



Analysis of coastal lagoon metabolism as a basis for management

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Abstract

This work was carried out in a shallow eutrophic coastal lagoon (St. André lagoon, SW Portugal) which is artificially opened to the sea each year in early spring. Macrophytes, mainly *Ruppia cirrhosa*, are keystone species in this ecosystem covering up to 60% of its total area with peak biomasses over 500 g DW m⁻². The main objectives were to study ecosystem metabolism, to evaluate the metabolic contribution to the community of the macrophyte stands and their influence in the development of thermal stratification and bottom oxygen depletion.

The work combined an experimental and a modelling methodology. The experimental approach included open water, mesocosm and microcosm seasonal experiments. During these experiments several physical, chemical and biological parameters were monitored in the lagoon and in plastic enclosures (mesocosms) for periods of 24 hours. The microcosm experiments followed the light-dark bottle technique. The simultaneous use of these different methodologies allowed the analysis of the contribution of the planktonic and benthic compartments to the ecosystem's oxygen budget.

The modelling work was based on the mathematical simulation of heat and gas exchanges in a vertically resolved water column, under different macrophyte densities. Several simulations were carried out, in order to investigate the importance of the macrophytes in the development of water column stratification and anoxia.

The simulation results suggest that macrophytes may greatly influence thermocline and oxycline development. This influence is proportional to their biomass and canopy height. It is suggested that controlled macrophyte biomass removal of up to 25% of available biomass in summer, may be useful in preventing bottom anoxia without compromising benthic net primary production.

Introduction and objectives

The metabolism of coastal lagoons is strongly influenced by freshwater inputs and the exchange processes with the adjacent sea (Barnes, 1980; Postma, 1981). Most lagoons located in the Portuguese West Coast are usually separated from the sea by a sand barrier. Natural opening processes are irregular and strictly dependent on the rainfall (Heydorn & Tinley, 1980; Hervé & Bruslé, 1981). In very rainy winters the high water level of the lagoons may cause discharges to the sea, opening a channel through the sand barrier

(Cancela da Fonseca, 1989). Usually the lagoon-sea exchange depends on a man-made channel for a period lasting from days to several weeks. The opening of these channels may prevent eutrophication and anoxia development, through the wash-out of organic matter and nutrients from the lagoons to the sea. Then, the uninterrupted sand barrier re-establishes and the lagoons return to their isolated condition.

During the exchange period with the sea, a marine renewal of the system occurs, enabling the colonisation by valuable marine species. There is export of dissolved and particulate organic and inorganic matter

in each tidal cycle. The efficiency of this washing-out process apparently depends on the lagoon water level before the opening process and on the local sea conditions. The macrophyte biomass decreases due to salinity shock and air exposure during low tide. Moreover, the brackish conditions of the lagoon are maintained.

The utmost importance of the lagoon-sea connection is related to the fact that many of these lagoons are dystrophic, i.e. eutrophic and thus subject to summer critical events involving intense nutrient releases from the sediment and faunal mortalities (Bamber et al., 1992).

St. André lagoon (Figure 1) (SW Portugal) is a land-locked coastal lagoon with a temporary connection to the sea. Usually in late March, when the lagoon water level is highest, a channel through the sand barrier is artificially opened, promoting water exchange with the sea. The juveniles of several marine species (e.g., *Anguilla anguilla*, *Dicentrarchus labrax*, *Sparus aurata*, *Mugil* sp.) enter into the lagoon during the short opening period (1–2 weeks). Annually, by 10–100 tons of these species (mainly *Anguilla anguilla*) are harvested. The lagoon is also used for recreational activities as beach visiting and bathing. The low average depth and the high water residence time are responsible for a strong macrophyte development dominated by *Ruppia cirrhosa* (Petagna) Grande and *Potamogeton pectinatus* L., and a high sediment organic content. Large accumulations of these plants and organic matter often cause ‘dystrophic crises’, especially during summers, when massive mortality among benthos and fish may occur (Bernardo, 1990). These events usually occur in years with weak connection to the sea and following several days of high temperatures and no wind.

High nutrient levels and shallow depth provide ideal conditions for high rates of primary production. In Table 1 the ranges of some physico-chemical and biological parameters of St. André lagoon are summarised.

During summer, under high temperature conditions due to shallow depth and isolation from the sea, the macrophyte biomass and the organic rich muds support intense respiration, and consequently anoxic conditions may occur. The high macrophyte biomass also restricts vertical mixing of the water column, further contributing to anoxic conditions.

