(T)
\]

\[
dDN/dt = R_{NC} \cdot \{k_{a} \cdot a(T) + k_{a0} \cdot a(T) \} \cdot Z
+ (1 - E_{a}) \cdot k_{gzf}(P) \cdot Z
- (k_{dec} + k_{az}) \cdot DN + k_{az} \cdot DO
+ Qk \cdot \max[(f_{na}(T) \cdot (U - DO)); 0]
\]

\[
dSN/dt = k_{a} \cdot DN - k_{a} \cdot SN \cdot a(T)
\]

Global model

\[
dDO/dt = \left\{ \psi \mu - k_{b}(T) \cdot f_{sg} \right\} \cdot U + R_{NC} \cdot \phi - k_{p} \cdot P
\]

\[
- R_{m} \cdot k_{m} \cdot NH_4^+ \cdot R_{SN} \cdot k_{dec}(DN)
+ SN \cdot a(T) + k_{rec}(DO_{nat} - DO)
\]

Functional forms used in the macroalgae model

\[
T_{SU} = T_{SUNH} + T_{SUNO}
\]

\[
T_{SUNH} = \left\{ V_{NH} \cdot NH_4^+ / (NH_4^+ + k_{NH}) \right\}
\]

\[
T_{SUNO} = \left\{ V_{NO} \cdot NO_3^- / (NO_3^- + k_{NO}) \right\}
\]

\[
\mu = \mu_{max} \cdot f_{a}(T) \cdot f_{a}(Q) \cdot f_{a}(PO_4^{3-})
\]

\[
f_{a}(I) = 1 - \exp(-I_{i}/I_{0})
\]

\[
f_{a}(T) = \left[ \frac{1}{[1 + \exp(-\gamma(T - \delta))]^{\eta}} \right]
\]

\[
f_{a}(Q) = (Q - Q_{min})/(Q - k_{c})
\]

\[
f_{a}(PO_4^{3-}) = PO_4^{3-} / (PO_4^{3-} + k_{cp})
\]

\[
I_{i} = I \exp[\epsilon_{a}P(z - 1) + \cdots + P(1)]
+ \epsilon_{a}[B(z - 1) + \cdots + B(1)] + \epsilon_{a}^{e}
\]

\[
f_{a}(T) = \frac{1}{[1 + \exp(-\gamma(T - \delta))]^{\eta}}
\]

Functional forms used in the phytoplankton model

\[
T_{SPNH} = R_{NC} \left( \frac{NH_4^+}{N_{tot}} \right) \phi
\]

\[
T_{SPNO} = R_{NC} \left( \frac{NO_3^-}{N_{tot}} \right) \phi
\]

\[
f(P) = \frac{P}{(P + k_{cp})}
\]

\[
\phi = \phi_{max} \cdot f(T) \cdot f(N) \cdot f(PO_4^{3-})
\]

\[
f(T) = \epsilon_{c} \cdot \exp(-\epsilon_{c} \cdot \exp(-\epsilon_{c} \cdot \exp(-\epsilon_{c} \cdot \exp(-\epsilon_{c})))
\]
The intrinsic mortality is linear for phytoplankton, Eq. (2), but is proportional to $U^2$ for the other community, Eq. (3). Phytoplankton is grazed by zooplankton, following a type II functional response, Eq. (23), while the predation of phytoplankton and macroalgae is shown in Fig. 2a, while Fig. 2b displays a non-periodical evolution, obtained by modifying the shading coefficients; examples of both patterns can be observed in the lagoon of Venice. Phytoplankton blooms are shorter and more intense than macroalgae ones, and they occur before the first macroalgae bloom and after the major macroalgae collapse. A comparative analysis of a whole set of simulations shows that the phytoplankton dynamic is sensitive to changes in external environmental conditions, whereas macroalgae evolution is less affected by external factors, because of the presence of inter-

$$N_{\text{tot}} = \text{NH}_4^+ + \text{NO}_3^-$$  \hspace{1cm} (31)

$$a(T) = 1.07(T^{2.20})$$  \hspace{1cm} (32)

