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The role of microphytobenthos on shallow coastal lagoons: a modelling approach

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Abstract Ria Formosa is a Region of Restricted Exchange given its limited connection to coastal water circulation. Furthermore, it is subject to several anthropogenic activities that can lead to an increase in nutrients and potentially to eutrophication. Previous studies have shown the importance of the benthic compartment, specifically the microphytobenthos (MPB) in this shallow coastal lagoon. The dCSTT–MPB model [new version of the dynamic Comprehensive Studies Task Team (dCSTT) model] here described couples the benthic and pelagic compartments. Due to the shallowness of the system, the benthic microalgae are one of the most important primary producers of the system. Preliminary results of the model show a large biomass of benthic microalgae, which strongly influences the pelagic chlorophyll concentration by resuspension. However, algae concentrations in the water column are relatively small due to the high flushing rate of the lagoon. The MPB community is mainly supported by nutrients in the pore water. A sensitivity analysis (SA) has revealed that the factors associated with the benthic compartment were the most important and sensitive to changes. Porosity, benthic chlorophyll recycling, loss of MPB due to grazing and the yield of microphytobenthic chlorophyll from nitrogen were some of the most sensitive parameters, as well as the ones associated with decay of particulate organic nitrogen. The development of our dCSTT–MPB model has itself provided insights into benthic function.

Keywords Microphytobenthos · Assimilative capacity · CSTT model · Eutrophication · Ria Formosa · Portugal

Introduction

Eutrophication and ecological modelling

In recent decades human related nutrient sources, such as agriculture, wastewater treatment plants, run-off, recreational activities and fossil fuel consumption (atmospheric deposition), have significantly increased the inputs of nutrients to coastal systems (Howarth and Marino 2006; Bricker et al. 2008). The accumulation

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of nutrients in coastal areas may also be favoured by the prevailing natural conditions, which is the case of the Regions of Restricted Exchange (RRE). These are enclosed areas which have only few points of water exchange with the sea (Tett et al. 2003). The accumulation of nutrients can lead to eutrophication events, which are considered one of the greatest threats to coastal ecosystem health (NRC 2000; Bricker et al. 2008). Eutrophication is defined by the Urban Waste Water Treatment Directive (UWWTD) as the 'enrichment of water by nutrients especially compounds of nitrogen and phosphorus, causing an accelerated growth of algae and higher forms of plant life to produce an undesirable disturbance to the balance of organisms present in the water and the quality of the water concerned' (CEC 1991).

Models that simulate the cycling of nutrients through primary producers and subsequent mineralization are therefore important to understand the system response to changes in nutrient inputs and to predict its future state. The model should be representative, but as simple as possible, so that it can be easily understood. Models are extremely useful to study eutrophication and the assimilative capacity of systems, which is 'a property of the environment defined as its ability to accommodate a particular activity, or rate of activity, without unacceptable impacts' (GESAMP 1986). By comparing the model output to the legally defined Ecological Quality Objectives (EcoQOs) for a specific site, models can help to diagnose eutrophication.

The CSTT (Comprehensive Studies Task Team) model was created to investigate the algal response to nutrient enrichment in British coastal waters (CSTT 1994, 1997). It is a steady-state model, assessing only the worst-case scenario. Such screening-models are useful for a rapid system evaluation (Bricker et al. 2003; Tett et al. 2003; Nobre et al. 2005). The results are normally very easy to interpret. This simple CSTT model was used to assess the trophic status of a number of European RREs, including the Ria Formosa, the subject of this paper, during the European Project OAERRE (Oceanographic Applications to Eutrophication in Regions of Restricted Exchange; Tett et al. 2003). Laurent et al. (2006) and Portilla et al. (2009) describe dynamic versions of the CSTT model, which were used to simulate the effects of aquaculture on seasonal cycles of phytoplankton and nutrients in Loch Creran, Scotland.

Shallow systems, as Ria Formosa, should be considered differently from other coastal systems for modelling purposes. The influence of sediments is crucial for nutrient and chlorophyll dynamics, as discussed by Falcão (1996), Newton et al. (2003), Newton and Mudge (2005), Murray et al. (2006) and Brito et al. (2009a). The most important source of nutrients to the lagoon dynamics is considered to be the sediments (Falcão 1996). Results from the application of the CSTT model to Ria Formosa suggested that rapid flushing removed nutrients and phytoplankton and so prevented eutrophication (Tett et al. 2003). However, the combination of modelling and field work undertaken in Ria Formosa has provided conflicting evidence on its trophic status (Tett et al. 2003; Newton et al. 2003; Nobre et al. 2005). Although certain areas within the Ria suffer from nutrient enrichment, hypoxia and algal mats, pelagic eutrophication symptoms are uncommon (Newton et al. 2003). Using a hybrid approach (ASSETS, which is a simple, screening model for the ASSessement of Estuarine Trophic Status, and an ecosystem model) Nobre et al. (2005) suggested that eutrophication symptoms are not present in the water column, although an excessive growth of macroalgal and dissolved oxygen fluctuation (in the bottom) were observed in areas with low water exchange (Newton and Icely 2006). Furthermore, these shallow systems have well-illuminated beds where phytobenthos can make an important contribution to the system's primary production. The phytobenthos includes seagrasses, seaweeds, and microphytobenthos (MPB). Brito et al. (2009a) showed that chlorophyll in benthic micro-algae exceeded that of phytoplankton by at least an order of magnitude in the Ria Formosa. Moreover, by living in the sediment surface, MPB cells take up considerable amounts of nutrients from the potentially large nutrient flux between the sediments and the water column. Pore water nitrogen concentrations are generally much higher than the concentrations found in the water column (for details see Brito et al. 2009a). This strong influence of sediments in shallow waters is a key difference between these systems and other coastal water bodies.

Several models have already included a MPB component. These include the ERSEM (European Regional Seas Ecosystem Model) for the Adriatic basin (Blackford 2002) and the one developed by

Murray and Parslow (1997) for Port Phillip Bay. They have both confirmed the importance of MPB for an appropriate assessment of shallow systems. However, Blackford (2002) indicates that his results are to be used only in a qualitative manner due to uncertainties about key parameters, and Murray and Parslow (1997) do not address the question of the temporal variation of MPB and acknowledge the need of further studies on MPB dynamics.

This study adds a benthic submodel, with state variables for microphytobenthic chlorophyll and pore water nutrients, to a dynamic CSTT model (dCSTT) which is similar to the one described in Laurent et al. (2006). We describe and justify the coupled dCSTT–MPB (dynamic version of the CSTT model coupled with MPB) model, present preliminary results and show the results of the sensitivity analysis (SA).

Methodology

Study site

Ria Formosa is a coastal mesotidal lagoon located in the southern coast of Portugal (36°58′N, 8°02′W to 37°03′N, 7°32′W, Newton and Mudge 2003). It covers an area of 100 km^2, and is 55 km long (E–W, from Cacela to Ancão) and 6 km wide (N–S) at its largest area (Asmus et al. 2000; Newton and Mudge 2003). The lagoon is very shallow with a mean depth of approximately 1.5 m (Nobre et al. 2005). Ria Formosa is separated from the sea by sand pits and has six inlets, where the water exchange between the lagoon and the sea takes place (Dias et al. 2009). The freshwater inputs are almost negligible (Nobre et al. 2005). The main sources of nutrients are point source discharges, sediment nutrient release and the run-off from fertilized areas.

The lagoon is of high ecological importance and is recognised within Portuguese legislation as a natural park and also internationally as a Ramsar wetland, a protected area under the Birds Directive (79/409/EEC) and a member of the Natura 2000 Network. The lagoon is a valuable socio-economic resource for the region mainly due to tourism, fisheries, aquaculture (especially shellfish) and salt extraction (Brito et al. 2010a).

Model development

The dCSTT–MPB model can be described in three main phases following Tett et al. (2007): conceptual, mathematical and numerical model. The conceptual model is our theoretical view of the relationships within the system. This has an associated error that derives from our incapacity to fully describe the systems we want to study. The mathematical model is represented by the differential equations that describe the processes and the relationships of each component of the system (state variables). The numerical model is the application of sets of data and forcing variables to our mathematical model. This model resulted from a scientific modelling process rather than an engineering modelling process. The former corresponds to the development phase, with formulation and rejection of scientific hypothesis. The latter is aimed at making a model that is reliable in prediction, based on previous models and using data for the calibration process as an essential step to provide a good agreement between model output and data.

Conceptual model

The conceptual model of the nutrient and algal interactions in shallow coastal lagoons is shown in Fig. 1. The model aims to simulate the nutrient and chlorophyll conditions in a shallow coastal lagoon with limited water exchange and receives nutrients from the surrounding areas.

Physics

The Ria is viewed as a single, well-mixed box, exchanging water with the sea at a constant daily rate, with the sea-bed forming the base of the box. All the other processes are also described as daily means.