In winter, episodic inputs of seawater overwhelming the sand barrier create density stratification in the deeper zones of the lagoon. Bottom waters of-

Table 1. Main characteristics of St. André lagoon (data from Bernardo, 1990)

Average area	150 ha
Average depth	135 cm
Max. depth	225–540 cm
Salinity	1.9–23.5 psu
Temperature	9.5–28.6 °C
Phosphate P-PO ₄	0.05–3.8 μmol l ⁻¹
Nitrate N-NO ₃	0.2–75.3 μmol l ⁻¹
Ammonia N-NH ₄	1.4–22.3 μmol l ⁻¹
Chl. <i>a</i>	1.8–61.9 mg m ⁻³
Macrophytes	94–438 g AFDW m ⁻²
Sediment org. matter	6.5–16.6%

ten become anoxic. Similarly, watershed inputs of freshwater during storms may also cause stratification (Cancela da Fonseca et al., 1989).

Photosynthetic organisms may intercept as much as 50% of incident light (Odum, 1971), thus blocking radiant energy transfer to depth. This bottom shading effect has been demonstrated in marine ecosystems by several authors (e.g., Taylor, 1993). It seems reasonable to expect that high-density stands of benthic macrophytes may produce a similar effect in shallow water ecosystems, such as the St. André lagoon, due to the shadowing of their leaves on the underlying water.

Eutrophication could possibly be reduced by harvesting macrophytes, therefore removing important quantities of nutrients and organic matter. This “cleaning” of the lagoon could contribute to its sustainable management, improving fish production and recreational usage. Macrophyte harvest for fertiliser has been a traditional activity in Portugal since at least the Middle Ages (Veiga de Oliveira et al., 1975). It is well established that macrophyte harvesting may prevent eutrophication phenomena in semi-enclosed water bodies (Thornton et al., 1995). It is also important to know the influence of this activity on water column stratification and bottom anoxia.

To be able to predict the occurrence of oxygen depletion it is important to quantify community photosynthesis and respiration. Since the contribution of the pelagic and benthic compartments to each of these processes will depend largely on water level and hydrodynamic mixing, it is also important to quantify the contributions of each compartment as a function of environmental conditions. Knowledge of which compartment contributes the most will make it possible to predict anoxia and to define preventive measures.

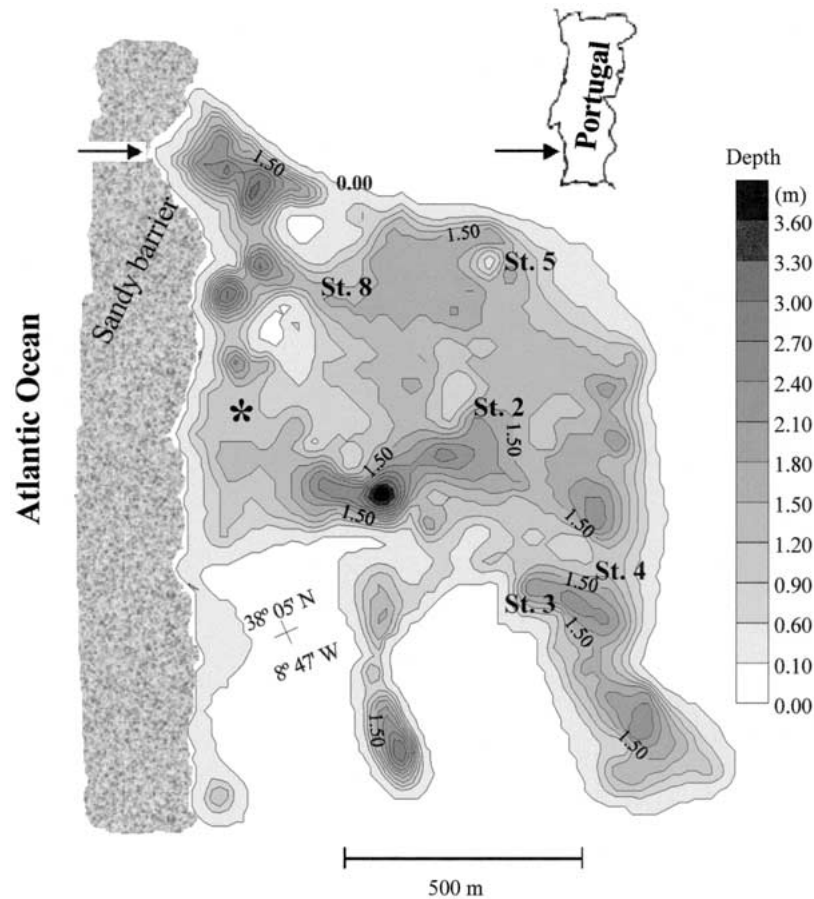


Figure 1. St. André Lagoon average depths reported to the lagoon margins (0.00), that are approximately 1.5 m above sea level. The arrow on the upper left corner shows the place where the Lagoon is artificially opened to the sea every Spring. The asterisk shows the place where the mesocosm experiments were carried out (see text).