### Table 1 (continued)

<table>
<thead>
<tr>
<th>Global model</th>
</tr>
</thead>
<tbody>
<tr>
<td>$x_1 = k_h x_2$</td>
</tr>
<tr>
<td>$k_h = \epsilon_p (0.5P(z) + P(z-1) + \cdots + P(1))$</td>
</tr>
<tr>
<td>$f(T) = [(T_a - T)/(T_a - T_i)]^{m(T_a - T_i)} + [T_a - T_i] \exp[a(T_a - T_i)]$ (27)</td>
</tr>
<tr>
<td>$f(N) = N_{\text{tot}}/(N_{\text{tot}} + k_{po})$ (28)</td>
</tr>
<tr>
<td>$f(PO_4^-(s)) = PO_4^-(s)/(PO_4^-(s) + k_{pp})$ (29)</td>
</tr>
<tr>
<td>$DO_{\text{sat}} = 14.6244 - 0.367134T^2 + 0.0044972T^2$ $- 0.0966S + 0.00005TS + 0.0002739S^2$ (30)</td>
</tr>
</tbody>
</table>

(continued)
Table 2
Parameters used in the model

**Parameters for Ulva**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \mu_{\text{max}} )</td>
<td>0.45</td>
<td>max specific growth rate ( (d^{-1}) )</td>
</tr>
<tr>
<td>( k_{\text{IC}} )</td>
<td>7</td>
<td>critical N quota level ( (\text{mg N/g dw}) )</td>
</tr>
<tr>
<td>( V_{\text{NH}} )</td>
<td>8.5</td>
<td>max specific uptake rate for ammonium ( (\text{mg N/g dw h}) )</td>
</tr>
<tr>
<td>( V_{\text{NO}} )</td>
<td>0.45</td>
<td>max specific uptake rate for nitrate ( (\text{mg N/g dw h}) )</td>
</tr>
<tr>
<td>( k_{\text{NH}} )</td>
<td>0.1</td>
<td>half saturation for ammonium ( (\text{mg N/l}) )</td>
</tr>
<tr>
<td>( k_{\text{NO}} )</td>
<td>0.05</td>
<td>half saturation for nitrate ( (\text{mg N/l}) )</td>
</tr>
<tr>
<td>( Q_{\text{max}} )</td>
<td>42</td>
<td>max value for N quota ( (\text{mg N/g dw}) )</td>
</tr>
<tr>
<td>( Q_{\text{min}} )</td>
<td>10</td>
<td>min value for N quota ( (\text{mg N/g dw}) )</td>
</tr>
<tr>
<td>( R_{\text{UPC}} )</td>
<td>2.5</td>
<td>stochiometric ratio ( \text{(mg P/g dw)} )</td>
</tr>
<tr>
<td>( k_{\text{PUC}} )</td>
<td>2.54</td>
<td>max respiration rate ( (\text{mg O}_2/\text{g dw h}) )</td>
</tr>
<tr>
<td>( \zeta )</td>
<td>0.2</td>
<td>temperature coefficient ( ^{\circ}C^{-1} )</td>
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<tr>
<td>( \zeta' )</td>
<td>0.3</td>
<td>temperature coefficient ( ^{\circ}C^{-1} )</td>
</tr>
<tr>
<td>( \theta )</td>
<td>12.5</td>
<td>temperature coefficient ( ^{\circ}C )</td>
</tr>
<tr>
<td>( \theta' )</td>
<td>10</td>
<td>temperature coefficient ( ^{\circ}C )</td>
</tr>
<tr>
<td>( I_{\text{h}} )</td>
<td>5800</td>
<td>photosynthetic efficiency parameter ( \text{(lux)} )</td>
</tr>
<tr>
<td>( k_{\text{PUL}} )</td>
<td>0.01</td>
<td>half saturation for ( \text{PO}_4^{3-} ) ( (\text{mg P/l}) )</td>
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<tr>
<td>( \epsilon_{\text{UL}} )</td>
<td>20</td>
<td>self-shading coefficient ( (\text{g C}^{-1}) )</td>
</tr>
<tr>
<td>( k_{\text{mUL}} )</td>
<td>0.005</td>
<td>mortality rate ( (\text{h}^{-1}) )</td>
</tr>
<tr>
<td>( \gamma )</td>
<td>0.84</td>
<td>coefficient ( \text{(mg O}_2/\text{g dw}) )</td>
</tr>
<tr>
<td>( \Psi )</td>
<td>1450</td>
<td>stochiometric ratio ( \text{(mg O}_2/\text{g dw}) )</td>
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**Parameters for phytoplankton**