Biogeochemistry

Water column processes act on the involved state variables, which are dissolved nutrients (nitrogen only, as Dissolved Available Inorganic Nitrogen—DAIN) and chlorophyll. The latter is in a microplankton compartment (Lee et al. 2003; Portilla et al. 2009), which includes the joint dynamics of phytoplankters and associated pelagic micro-heterotrophs. The new benthic submodel deals with a thin

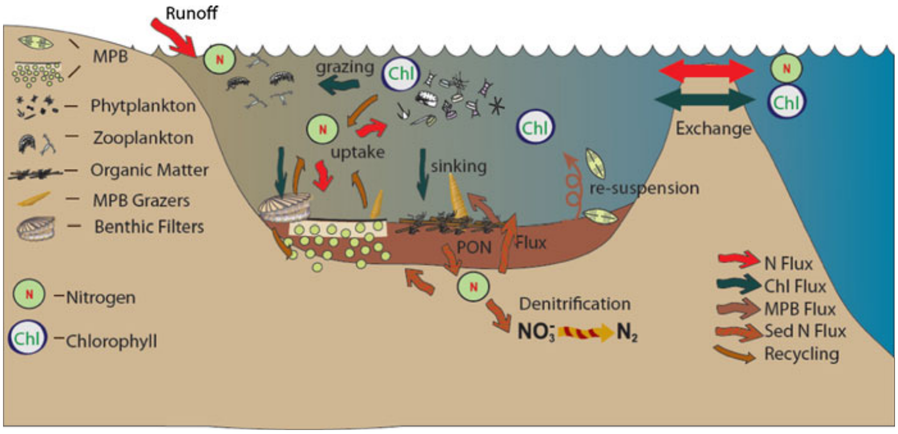

Fig. 1 Diagram representation of the conceptual model. Illustration symbols from the Integration and Application Network (http://ian.umces.edu)

superficial layer of sediments and adds state variables for the concentration of DAIN in pore water and for the amount of microphytobenthic chlorophyll per unit area. As for the water column, we assume that there are benthic micro-heterotrophs closely coupled to the benthic micro-autrophs. However, whereas microplankton growth is conventionally parameterized in terms of specific growth rates multiplied by biomass, microphytobenthic growth involves a novel parameterization in terms of the capture of fluxes of photons and nutrients (Fig. 2).

Mathematical model

The following equation can be used to describe one or more water quality variables (*Y*) of the dCSTT–MPB or similar models such as the LESV (Loch Ecosystem State Vector) model presented by Portilla et al. (2009):

$$\frac{\partial Y}{\partial t} = -\nabla \varphi_Y + \beta_Y + \frac{\partial \Gamma_Y}{\partial V} \tag{1}$$

The first term $(-\nabla \varphi_Y)$ is the divergence of physical transport fluxes at a point. It represents the physical transport and gives the rate of change of the variable as a result of a set of water exchanges. In a spatially complex model, the physical transport may occur along three axes as a result of different processes, such as advection and diffusion. In this single box model, the physical term represents the exchange of a certain state variable with the sea, along exclusively one axis, plus vertical exchange with the sediment. Thus for nutrients:

$$-\nabla \varphi_Y = E(S_0 - S) + \frac{\phi_s}{H} \tag{2}$$

where *E* is the exchange rate (day^{-1}), which will be described below in this section; *S* corresponds to the nutrient concentration ($\mathrm{mmol\ m^{-3}}$) in the water column; ϕ_s is the positive nutrient flux from the sediment to the water column ($\mathrm{mmol\ m^{-2}\ day^{-1}}$); and *H* is the mean depth (m). The subscript 0 refers to the concentrations outside the lagoon.

The bio-chemical term (β_Y) consists in the biological and chemical transformations of the state variable, such as growth or loss. The beta-terms are part of the model that contains the most detail and is a key addition in the present study. These terms are expanded in Eqs. 4–7. The final term $(\partial \Gamma_Y / \partial V)$ gives the input/flux to the system, such as from a water treatment plant or a fish farm or the loss to the farm of the state variable.

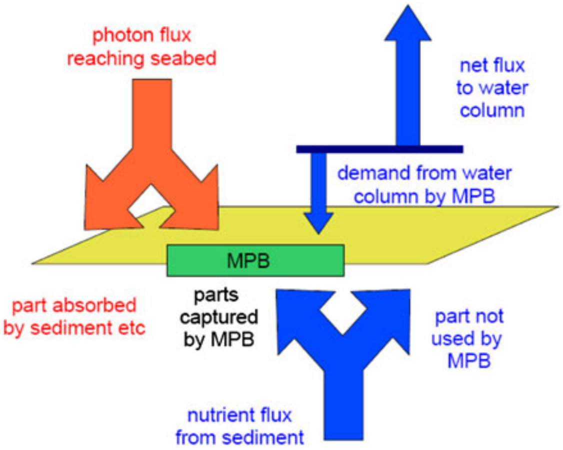

Fig. 2 Scheme of the nitrogen and light fluxes which influence MPB growth

The inputs have origin from local anthropogenic or land-derived sources. In this model, a possible solution for $\partial\Gamma_Y/\partial V$, as a daily variation of the influx of nutrients to the water column is:

$$\frac{\partial\Gamma_Y}{\partial V} = \frac{Si}{V} \tag{3}$$

The mathematical model is constituted by four differential equations, one for each state variable: S (nitrogen in the water column), X_p (pelagic chlorophyll in the water column), X_b (microphytobenthic chlorophyll within the sediments) and S_s (nitrogen in the pore water).

$$\frac{\partial S}{\partial t} = E\cdot(S_0 - S) - \frac{\mu_p X_p}{q} + e\cdot L_p\cdot\frac{X_p}{q} + e\cdot L_{bf}\cdot\frac{X_p}{q} + \frac{S_i}{V} + \frac{\phi_s - \frac{\mu X_b}{q_b}}{H} \quad \left(\text{mmol m}^{-3}\ \text{day}^{-1}\right) \tag{4}$$

$$\frac{\partial X_p}{\partial t} = E\cdot\left(X_0 - X_p\right) + \mu_p X_p - \left(L_p + L_{bf}\right)\cdot X_p + \frac{c_3\cdot L_{br}\cdot X_b}{H} - \frac{sk}{H}\cdot X_p \quad \left(\text{mg chl m}^{-3}\ \text{day}^{-1}\right) \tag{5}$$

$$\frac{\partial X_b}{\partial t} = \mu X_b - L_g\cdot X_b + sk\cdot X_p - c_3\cdot L_{br}\cdot X_b \quad \left(\text{mg chl m}^{-2}\ \text{day}^{-1}\right) \tag{6}$$

$$\frac{\partial S_s}{\partial t} = \frac{\frac{e_b\cdot L_g\cdot X_b}{h_s}}{q_b\cdot p} + \frac{(1-e)\cdot L_{bf}\cdot X_p}{q\cdot p}\cdot\frac{V}{A\cdot h_s} + \frac{\frac{PON}{A\cdot h_s}\cdot d}{p} - den\cdot S_s - \frac{\phi_s}{h_s\cdot p} \quad \left(\text{mmol m}^{-3}\ \text{day}^{-1}\right) \tag{7}$$

where Si corresponds to the total amount of nutrient inputs per day (mmol day^{-1}) to the water column, except fluxes from sediments, and V is the average volume (m^3) of the lagoon. We separate the gamma term from the flux divergence because the gamma term is not associated with significant flows of water. In this case, the gamma term corresponds to the local anthropogenic and/or land-derived inputs. Some state variables may be described by only part of the equation, i.e. with some terms having no representation. This is what happens with the benthic state variables, such as the MPB, which do not have any exchange with the sea, but do have a sediment–water exchange because of resuspension.

The development of a model raises issues of notation. It is essential that all variables are well defined and described. It is also desirable that the notation system follows the standards or conventions of the scientific discipline in which it operates. For simplicity and logical sequence, notation used by the simple CSTT model (CSTT 1994, 1997) and recent modifications, such as dCSTT (Laurent et al. 2006) and LESV (Tett et al. 2007), was generally followed with some adjustments.

The subscript 0 (outside) always refers to the concentrations in the sea and the subscript i refers to inputs, in this case of nutrients (S_i, mmol day^{-1}) to the box. The subscript b refers to MPB. E is the exchange rate of waters between inside and outside the lagoon (day^{-1}), V is the volume (m^3), e is the fraction of grazed chlorophyll that is recycled, q is the yield of chlorophyll from nutrients (mg chl mmol^{-1}), H is the mean depth of the lagoon (m), L_p is phytoplankton loss rate (day^{-1}), μ is growth rate (day^{-1}), L_{bf} is the loss rate of phytoplankton chlorophyll due to filter-feeders (day^{-1}) and ϕ_s is the nutrient flux from the sediments to the water column, which is assumed to result from molecular diffusion and PON is the sediment particulate organic nitrogen in mmol (Table 1). The positive value of the flux corresponds to a flux into the water column. L_{br} is the loss rate of MPB chlorophyll to the water column (day^{-1}), c_3 is the proportion of MPB on the surface of the sediment, A is the area (m^2), L_g is the grazing rate (day^{-1}), sk is the sinking rate (day^{-1}) of phytoplankton, p is porosity, h_s is the thickness of the pore water sediment layer (m), d is the decay rate of PON (day^{-1}) and den is the denitrification rate (day^{-1}). See Tables 1, 2, 3, 4 and 5 for specific values.