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<tr>
<th>Parameter</th>
<th>Value</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>( \varphi_{\text{max}} )</td>
<td>0.12</td>
<td>max specific growth rate ( (h^{-1}) )</td>
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<tr>
<td>( k_{\text{PN}} )</td>
<td>0.05</td>
<td>half-saturation for N ( (\text{mg N/l}) )</td>
</tr>
<tr>
<td>( k_{\text{PP}} )</td>
<td>0.01</td>
<td>half-saturation for ( \text{PO}_4^{3-} ) ( (\text{mg P/l}) )</td>
</tr>
<tr>
<td>( T_{\text{a}} )</td>
<td>35</td>
<td>temperature inhibition threshold growth ( (^{\circ}C) )</td>
</tr>
<tr>
<td>( T_{o} )</td>
<td>31</td>
<td>optimal temperature for growth ( (^{\circ}C) )</td>
</tr>
<tr>
<td>( I_{\text{op}} )</td>
<td>50000</td>
<td>optimal irradiance level growth ( \text{(lux)} )</td>
</tr>
<tr>
<td>( \epsilon_{\text{P}} )</td>
<td>0.001</td>
<td>self-shading coefficients ( (\text{g C}^{-1}) )</td>
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<tr>
<td>( k_{\text{PP}} )</td>
<td>0.004</td>
<td>respiration rate ( (\text{h}^{-1}) )</td>
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<tr>
<td>( k_{\text{mP}} )</td>
<td>0.005</td>
<td>mortality rate ( (\text{h}^{-1}) )</td>
</tr>
<tr>
<td>( k_{\text{sedP}} )</td>
<td>0.0005</td>
<td>sedimentation rate ( (\text{m/h}) )</td>
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<tr>
<td>( R_{\text{NC}} )</td>
<td>0.15</td>
<td>stochiometric ratio ( (\text{mg N/mg C}) )</td>
</tr>
<tr>
<td>( R_{\text{PC}} )</td>
<td>0.023</td>
<td>stochiometric ratio ( (\text{mg P/mg C}) )</td>
</tr>
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**Parameters for zooplankton**

<table>
<thead>
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<th>Parameter</th>
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<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>( k_{\text{oz}} )</td>
<td>0.05</td>
<td>grazing rate ( (\text{h}^{-1}) )</td>
</tr>
<tr>
<td>( k_{\text{mZ}} )</td>
<td>0.005</td>
<td>mortality rate ( (\text{h}^{-1}) )</td>
</tr>
<tr>
<td>( E_{\text{f}} )</td>
<td>0.7</td>
<td>grazing efficiency ( (\text{h}^{-1}) )</td>
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<tr>
<td>( k_{\text{exz}} )</td>
<td>0.002</td>
<td>excretion rate ( (\text{h}^{-1}) )</td>
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<tr>
<td>( k_{\text{PZ}} )</td>
<td>1.0</td>
<td>half-saturation for grazing ( (\text{mg C/l}) )</td>
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Table 2 (continued)

<table>
<thead>
<tr>
<th>Others Parameters</th>
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<tr>
<td>( k_{\text{sed}} )</td>
<td>0.004</td>
<td>sedimentation rate ( (\text{m/h}) )</td>
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<tr>
<td>( k_{\text{nit}} )</td>
<td>0.0023</td>
<td>nitrification rate ( (\text{h}^{-1}) )</td>
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<td>( k_{\text{dec}} )</td>
<td>0.0048</td>
<td>decay rate ( (\text{h}^{-1}) )</td>
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<tr>
<td>( k_{\text{rear}} )</td>
<td>0.045</td>
<td>reaeration rate ( (\text{h}^{-1}) )</td>
</tr>
<tr>
<td>( \epsilon_{\text{w}} )</td>
<td>0.4</td>
<td>water extinction coefficients</td>
</tr>
<tr>
<td>( S )</td>
<td>30</td>
<td>average salinity of the Venice lagoon</td>
</tr>
<tr>
<td>( R_{\text{nit}} )</td>
<td>4.5</td>
<td>stochiometric ratio</td>
</tr>
<tr>
<td>( R_{\text{ON}} )</td>
<td>17.7</td>
<td>stochiometric ratio ( (\text{mg O/mg N}) )</td>
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<tr>
<td>( R_{\text{OC}} )</td>
<td>2.66</td>
<td>stochiometric ratio ( (\text{mg O/mg C}) )</td>
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</table>

**Fig. 2.** Time evolution of phytoplankton and macroalgae in simulations obtained with the 1D reaction diffusion model for different value of the shading coefficient.
Fig. 3. Initial condition for Ulva as derived from remote sensing image (a), spatial distribution of Ulva density on day 210 of the first year of simulation (b), day 80 of the second year of simulation (c) and day 210 of the second year of simulation (d).

4. Results and discussion

4.1. Analysis of the evolution in the reference scenario of forcing functions

The 3D model allows one to study the ecosystem in realistic conditions of inflows and outflows of nutrients. In a first simulation, the initial density of macroalgae has been taken as a constant for the whole area, in order to check if the model would succeed in giving rise to temporal and spatial patterns. This simulation confirms that Ulva colonies survive only in shallower areas, less than 2 meters deep, whereas the distribution of phytoplankton is not correlated with the bathymetry. The spatial distribution of Ulva colonies is explained by the low solar radiation which reaches the bottom below that depth, in an environment characterized by a low transparency.

Spatial distributions closer to the observed ones have been obtained by assigning the initial condition for Ulva on the basis of a remote sensing image: initial Ulva density has been set to a constant value in the black area of Fig. 3a, and zero elsewhere (Solidoro et al., 1996a). Initial conditions have a considerable influence on the spatial distribution, but do not modify the essential features of the seasonal evolution. The model has been run for two consecutive years, using the same yearly scenario of nutrient inputs and meteorclimatic conditions. In this way, it is possible to analyze the contraction of Ulva colonies during the first winter, and their expansion, starting from a situation given by the model itself. The overall
seasonal evolution of *Ulva r.* has been summarized by computing the temporal evolution of *Ulva r.* total biomass, its maximum density and the area covered by macroalgae colonies. These three indices start increasing in March, when light and temperature conditions become favourable for *Ulva* growth. Macroalgae reach very high standing crops at the end of the spring, (12 kg ww/m$^2$), when they cover more than 4000 cells, with a total biomass of $15 \cdot 10^6$ kg ww. Productivity decreases in autumn, and during the winter *ulva* colonies cover a small area, with a biomass density greater than 0.1 kg/m$^2$ in less than 150 nodes.

The spatial distributions of biomass, at three significant stages of the evolution outlined above, are shown in Fig. 3. *Ulva* colonies spread quite easily in contiguous areas, where they find favourable conditions: see the difference between Fig. 3a, representing the initial situation, and Fig. 3b, which shows the spatial distribution at day 210, when biomass density is at its maximum in the first year. The colonization can be stopped or slowed down by the presence of a natural barrier, such as deep channels or large areas in which the conditions are adverse to the development. For instance, the channel between areas b and c, marked in Fig. 1, has not been invaded by macroalgae. After the winter decrease, which is noticeable in Fig. 3c, macroalgae start expanding again and reach the spatial distribution of Fig. 3d at day 210 of the second year, when their density is again at its maximum. This simulated spatial pattern is in reasonable agreement with that obtained from field data shown in Fig. 4, which was sampled in 1987 (Sfriso et al., 1989). The two spatial distributions look similar, even though the simulation has been run using an averaged meteorclimatic scenario; results could be improved by using actual data.

The spatial distribution of macroalgae within a colony depends on the intraspecific competition for nutrients. Biomass density is higher in the new colonies, and on the edge of the old ones, where the concentration of quota is maintained above the limiting threshold by the fluxes of nutrients from the surroundings. The edge of a colony acts as a barrier, which strongly decreases the nutrient concentration in the water that reaches its core. This description is supported by the distributions of NH$_4^+$, presented in Fig. 5a, and of internal nitrogen in *Ulva* (quota) presented in Fig. 5b, both taken at day 210 of the second year. Comparing figures Fig. 5a and Fig. 3d, it can be noted that the nutrient is supplied by the channels, where its concentration is higher, and is almost totally assimilated in the shallow areas where *Ulva* is present. The nitrogen taken up is stored as quota, whose value is much higher at the edge of the colonies than in their cores (Fig. 5b). This simulation suggests that the nitrogen supplied from the city of Venice is readily assimilated and, therefore, that sewage immissions could represent important sources of nutrients.

The dynamic of *Ulva* colonies outlined above can be followed by plotting the seasonal evolution along one of its sections, as has been done in Fig. 6 for section, A–A', which crosses the areas labelled as a, b, c, d, in Fig. 1. Water depth along the section is reported at the top of the figures. We focused first on area b, because it presents the typical evolution pattern for shallow water. This zone is 1 m deep and, since it is surrounded by a

![Fig. 4. Experimental distribution of *Ulva* in July 1987 as measured by Sfriso et al., 1989.](image-url)
Fig. 5. Spatial distribution of nitrogen concentration (a) and quota (b) on day 210 of the second year of simulation.

is very close to the deepest channel and rich in nutrients; the biomass peak, which was barely noticeable at the end of the summer (day 252) increases up to 6 kg ww/m².