Table 1 General parameters used in the model

Term	Description	Value	Units	Source
S_0	Seawater nutrient concentration	2.3	mmol m^{-3}	Data
S_i	Nutrient input from all sources except sea	78×10^6	mmol day^{-1}	Tett et al. (2003)
X_0	Seawater chlorophyll concentration	1.75	mg chl m^{-3}	Tett et al. (2003) and data
E	Exchange rate	0.5	day^{-1}	Tett et al. (2003)
V	Volume of Ria Formosa	88×10^6	m^3	Tett et al. (2003)
A	Area of Ria Formosa	53×10^6	m^2	Newton and Mudge (2003)
H	Mean depth of Ria Formosa	1.5	m	Tett et al. (2003)
q	Chlorophyll yield from limiting nutrient (N)	1.1	mg chl $mmol^{-1}$	Tett et al. (2003)
q_b	MPB chlorophyll yield from limiting nutrient	4	mg chl $mmol^{-1}$	Brito et al. (2010b)
e	Proportion of grazed nutrient that is recycled	0.5	–	Laurent et al. (2006)
e_b	Proportion of grazed nutrient that is recycled for MPB	0.5	–	Adapted from Laurent et al. (2006)
L_p	Loss rate of phytoplankton due to benthic pelagic grazers	0.05	day^{-1}	Adapted from Tett et al. (2003)
L_{bf}	Loss rate of phytoplankton due to filter feeders	0.9	day^{-1}	Data and Sobral (1995)
L_g	Loss rate of MPB due to grazing	0.1	day^{-1}	Adapted from Blackford (2002)
sk	Sinking rate of pelagic chlorophyll	1	m day^{-1}	Mann and Lazier (1996)
c_3	Proportion of MPB on the sediment surface	0.15	–	Estimated
PON	Particulate Organic Nitrogen in the sediments	5×10^8	mmol	Serpa et al. (2007)
d	Decay rate of sediment PON	0.1	day^{-1}	Adjusted
p	Porosity of sediment	0.5	–	Data
Den	Denitrification rate	0.01	day^{-1}	Adapted from Murray and Parslow (1997)
h_s	Thickness of the modelled sediment layer	0.05	m	Data
Φ	Photosynthetic yield	40	nmol C μE^{-1}	Tett (1990), Tett et al. (1993)
χ	Chlorophyll-carbon ratio	0.4	mg chl (mg-at organic C)$^{-1}$	Portilla et al. (2009)
k	Conversion factor	8.64×10^{-2}	s day^{-1} milli(nano)$^{-1}$	
$\mu_{\max(20)}$	MPB maximum growth rate at 20°C	1.5	day^{-1}	Lee et al. (2003)
Q_{10}	Increase in metabolism activity due to an increase of 10°C in temperature	2		Eppley (1972)
Ti	Temperature	Variable	°C	Data

Adjusted means that the value used was the one that allowed the best correspondence with data

Adapted means that values from phytoplankton were used for MPB, when the latter were not available

Uptake of nutrients by algae

The conversion of nutrients to microalgal chlorophyll is very important in this model. It is one of the most important links in terms of eutrophication. It is now widely accepted that algae growth may be nutrient-controlled. The growth depends mainly on the limiting nutrient content inside the cell. However, this leads to complex cell-quota models (Droop 1983) and as such the derivation of a simpler way to establish this link has been proposed, which is the ratio of chlorophyll formed from the limiting nutrient assimilated—q (Gowen et al. 1992; Edwards et al. 2003). So, the loss term of nutrients is simply defined for algae as:

Table 2 Initial values of each state variable of the model and boundary conditions

Symbol		Initial values	Boundary conditions
S	Nutrient concentration	2 mmol m^{-3}	2.3 mmol m^{-3} (S_0)
X	Chlorophyll concentration	2 mg chl m^{-3}	1.75 mg chl m^{-3} (X_0)
X_b	MPB chlorophyll concentration	200 mg chl m^{-2}	(Water column)
S_s	Pore water nutrient concentration	100 mmol m^{-3}	(Water column)

Table 3 Resuspension: equations and parameters

Term	Description	Value	Units	Source
w	Wind velocity	Variable	m s^{-1}	Data
$w_{\max}$	Wind velocity (maximum)	12.8	m s^{-1}	Data
L_{br}	Resuspension of superficial fraction of MPB	Variable	day^{-1}	[a]
L_t	Tidal driven re-suspension rate	0.075	day^{-1}	[a]
L_w	Wind driven re-suspension rate	0.20	day^{-1}	[a]

The following equations describe the re-suspension of MPB cells caused by wind and tide

Re-suspension of MPB cells	$L_{br} = rtide + rwind$
Re-suspension caused by tide	$rtide = \sin(48 \cdot \pi \cdot t/365 + 162) \cdot 0.002 + L_t$
Re-suspension caused by wind	$rwind = \left(\frac{w}{w_{\max}}\right) \cdot L_w$

[a] These values were adjusted in order to obtain a value of L_{br} of 0.1 day^{-1}(Guarini et al. 2008), i.e. the re-suspension rate is variable with term calibrated against Guarini et al. (2008). Following these formulations, the tidal effect is stronger than the action of wind, which is in accordance with results of Brito et al. (2010a)

$$\text{Uptake} = \frac{\mu \cdot X}{q} \quad \left(\text{mmol m}^{-3}\ \text{day}^{-1}\right) \tag{8}$$

Biological production

The growth rate of phytoplankton is either light or nutrient limited which can be represented by the following equation:

$$\mu(S,I) = \min[f(I), f(S)] \quad \left(\text{mmol m}^{-3}\ \text{day}^{-1}\right) \tag{9}$$

The growth rate equation is defined by a function dependent on the Photosynthetic Active Radiation (PAR; I) and a temperature dependent, Monod-type, nutrient-limited growth function (Portilla et al. 2009). Details are presented and discussed by Portilla et al. (2009).

For MPB, our approach involves equations that deal with MPB biomass increase (mg chl m^{-2} day^{-1}) and not growth rates (day^{-1}). This approach is novel in describing algal growth and was developed due to the incapacity of the standard growth equations (e.g. Monod model) to describe MPB growth. This became clear during the model development process (data not shown). Thus:

$$\mu X_b = \min[f(\phi), f(I), f(\theta)] \quad \left(\text{mg chl m}^{-2}\ \text{day}^{-1}\right) \tag{10}$$

MPB growth comprises the relationship between biomass increase and the fluxes of photons (I), nutrients (ϕ, mostly from within the sediment) and a function of the temperature (θ). The function $f(\theta)$ sets an upper limit in algal physiology to the rate of biomass production. It can be expanded as:

$$f(\theta) = \mu(\theta) \cdot X_b \tag{11}$$

The nutrient saturated growth rate, controlled by algal physiology and considering a temperature of 20°C follows the approach described by Lee et al. (2003). The growth rate is described as:

$$\mu(\theta) = \mu_{\max(20)} \cdot Q_{10}^{\left(\frac{Ti-20}{10}\right)} \tag{12}$$

where $\mu_{\max(20)}$ is the maximum growth rate at a temperature of 20°C, Q_{10} is a multiplicative factor

Table 4 MPB nutrient limited growth: equations and parameters

Term	Description	Value	Units	Source
c_3	Proportion of MPB on the sediment surface	0.15	–	Calculated[a]
p	Porosity of sediment	0.5	–	Data
D_m	Molecular diffusion coefficient in sediment pore water	1.66×10^{-4}	$m^2\ day^{-1}$	Murray et al. (2006)
τ	Tortuosity of sediment pores	1.3	–	Jackson et al. (2002)
a_S^*	'Nutrient absorption cross-section'	0.03	$m^2\ mg^{-1}$	Estimated
h_b	Thickness of the superficial sediment layer	0.001	m	Brito et al. (2010b)
h_{bbl}	Thickness of the benthic boundary layer	0.001	m	Di Toro (2001), Murray et al. (2006)
S_n	Nutrient 'notional' concentration at MPB cell surface	1	$mmol\ m^{-3}$	[b]
c_5	Mean illuminated fraction of day, during which MPB can migrate to the surface	0.5	–	Data
c_6	Mean tidally drying fraction of sediment surface	0.3	–	Data

The following equations describe the nutrient-limited growth of MPB

Proportion of sediment flux intercepted by MPB	$c_2 = \left(1 - e^{-a_s^* \cdot (1-c_3) \cdot X_b}\right)$	[1]
Benthic nutrient flux	$\phi_s = D_m \cdot \frac{\partial S}{\partial z}\vert ss \cdot \frac{p}{\tau}$	[2]
Proportion of nutrient flux from water column intercepted by MPB	$c_4 = \left(1 - e^{-a_s^* \cdot c_3 \cdot X_b}\right)$	[1]
Water column nutrient flux	$\phi_w = D_m \cdot \frac{\partial S}{\partial z}\vert_{bbl}$	[2]
Fraction of cells that are in the sediment surface[a]	$c_3 = c_5 \cdot c_6$	[3]
Nutrient gradient in the superficial sediment	$\frac{\partial S}{\partial z}\vert_{ss} = \frac{S_s - S}{h_b + h_{bbl}}$	[4]
Nutrient gradient in the benthic boundary layer[b]	$\frac{\partial S}{\partial z}\vert_{bbl} \approx \max\left(0, \frac{S_w - S_n}{h_{bbl}}\right)$	[5]
MPB maximum biomass	$X_{b,\max(S)} = \frac{q_b \cdot (\phi_s + \phi_w)}{L_g + L_{br}}$	[6]

[1] MPB take nutrients up from the intercepted part of the nutrient flux from the sediments to the water column and from the intercepted part of the nutrient flux from the water column to the cells. The nutrient absorption cross-section parameter, a_s^* was estimated considering diatom cell dimension taken from Jesus et al. (2005), analogous to the light absorption cross-section

[2] The benthic nutrient flux (Φ_s) is assumed to result from molecular diffusion in sediment pore water. The water column nutrient flux (Φ_w) is assumed to result from molecular diffusion across the benthic boundary layer or viscous layer, which separates the sea-bed from the main part of the water column. There is an important conceptual difference between Φ_s and Φ_w. Φ_s is a real flux and the part $(1 - c_2)$. Φ_s, not consumed by algae, goes directly to the water column nutrient stock. The other is a potential flux and only the part consumed by algae is realized. The unused $(1 - c_4)$. Φ_s does not happen

[3] The surface fraction (c_3) is a complicated function of time in the tidal cycle, time of day, height relative to low water. The type of sediment may also be important. Several studies have reported the vertical migration of microalgae due to the joint stimulus of tide and light (e.g. Serôdio et al. 1997, 2005; Jesus et al. 2005). Microalgae tend to preferentially migrate to the sediment surface during daylight and as water level falls. The CSTT–MPB model works with daily values and does not resolve processes within the diel cycle. Therefore, a single value that averaged all processes was used

[4] The nutrient gradient in the superficial sediment is positive when the concentration in the pore water is higher than that in the water column resulting in a flux into the water column

[5] In principle, S_n is less than S_w because of the uptake by cells and it cannot fall too close to zero, which would lead to the termination of trans-wall nutrient transport

[6] Considering that all the benthic and the water column nutrient flux is captured by algae

that represents the increase to the double of metabolism activity due to an increase of 10°C in temperature and Ti is the temperature observed in the Ria. This general equation is in agreement with Droop (1968), Eppley and Strickland (1968) and Eppley (1972).

Table 5 MPB light limited growth: equations and parameters

Term	Description	Value	Units	Source
V_{hw}	Volume of Ria Formosa (high water)	140×10^6	m^3	Mudge et al. (2008)
A	Area of Ria Formosa	53×10^6	m^2	Newton and Mudge (2003)
h_b	Thickness of the superficial sediment layer	0.001	m	Brito et al. (2010b)
p	Porosity	0.5	–	Data
I_0	24-h mean surface PAR	Variable	$\mu E\ m^{-2}\ s^{-1}$	Data
R	Proportion of reflected PAR from sea-bed (sea albedo)	0.5	–	Data
K_d	PAR diffuse attenuation coefficient in the lagoon	0.7	m^{-1}	Data
m_2	Corrects for losses due to the surface reflection and hyperexponential decay	0.7	–	Tett (1990) and adjusted to Ria
a^*_{pH}	Absorption cross-section of photosynthetic pigments	0.02	$m^2\ mg^{-1}$	Portilla et al. (2009)
a^*_{NP}	Absorption cross-section of photoprotective pigments	0.02	$m^2\ mg^{-1}$	Taken as the same as a^*_{pH}
a^*_{PM}	Absorption cross-section of particulate matter	3×10^{-6}	$m^2\ mg^{-1}$	Devlin et al. (2008)
ρ_s	Density of dry sediment	2.16×10^9	$mg\ m^{-3}$	Data
$r_{0,a}$	Algal basal respiration rate	0.05	day^{-1}	Lee et al. (2003)
$r_{0,h}$	Heterotroph basal respiration rate	0.03	day^{-1}	Lee et al. (2003)
b_a	Slope of graph of algal respiration on growth rate	0.5	–	Lee et al. (2003)
b_h	Slope of graph of heterotroph respiration on growth rate	1.5	–	Lee et al. (2003)
η	Heterotroph fraction	0.125	–	Portilla et al. (2009)

The following equations describe the light-limited growth of MPB

Proportion of the photons in I_0 absorbed by algae on the sediment surface	$c_{1s} = \left(1 - e^{-a_{PH,s} \cdot h_b}\right) \cdot R$	[1]
Proportion of the photons in I_s absorbed by algae inside the sediment	$c_{1b} = \frac{a_{PH,b} \cdot h_b}{a \cdot h_b} \cdot (1 - R)$	[1]
24-h mean PAR on the sediment	$I_s = m_2 \cdot I_0 \cdot \frac{1 - e^{-K_d \cdot h_{hw}}}{K_d \cdot h_{hw}}$	[2]
Depth at high water	$h_{hw} = V_{hw}/A$	[3]
Absorption (m^{-1}) by superficial algae	$a_{PH,s} = c_3 \cdot a^*_{PH} \cdot X_b \cdot h_b^{-1}$	
Absorption (m^{-1}) by in-sediment algae	$a_{PH,b} = (1 - c_3) \cdot a^*_{PH} \cdot X_b \cdot h_b^{-1}$	
Total benthic absorption (m^{-1})	$a = (1 - c_3) \cdot \left(a^*_{PH} + a^*_{NP}\right) \cdot X_b \cdot h_b + a^*_{PM} \cdot PM$	[4]
Fraction of cells that are in the sediment surface	$c_3 = c_5 \cdot c_6$	[5]
Particulate matter	$PM = \rho_s \cdot (1 - p)$	
Microbenthic respiration	$r = r_0 + b \cdot \mu$	[6]
Basal respiration	$r_0 = r_{0,a} \cdot (1 - \eta) + r_{0,h} \cdot \eta \cdot (1 + b_a)$	[7]
Respiration slope	$b = b_a \cdot (1 + b_h \cdot \eta) + b_h \cdot \eta$	[7]

Table 5 continued

Term	Description	Value	Units	Source
MPB maximum biomass		$X_{b,\max(I)} = \frac{k\cdot(c_3\cdot I_0+(1-c_3)\cdot I_s)\cdot\Phi\cdot\chi}{L\cdot(1+b)+r_0}$		[8]

[1] Ria Formosa experiences different water levels according to the tidal cycle, which may strongly affect the radiation in the sediment surface. In this model it is assumed that microalgae cells migrate into the sediment surface during emersion. Under dry these conditions, cells are exposed to I_0 rather than I_s

[2] Assuming that each depth interval corresponds to an equal proportion of sea-bed, then this mean PAR can be equated with the mean PAR in the water column when the Ria is flooded

[3] The depth h_{hw} might be higher or smaller than H, depending on the relative area of the Ria above mid-water

[4] The algal pigments that capture the fraction of PAR used for photosynthesis have to compete with other 'Optically Active Constituents' (OAC), mainly non-photosynthetic pigments and sediment particles (see Fig. 2). The thickness of the superficial layer (h_b), corresponding to the euphotic zone of the sediment, was assessed experimentally in the laboratory

[5] See Table 4

[6] The microbenthic respiration (r) is assumed to include a basal (r_0) and a growth dependent ($b.\mu$) component

[7] The two parameters involved in the equation, the basal respiration (r_0) and the respiration slope (b), were calculated from autotroph and heterotroph parameters as described in the microplankton model (Tett et al. 2007)

[8] Considering that all available photons are captured by algae

Nutrient limited growth

It is well accepted that MPB cells are present at the sediment surface and within the sediment (see for example, Underwood and Paterson 2003; Cartaxana et al. 2006). Cells at the top of the sediment should be able to uptake nutrients from the water column and from the pore water. Therefore, the nutrient limited increase of MPB depends on nutrient flux from the sediment and nutrient supply from the water column. Thus:

$$\mu X_b = q_b \cdot (c_2 \cdot \phi_s + c_4 \phi_w) \quad \left(\text{mg chl m}^{-2}\ \text{day}^{-1}\right) \tag{13}$$

where c_2 is the proportion of the sediment flux that is captured by benthic algae, which depends on algal biomass, ϕ_s is the nutrient flux from the sediment into the water column, c_4 is the proportion of the water nutrient that is captured by benthic algae, which again, depends on algal biomass, and ϕ_w is the nutrient flux from the water column to algae on the surface of the sediment. The yield q_b for MPB was estimated by Brito et al. (2010b) and is used in this modelling approach. Equation 13 assumes that the source of nutrients for MPB cells within the sediment comes from algal interception of a fixed sediment nutrient flux.