4.2. Dynamic of anoxic crisis

One of the main reasons for studying the dynamics of Ulva r. is the strong effect that this community exerts on the oxygen balance. DO is close to saturation along the major channels, and well above it, concurrently with algae blooms. Vertical discretization turns out to be very important in order to create a realistic simulation, because the vertical distribution of nutrients and DO, combined with the effects of shading and self shading, enable the reproduction of the dynamics of the anoxic crisis. Above a certain level of biomass, Ulva respiration and bacterial mineralization cause the depletion of DO, which becomes extremely low in the core of Ulva colonies, especially in the early morning. The crisis can persist in the bottom layers, where photosynthetic activity is reduced by nutrients depletion and self-shading. Since the lack of oxygen has a feedback effect on the rate of Ulva mortality, the oxygen demand for mineralization further increases. In these conditions, a local anoxia can cause a general dystrophic crisis, if reareation cannot restore the oxygen balance. As a consequence, the population of Ulva suddenly collapses. This is illustrated in Fig. 7, which shows the spatial distribution before, Fig. 7a, and just after the crisis. The phytoplanktonic pool can take advantage of the large amount of nutrients released by the decomposition of Ulva. In fact, phytoplankton, which behaves as a passive tracer, is less sensitive to local phenomena. This succession can be observed in the ecosystem and is correctly reproduced by the model, as discussed in Solidoro et al. (1997a).

4.3. Long term simulation under different scenarios of external forcings

Because of the intrinsically variable nature of real forcing functions, and the complexity of the ecosystem, an investigation of steady states would make little sense, even if the model eventually...
reached a steady state evolution, when driven by the same forcings for many years. For this reason, we have focused our attention on the modality of expansion of Ulva colonies within a few years, trying to understand how different scenarios of loads of nutrients and light intensity affect the spatial distribution of Ulva r.

A reference scenario, called ‘ref’, has been obtained by running the model for three consecutive years, with the same forcings used in the above two year simulation. Another two scenarios have been obtained by running the model as above for two years, and then modifying the forcings for the third year: in the scenario labelled ‘nutlim’, nutrients loads have been halved, while in the one labelled ‘lightlim’, incident light intensity has been reduced by 30%. The results are compared in Fig. 8, which displays the spatial distribution of the
5. Conclusions

The model here discussed represents the first attempt at including the dynamic of macroalgae in a 3D water quality model of a coastal basin. The application to the lagoon of Venice is particularly interesting, because this ecosystem has been studied from many points of view, due to its peculiarity. The model has proved to be an effective tool for studying primary production in an eutrophic environment, where macro and microalgae are both present. A 3D model gives one the possibility to investigate the competition between the two communities of producers, as well as the intraspecific competition among and within Ulva colonies.

The two communities compete for the available nutrients, but their coexistence, or their extinction, is mainly regulated by the physical factors connected with light intensity, such as the depth...
of the water column, and shading coefficients, and by their photosynthetic efficiencies. Vertical discretization turns out to be very important in improving the results, because it emphasizes the effects of the reareation as well as those of shading and self-shading.

The simulations here presented show that Ulva colonies survive only in shallow areas and that the colonization of Ulva is slowed down by natural barriers, such as deep channels; whereas the distribution of phytoplankton is not correlated with the bathimetry. The simulated spatial patterns are in reasonable agreement with those obtained from field data. The dynamic of anoxic crises is also correctly reproduced.

The density distribution of Ulva is mainly determined by the availability of nutrients and, therefore, the density is higher in areas closest to the main channels. Within a colony, the intraspecific competition for nutrients gives rise to a typical spatial distribution: biomass density is higher in the new colonies and on the edge of the old ones.
Even though, at this stage, the model cannot be used as a predictive tool, it can give useful qualitative indications about the long term dynamic of the ecosystem, under different scenarios of meteorological conditions and input of nutrients. The results, presented in Section 4, show that the effects of a consistent reduction in input are counterintuitive and difficult to analyze. This confirms the importance of taking into account the interaction between primary production and transport phenomena.

References