Light limited growth

The net photosynthetic production limited by light depends on capture of light, conversion efficiencies and losses due to respiration of cells. Ria Formosa experiences different water levels according to the tidal cycle, which may strongly affect the radiation in the sediment surface. In this model, we separate the growth that occurs under different light conditions (I_0 and I_s). It is assumed that microalgae cells migrate into the sediment surface during part of the day, especially during daytime and emersion (Jesus et al. 2005). Under these conditions, cells are exposed to I_0 rather than I_s. Therefore, the use of a two-part light limited function, considering both irradiance conditions, is outstanding. Thus:

$$\mu X_b = k \cdot (c_{1s} \cdot I_0 + c_{1b} \cdot I_s) \cdot \Phi\chi - r \cdot X_b \quad \left(\text{mg chl m}^{-2}\ \text{day}^{-1}\right) \tag{14}$$

where k converts units from s^{-1} to day^{-1} and from ng to mg, c_{1s} is the proportion of the photons in I_0

absorbed by algae on the sediment surface, I_0 is the 24-h mean surface PAR, c_{1b} is the proportion of the photons in I_s absorbed by algae inside the sediment, I_s is now the 24-h PAR on the top of the sediment, averaged over the lagoon, Φ is the photosynthetic yield, χ is a conversion factor (mg chl (mg-at organic C)$^{-1}$) and r is the respiration rate (below).

The model also assumes that all particles that influence the light absorption are uniformly distributed within the sediment, except the fraction c_3 of cells that are in the sediment surface.

Numerical model

Parameters used through the dCSTT–MPB model are described in Table 1. In some cases, specific parameters were not available for the MPB. For these, values for phytoplankton were taken. This is expressed in the table as 'adapted'. Other parameters, such as the decay of PON (day^{-1}) were 'adjusted' to observations, which means that the value used was the one that allowed the best correspondence with data. Further work is needed in order to obtain appropriate estimates. Table 2 presents the initial values of each state variable and the boundary conditions.

Physical model

Exchange Ria Formosa is a mesotidal lagoon. Tides are semidiurnal, i.e. with two high tides and two low tides per day. The lagoon is shallow and it was estimated by Tett et al. (2003) that 50–75% of the water in the lagoon is exchanged daily by tides. This exchange is therefore key in the understanding of the dynamics of the states variables in this model. The exchange rate is considered to be the instantaneous probability of any small packet of water being lost from the RRE to the sea and replaced by a packet of the same volume but having a different content from the sea (Tett et al. 2003). The value for the exchange rate used in this model is 0.5 day^{-1} because in this case the worst-case scenario is considered.

Sinking and resuspension of algae The algal cells in the water column tend to sink to the bottom. This process influences the MPB chlorophyll concentration since it constitutes an inflow of chlorophyll to the sediment surface. MPB cells on the sediment surface, the fraction c_3, which is discussed below, are subject to several potential losses. They may be grazed or also be suspended into the water column during immersion. Benthic microalgae are heavier than water, and lie within a viscous layer. However, irregularities in the sea-bed disrupt the smooth flow and may cause small eddies. These eddies have a vertical component and once in contact with the biofilm, it may lift up cells. The result may solely be a tumbling motion, in which cells would move along the sea-bed rather than being lifted into the water column. In other cases cells would be elevated into regions of stronger turbulence in which the upwards motions exceed the sinking speed (see Table 3 for details on equations used). In order to improve the model, the sinking of benthic microalgae cells should also be considered. Obviously, benthic and pelagic cells have different sinking speeds due to their different size and weight. Therefore the addition of another state variable, representing the benthic algae suspended in the water column would be a logical improvement in the future. It was not considered in this work due to difficulties in the implementation and validation of results, since no data are available.

Biochemical model

Biological production The growth rate of phytoplankton is either light or nutrient limited, as described in Eq. 9. Details are provided in Portilla et al. (2009). The values of the parameters used are presented in Table 1.

For MPB, our approach involves equations that deal with MPB growth and not growth rates, which is one of the novel aspects of this study. A detailed description of the equations used in this model and correspondent parameters is present in Tables 4 (nutrient limited growth) and 5 (light limited growth).

Vertical migration and surface fraction The surface fraction specifies the proportion of MPB able to consume nutrients from the water column. Several studies have reported the vertical migration of microalgae due to the joint stimulus of tide and light (e.g. Serôdio et al. 1997, 2005; Jesus et al. 2005). Microalgae tend to preferentially migrate to the sediment surface during daylight and as the water level falls. However, it has been suggested that MPB cells can be constantly migrating from the surface to deeper layers and vice versa (Serôdio et al. 2005). By doing this, they exclude themselves from the greater light availability at the surface and water column supply of nutrients, at certain times and conditions.

The yield of chlorophyll from nutrient The yield of pelagic chlorophyll from assimilated nitrogen, q, was fully investigated by Gowen et al. (1992), Edwards (2001), and Edwards et al. (2003, 2005). The use of this parameter is a distinctive feature of the CSTT and dCSTT models.

In our model, the value of 1.1 mg chl (mmol N)$^{-1}$ proposed by Tett et al. (2003) was used for pelagic algae. For benthic chlorophyll, a value of 4 mg chl (mmol N)$^{-1}$ was used. This value was obtained from previous investigations, described in Brito et al. (2010b).

Discharges/inputs to the water column—the $\partial \Gamma_Y / \partial V$ terms

This part of the model is only composed by nutrient inputs from local anthropogenic or land-derived sources, as explained before in Eq. 3.

Numerical methods

The dCSTT–MPB model was implemented in MATLAB software (version 7). The MATLAB numerical integration function used was ode23, which is based in the Runge–Kutta integration method. This method is more precise than others, such as the Euler's method. Moreover, it is a one-step solver, which means that this solver only needs the solution immediately preceding the time point. Some other solvers of the ode family also need other solution points of the simulation. This means that the simulation would be time consuming, which is avoided using ode23. In addition, this solver also chooses the best time-step to use in the simulation.

Forcing variables and data

The biochemical model uses irradiance data in the growth equations. Irradiance (24-h mean of PAR at sea-surface in μE m^{-2} s^{-1}) was estimated by applying an algorithm based on the astronomical equations suggested by Kirk (1994) to cloud cover data from the Instituto de Metereologia de Portugal.

Wind velocity (m s^{-1}) data were used to describe the resuspension of MPB caused by wind action. Wind velocity data were obtained from the European Project OAERRE database for the years between 1990 and 2002 (Caetano et al. 2002).

Water temperature (°C) data were also used in the growth equations of phytoplankton and MPB. Data were collected from Ria Formosa lagoon every 2 weeks. Then, data were linearly interpolated to obtain daily values.

Pelagic and benthic chlorophyll concentrations were measured from April to October 2006 and from March 2007 to February 2008 (Brito et al. 2009a, b). Nutrient concentrations in the water column and within the sediments were also collected to test and improve the model (Brito et al. 2009b).

Sensitivity analysis

Sensitivity analysis (SA) is recognized as an essential step in the model development process, allowing identification of the most critical processes and parameters in a model (Campolongo et al. 2007; Cossarini and Solidoro 2008; Portilla et al. 2009). Several SA strategies exist (Kohberger et al. 1978; Campolongo et al. 2007; Cossarini and Solidoro 2008; Saltelli et al. 2008). Here, we have applied a screening SA, based on a randomised one-at-a-time (OAT) parameter change design, described by Kohberger et al. (1978) and Morris (1991), and revised by Campolongo et al. (2007). The effects of changing one factor are assessed using an indicator, μ_{SA}, for the overall influence of the factor on the final output of the model (Morris 1991; Campolongo et al. 2007; Portilla et al. 2009). This indicator is itself sensitive to state variables with greater magnitudes. A second indicator, μ^*_{SA} involves the standardization of the model output (Kohberger et al. 1978).

Each model factor X_i with $i = 1,\ldots, k$, was assumed to vary across p selected levels in the space of the input factors. The levels covered ±50% of the initial parameter value. For a given value of X, the effect of the ith impact factor is defined as:

$$d_i = \frac{f(X + \Delta X_i) - f(X)}{\Delta X_i / X_i} \tag{15}$$

where $\Delta X_i/X_i$ is a value in $\{1/(p-1),\ldots, 1 - 1/(p-1)\}$ and p is the number of levels considered in the assessment, which in this case is two (±50% of the initial parameter value; Campolongo et al. 2007). Resulting values of μ_{SA}, which is the mean of d_i, were ranked. The d_i distribution may contain positive and negative elements resulting from the increase or decrease of the input factor value. These elements may cancel each other out and thus incorrectly produce a low value of μ_{SA}, indicating a negligible effect. Therefore, Campolongo et al. (2007) suggested the use of μ^*_{SA} which is the estimate of the mean of the distribution of the absolute values. In this case:

$$d_i^* = \frac{(f(X + \Delta X_i) - f(X))/f(X)}{\Delta X_i/X_i} \tag{16}$$

The levels of parameter change considered in this analysis were ±50%. The indicator μ^*_{SA} was calculated for each state variable and each parameter. A variation from 0 to 1 of μ^*_{SA} indicates that the model is insensitive to the parameter change. A value of 1 indicates a linear relationship between the model and the parameter change. Values above 1 indicate that the model is sensitive to the change of parameter.

Model validation

The robustness of the fit was investigated by doing a linear regression using the least squares method. The statistical coefficient of determination (R^2) provides a measure of the model performance. This procedure was done by comparing data collected during the years of 2006 and 2007–2008 and the model output for the four state variables. The perfect agreement between data and model output is yielded by a regression slope of 1.

Results

Model

Nitrogen concentrations in the water column are predicted to vary from around 2 to 10 mmol m^{-3}, with higher values during the winter and lower during the summer (Fig. 3a). The model predicts a variation in pelagic chlorophyll concentrations of approximately 1 mg chl m^{-3} through the year (Fig. 3b). Concentrations are expected to be slightly higher during the summer, when compared with the winter. The pattern of variation of chlorophyll and nitrogen concentrations within the sediments is expected to be similar through the year (Fig. 3c, d). MPB chlorophyll concentrations would vary from 200 to around 250 mg chl m^{-2} with higher values during the summer and a strong decrease

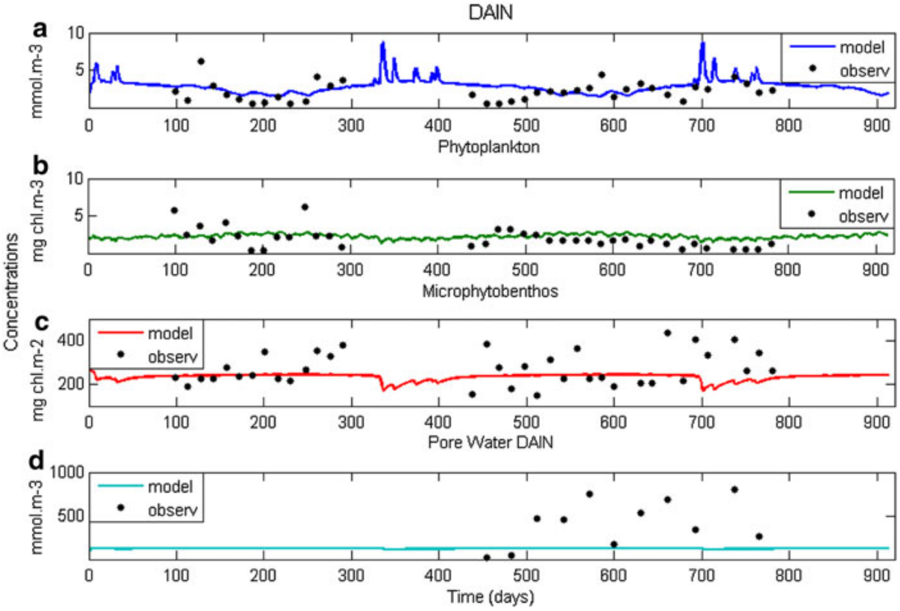

Fig. 3 Observations (*black dots*; from March 2006 to February 2008) and simulation output of **a** DAIN (*blue*; mmol m^{-3}) in the water column; **b** pelagic chlorophyll (*green*; mg chl m^{-3}); **c** benthic chlorophyll (*red*; mg chl m^{-2}); and **d** DAIN in pore water (*light blue*; mmol m^{-3}) during a period of approximately 2 years and a half (913 days)

in the winter. Nitrogen concentration in the pore water would vary from 110 to 130 mmol m^{-3}.

The predicted DAIN concentrations in the water column are within the observed range of variation, except for winter, when the model predicts a strong increase in the pelagic nutrient concentrations due to the lower abundance, and therefore nutrient demand, of MPB. Pelagic chlorophyll concentrations are within the range of variation found in Ria Formosa. MPB chlorophyll concentrations are mostly within the ranges obtained during sampling (Brito et al. 2009b). However, the lower values obtained in the winter were not observed in the lagoon (Fig. 3c). This is due to the fact that the MPB growth changes from nutrient limited (throughout the year) to light limited. From the model development process, it was clear that the pore water DAIN concentrations simulated by the model are strongly affected by the MPB concentrations, and are also lower during the winter due to the decrease in recycled MPB chlorophyll. Both pore water DAIN and benthic chlorophyll are highly variable throughout the year (Fig. 3c, d).

As presented before in this section, this approach for describing the MPB dynamics, allows the calculation of the maximum possible value of chlorophyll concentration (Tables 4, 5). According to the model simulation, the maximum value is of 392 mg chl m^{-2}, defined by the light limited growth rate, which is the one that allows higher values of chlorophyll concentration.

The linear regression showed a weak agreement between the model output and observation for both periods, 2006 and 2007–2008 separately. The coefficients of determination obtained were very low for all the state variables, as presented in Table 3. Moreover, none of them were significant ($p > 0.05$) (Table 6).

Table 6 Agreement between model output and observations

Year	Variables	R^2
2006	DAIN	0.26
	Phyto	0.07
	MPB	0.20
2007–2008	DAIN	0.11
	Phyto	0.10
	MPB	0.14
	PW DAIN	0.06

Sensitivity analysis

The input factors that caused the largest change in the model simulation, following the first approach, the relative absolute change, are represented in Fig. 4 by dark shades. Our results clearly indicate that variations in all input factors have a greater effect on the benthic components of the system, on both the MPB and the pore water nutrients. This is due to the fact that the concentrations of the benthic elements are in one or two orders of magnitude higher than the concentrations simulated for pelagic elements. The physical characteristics of this lagoon system are important in the model. Variations in the exchange rate (E) produce a relatively high variation in the output of DAIN concentration in the water column. However, this fact is masked by the importance of the benthic compartments (Figs. 4, 5). If the exchange rate is lower than normal, the nutrient concentrations in the water column will increase due to their accumulation in the system. Porosity is another input factor that is extremely important both for pelagic and benthic compartments. This factor is essential for the fluxes equations, having a great impact in the diffusion of nutrients from the sediments to the water column and therefore in the amount of nutrients that is captured by MPB (Table 4). It also affects the MPB growth by interfering with the uptake of nutrients by MPB. Regarding the group of factors that includes the chlorophyll and nutrient related parameters, it is clear that the parameters directly associated with benthic processes are the ones that cause the largest variations. The yield of MPB chlorophyll from nutrients (q_b) has a key role in the calculation of the MPB chlorophyll concentrations by the model. The yield of chlorophyll from nutrients was previously identified as a key factor for phytoplankton by Portilla et al. (2009) using a different version of the CSTT model (LESV model) which only considers the pelagic compartments. The benthic chlorophyll fraction that is recycled (e_b) is also critical in this model both for MPB and pore water nutrients. If the value of the e_b factor is higher than the original value, the amount of matter that will be recycled rises and leads to an increase in the pore water concentrations. This is favourable for an increase in the MPB concentrations, as well. The loss rate of MPB due to grazing (L_g) has a direct effect on MPB chlorophyll concentrations.

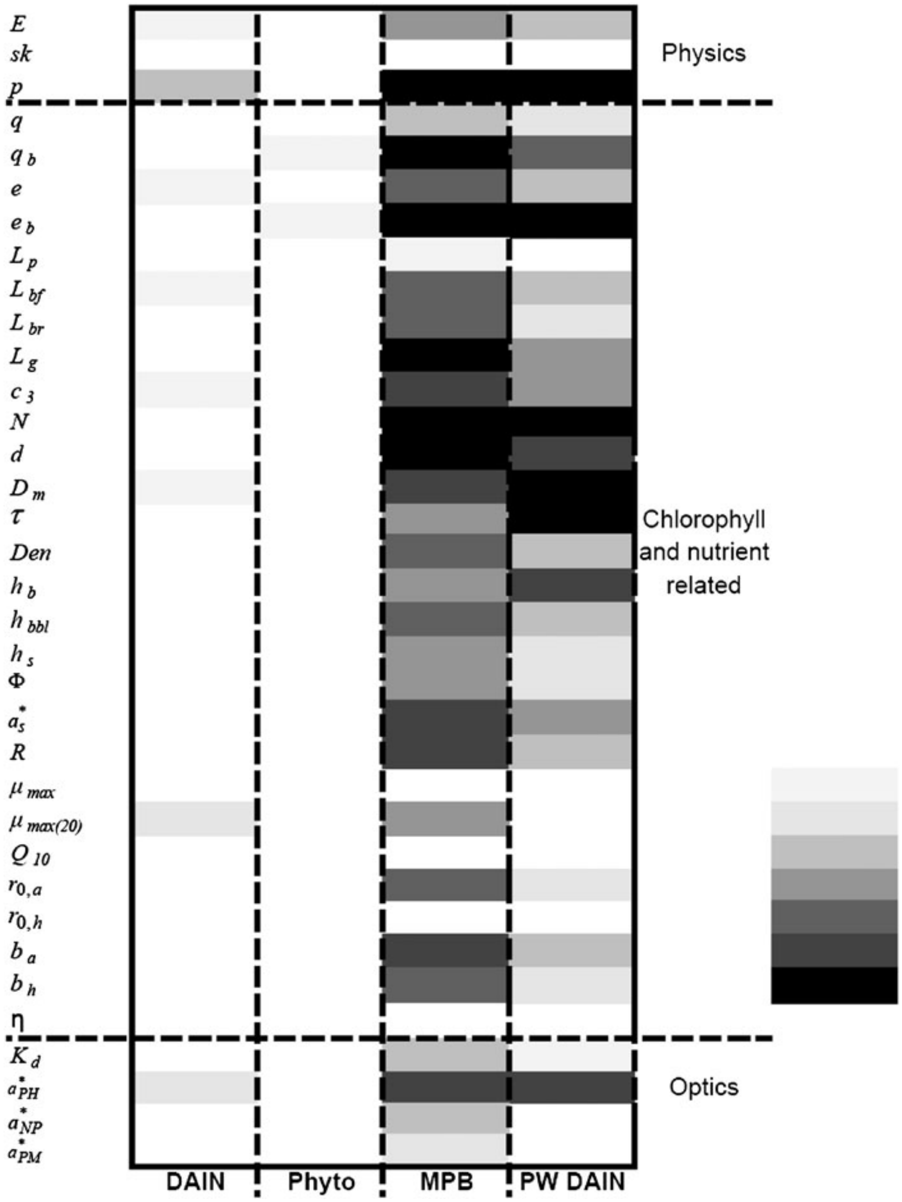

Fig. 4 Parameter change effect as a function of the state variables following the relative absolute change method. The *darkest colour* correspond to the highest score in the μ_{SA} indicator. Scores under the 50th quantile of all the effect considered were not included

All the other input factors with large effects on the benthic components have a close relationship with pore water concentrations and fluxes, such as the nitrogen input (N), the decay rate (d), the diffusion coefficient (D_m) and tortuosity (τ). The absorption cross section of photosynthetic pigments $\left(a_{PH}^*\right)$ is the only input factor from the 'optics' group that has a relatively high effect on the model output. A higher value of this input factor would lead to an increase of the photosynthetic efficiency of MPB.

The parameters that caused the largest impact in the model, following the second approach, the standardized change, are represented in Fig. 5. The main results are similar to the ones obtained with the previous approach. It is clear that porosity (p) is a

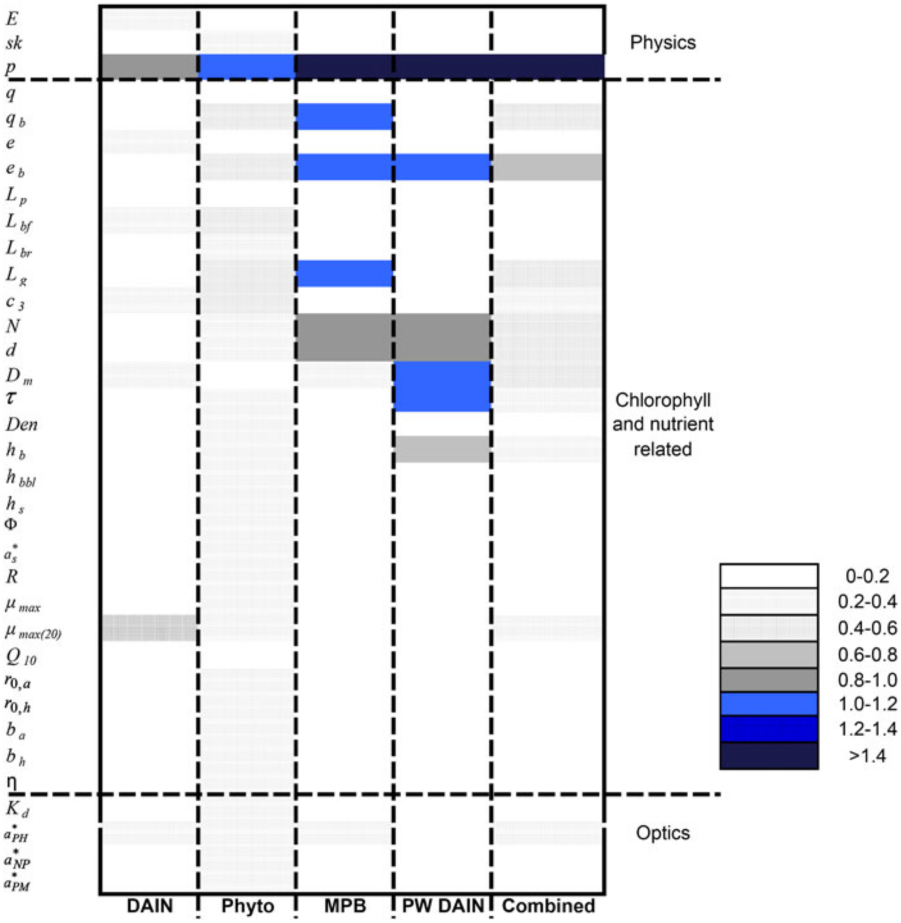

Fig. 5 Parameter change effect as a function of the state variables, following the standardized change method, represented as the μ^*_{SA} indicator values. The *darkest colour* correspond to the highest value of the μ^*_{SA} indicator

parameter to which the model is more sensitive, which was also indicated previously. In fact, porosity has the largest impact in all the state variables of the model. The yield of microphytobenthic chlorophyll from nitrogen (q_b) was also confirmed as one important parameter for MPB, as well as, the benthic chlorophyll fraction that is recycled (e_b), which has also an important effect on pore water nutrient concentrations. The parameters that are linked to the nutrient fluxes such as the diffusion coefficient (D_m) and tortuosity (τ) have also an important effect on the benthic variables, as also indicated previously. Finally, it is interesting to note that combining the four state variables, the model is only sensitive to one parameter, porosity, which has a strong effect in the model output.

Estimating assimilative capacity

The assimilative capacity of a system is its ability to accommodate waste products without breaching any of the ECoQOs defined for the specific area. However, no ECoQOs have yet been defined and established for Portuguese waters, and more specifically to the Ria Formosa lagoon. In this approach, the standards suggested by Crane et al. (2006) and Tett et al. (2007) for DAIN (winter values—10 µM or 10 mmol m^{-3}) and phytoplankton chlorophyll (spring/summer values—10 mg m^{-3}) concentrations were taken and applied in this analysis. In the future this analysis should be performed with specific reference conditions and ECoQOs for Ria Formosa, as required by the Water Framework Directive.

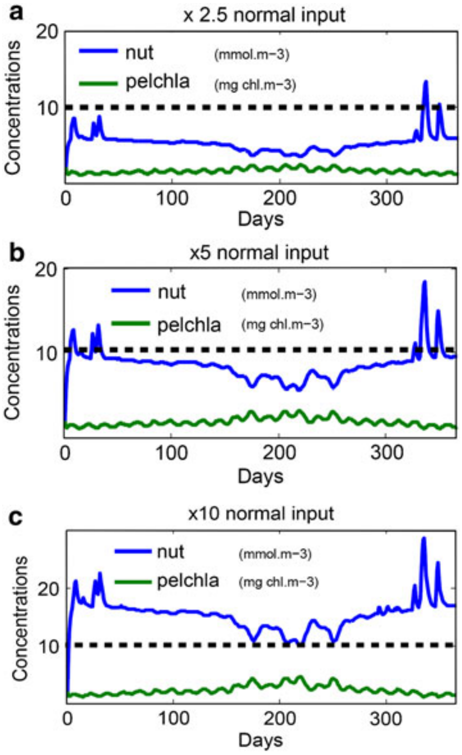

Fig. 6 Model output for DAIN (‘nut’; mmol m^{-3}) and pelagic chlorophyll (‘pelchla’; mg chl m^{-3}) concentrations with nitrogen input increased by a factor of 2.5 (**a**), 5 (**b**) and 10 (**c**). Threshold for DAIN and pelagic chlorophyll concentrations is shown in each figure (*black dashed line*)

A series of simulations were carried out in which the nitrogen input to the lagoon system was increased by a factor of 2.5, 5 and 10. The output of these simulations is presented in Fig. 6. Figures include the indicative threshold for DAIN and pelagic chlorophyll concentrations. Nitrogen inputs to the lagoon were increase by a factor of 2.5 and the threshold for DAIN concentrations was reached and exceeded, as illustrated in Fig. 7a.

Enrichment of nutrient concentrations in the lagoon would not produce a clear response from the algal community. Pelagic chlorophyll concentrations were maintained far below the threshold during all the simulations performed (Fig. 7b). Benthic chlorophyll concentrations did not suffer from a strong influence in nutrient enrichment either and concentrations were kept similar to the ones obtained using normal values of nitrogen input. In summary, the DAIN threshold was breached by doubling the nitrogen input and the chlorophyll threshold was not reached, even with an increase of the nitrogen input by a factor of 10.

Discussion

During the past two decades a number of models have dynamically coupled benthic and pelagic ecosystems (e.g. Baretta et al. 1995) but with the emphasis on the sediment’s role in remineralisation in water columns in which not enough light reaches the sea-bed to allow benthic photosynthesis. Although there has been much interest in the detailed biology and photosynthetic abilities of MPB (Jesus et al. 2005; Serôdio et al. 2005), little of this has been applied into models capable of simulating seasonal cycles of microphytobenthic production, and the role of benthic micro-algae in nutrient cycling has been limited. As far as we know, only Blackford (2002) has reported such a model.

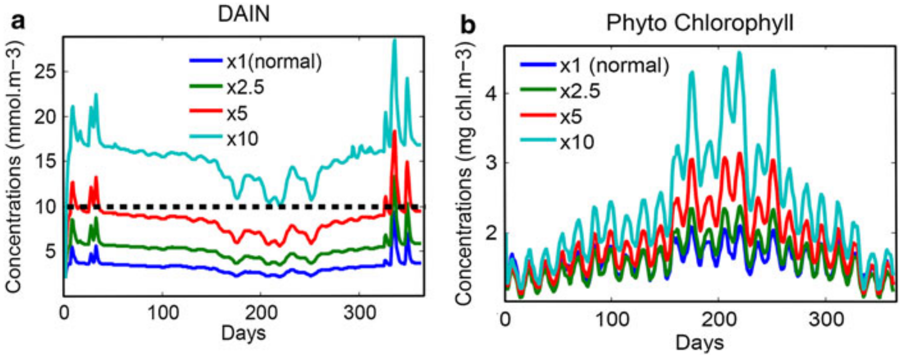

Fig. 7 DAIN concentration (**a**; mmol m^{-3}) and pelagic chlorophyll concentration (**b**; mg chl m^{-3}) variations using different multipliers of the nitrogen input parameter (2.5, 5 and 10)

Blackford (2002) added a compartment for benthic diatoms to the ERSEM model and applied the extended model to water columns in the Adriatic with depths from 5 to 25 m. ‘The benthic algae were modelled in a way conceptually similar to that employed by ERSEM’s phytoplankton’, using Cell Quota kinetics for N and P uptake and growth, direct limitation of growth by ambient dissolved silica concentration and temperature control of maximum uptake rates including carbon dioxide. Biomass change was a product of specific growth and loss rates, multiplied by biomass. Simulated MPB biomass showed a strong seasonal cycle as a result of a combination of light-limitation and lower temperature in the winter; the amplitude of the cycle was least in the shallowest water column.

The present model is intentionally simpler than ERSEM, in physical structure (only one sediment layer rather than 3, for example), in its restricted set of state variables (no multicellular pelagic and benthic grazers, for example, with grazing as a constant loss rate) and its simplified process parameterization (temperature dependent Monod growth for phytoplankton and flux sharing for MPB). In its use of parameterizations that implicitly subtract microheterotroph losses from photo-autotroph production, and in the use of flux parameterizations for MPB, the present model’s conceptual scheme is distinctly different from that of ERSEM. It also uses the CSTT strategy, in which nutrient depletion is a consequence of algal growth, the latter being linked to the former by a yield term (Gowen et al. 1992; Edwards et al. 2003). Finally, the present model allows some benthic–pelagic exchange of autotrophs, likely to be important in shallow, tidally-stirred waters.

Characteristic behaviour of benthic diatoms is reported as including migrations to and from the surface of the sediment, for reasons that include avoiding resuspension, and acquiring photons (e.g. Serôdio et al. 1997). We have included these processes in the present model, albeit parameterized more simply than in the more detailed model used by Guarini et al. (2008) to simulate the spatial dynamics of MPB over tidal cycles in the Marennés-Oleron Bay on the French Atlantic coast.

There are several arguments for simplicity in modelling. These include ‘Occam’s razor’ (‘it is vain to do with more what can be done with less’, or, ‘do not unnecessarily multiply entities’), best treated as practical advice to work from simple to more complex, and the arguments explored by Fulton et al. (2004), who showed that physiological details are not always needed in biogeochemical marine ecosystem models: simpler formulations can be adequate for learning and general predictive purposes—with consequent lower developmental, computational and maintenance costs. These are the arguments that led to the CSTT model, which has been made more complicated only from necessity.

Summarizing, there are three aspects that are novel and were introduced in this article: the application of the CSTT concepts to the sediment, especially the MPB yield of chlorophyll from nutrients; the use of a flux capture approach for microbenthic biomass increase, rather than a parameterization involving specific growth rates as a function of PAR and nutrient concentration; and taking some account of MPB migratory behaviour in an ecosystem model. These contribute towards the development of useful models for the management of systems and interpretation of events such as eutrophication.

In general terms simulated values of state variables are of the correct order of magnitude (with little adjustment of model parameters, most of which are taken from literature or other work). The model show, however, little time variation and most of the R^2 coefficients are below 0.26. Simulated MPB chlorophyll, for example, decreased for a few weeks during mid-winter, but otherwise remained constantly high. This would seem to contrast with the results of Blackford (2002), who simulated more strongly defined seasonal cycles of microphytobenthic biomass in the Adriatic. However, extrapolation of his simulations to water depth corresponding to that of the Ria Formosa might produce similar results to ours, with light-limitation being important only during the darkest days of the year. Equally importantly, an analysis of the spatial and temporal scales of variation in MPB chlorophyll reported by Brito et al. (2009b) showed that the seasonal component was very weak (5% of the total), variation coming mainly from spatial heterogeneity (61%). Thus we might conclude that the model has simulated benthic variables as well as could be expected for a single box simplification of a spatially complicated region, and that the variation shown in the observations results from small-scale processes that are not included in the model. Understanding these processes would be interesting but might not help us understand nutrient cycling on the scale of the whole Ria, which is to say that they can be treated as stochastic in relation to the model.

The model developed predicts DAIN concentrations (water column and sediments) within the range of the observed variation. Moreover, the range of variation predicted is in accordance with the results obtained by Serpa et al. (2007) using a biogeochemical model just for nutrients and considering the denitrification process. The model predicts a well defined pattern for the variation of pelagic chlorophyll concentrations, which is mainly influenced by the resuspension of benthic chlorophyll, especially by the action of spring and neap tides. This is clear in the output due to the periodicity of the peaks. It would thus seem, from the simulations, that MPB play a major role in the over-all dynamics of (benthic + pelagic) chlorophyll in the Ria. MPB may represent up to 99% of the total chlorophyll of the system, when considering phytoplankton (also discussed in Brito et al. 2010a). The high flushing rate of the lagoon, as well as the large grazing pressure by benthic organisms leads to a strong reduction in the phytoplankton biomass, which is compensated by the resuspension of benthic algae. Due to the large concentration of benthic chlorophyll, as observed and predicted by the model, a small rate of daily resuspension (around 0.5–1% of the fraction c_3 of the MPB community) is sufficient to keep the system within these conditions. Moreover recent studies, such as Cloern and Jassby (2008) have reported the absence of recurrent temporal variation of phytoplankton over 150 sites at the land-sea interface caused by the complex interactions between the processes that affect phytoplankton. This is therefore another factor that is responsible for the difficulty in predicting the temporal variation of primary producers at these sites. The pelagic and benthic interactions in shallow lagoons, like Ria Formosa should be further explored.

The high pore water DAIN concentrations are the major source of nutrients for the large microphytobenthic algal community as evidenced by the data obtained when assembling the model. Through the nutrient flux from the sediments to the water column, MPB always have a large amount of available resources to grow. Alternative parameterizations, using standard functions such as the Monod type and a *P–I* curve for growth were explored but resulted in low concentrations of MPB chlorophyll and extremely poor agreement with data (for details see Brito 2010). This motivated the development of this new approach based on fluxes.

Under normal conditions, the MPB absorb most of the flux from the sediment pore water. Thus, if the benthic chlorophyll concentrations decrease by any reason, the nutrient flux into the water column increases strongly. This is what happens in the model during the winter and could happen in response to global change. If less light reached the seabed because of sea level rise and increased water turbidity due to more stirring, the MPB community might decrease, and hence relinquish some of its nutrient-absorbing role.

Considered in terms of hypothesis testing: the agreement of benthic observations with simulations tells us that our current conceptual model cannot be rejected for the Ria as a whole—although it clearly fails to capture some important processes at the local (sampling site) level.

The SA indicates that the ecosystem behaviour is more sensitive to the benthic components/processes, including benthic physics and biology, than to the pelagic sector. The yield of chlorophyll from nutrients was previously identified as a key factor for phytoplankton by Portilla et al. (2009) using a different version of the CSTT model (LESV model) which only considers the pelagic compartments. This was also confirmed in this study. Both yields of phytoplankton and MPB chlorophyll from nitrogen were confirmed to be some of the most important parameters for these two state variables. Another important parameter, the recycling factor e_b needs further investigation. For MPB, the parameters involved in the nitrogen cycle were also very important, which, once more, indicates the importance of pore water nutrients.

Given the importance of these factors, they should be carefully evaluated in future applications of this model. Porosity is easily evaluated by field and laboratorial work and should always be assessed. The yield of microphytobenthic chlorophyll from nutrients was estimated through an experimental approach (for details see Brito et al. 2010a). Similar evaluations have also been carried out in the past for pelagic communities (e.g. Edwards et al. 2003, 2005). Further work on nutrient recycling and grazing pressure should be seriously considered in the future to improve our understanding of the system.

The optical parameters did not show a great effect on the model output. The analysis of the model output and field data indicate that photosynthetic communities do not have a strong dependence on light, because light does not seem to be limiting the algal growth (both pelagic and benthic) in this shallow lagoon.

The assimilative capacity estimate obtained through this exercise indicates that an increase in nitrogen inputs by a factor of 2.5 may be sufficient to breach the established threshold during the winter. This would occur if the same conditions exist, i.e. considering the lower values of benthic chlorophyll during the winter. Moreover, no chlorophyll threshold is reached even considering a nitrogen input increase by a factor of 10, which may be due to the high flushing rate in the lagoon.

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