The objective of this work in the St. André lagoon is to answer the following questions:

- (1) What is the relative contribution of the different autotrophic compartments in the community metabolism?
- (2) What are the time-scales for the development of thermal stratification?
- (3) What is the influence of the macrophytes in the development of water column thermal stratification and bottom anoxia?

Materials and methods

Several experimental and modelling approaches were used. Mesocosm and microcosm experiments were carried out *in situ*. Also six sampling campaigns were carried out in Santo André lagoon covering all seasons - July 1996, December 1996, September 1997,

December 1997, March 1998 and June 1998. The experimental results obtained from the mesocosm and the microcosm experiments were used to compute lagoon metabolism in terms of oxygen production and consumption.

Mesocosm experiments

Two types of mesocosms were used to isolate ecosystem components. Some mesocosms contained only water (Pelagic (P)-mesocosms) and others contained water, sediments and also macrophytes when these were present in the lagoon (Bentho-Pelagic (BP)-mesocosms). The P-mesocosms consisted of a transparent polyethylene cylinder with the bottom closed (Figure 2). The BP-mesocosms were similar to the pelagic ones except in their lower end, which was open and made of PVC, so that they could be pushed into the sediments (Figure 2). A plastic net was placed

inside the mesocosm walls to reinforce the whole structure. The diameter of the mesocosms was 45 cm. Their height depended on the depth of the lagoon at the place where the experiments took place (Figure 1) and varied from ca. 50 to 100 cm, corresponding to a volume of 79 to 159 dm³. Three replicates were used in all mesocosm experiments.

After placing the mesocosms in the lagoon near the sandy barrier (Figure 1), sampling for dissolved oxygen (D.O.) was carried out every 3 hours for a 24-hour period, in the lagoon and in the mesocosms. Simultaneously, sensors were used to measure underwater light intensity just below the surface and above the bottom (Quantum sensor LI-COR mod. 193AS), pH (pH meter ESD, Engineered Systems & Designs, model 69), temperature and salinity (S-C-T meter YSI model 33). Dissolved oxygen samples were chemically fixed *in situ* and analysed in the laboratory by the Winkler method (A.P.H.A., 1992). Each mesocosm was sampled nine times per sampling campaign, for all the parameters described above, except in the first campaign, in July 1996, when eight samples were taken. At the end of each campaign the mesocosms were removed.

At the end of the experiments water samples were collected for pigment analysis. These were analysed by fluorimetry according to Strickland & Parsons (1968). Sediment samples for macrophyte biomass were also collected from inside the area previously covered by the BP-mesocosms, using a 16 cm diameter cylindrical sampler "core" (Menéndez & Comín, 1989). Plants and sediment were sorted from the core through a 5 mm mesh bag and sieved in the water. Samples were transported to the laboratory and frozen (−18 °C) until subsequent analysis. Plant material was then separated, dried at 105 °C for about 24 hours and finally weighed.

Oxygen budget calculations

The diurnal oxygen curves obtained for each mesocosm and for the lagoon were used to calculate oxygen diffusion across the surface (D), net primary production (NPP), respiration (R) and gross primary production (GPP). Equation (1) describes the D.O. depth integrated mass balance. In the mesocosms the horizontal diffusion and advection terms are zero.

$$\frac{dC}{dt} = GPP - R + k_{\text{air-water}} \left(\frac{C_s - C_o}{C_s} \right) + k \frac{\partial C_w}{\partial x} + k \frac{\partial C_w}{\partial y} + A, \quad (1)$$

where, C_s and C_o are saturation and depth integrated oxygen concentrations (g O₂ m^{−2}) in the time interval δt ; GPP , gross primary production (g O₂ m^{−2} h^{−1}); R , respiration (g O₂ m^{−2} h^{−1}); $K_{\text{air-water}}$, gas-transfer coefficient (g O₂ m^{−2} h^{−1}); $\partial C_x / \partial x$ and $\partial C_x / \partial y$, horizontal D.O. concentration gradients (g O₂ m^{−3} m^{−1}); k , horizontal eddy diffusion (m^{−2} h^{−1}); A , net oxygen advection (g O₂ m^{−2} h^{−1}).

Overnight oxygen dynamics in the mesocosm at two different time intervals (1 and 2) is described by (2) and (3):

$$\frac{dC_1}{dt_1} = -R + k_{\text{air-water}} \left(\frac{C_{s1} - C_{o1}}{C_{s1}} \right), \quad (2)$$

$$\frac{dC_2}{dt_2} = -R + k_{\text{air-water}} \left(\frac{C_{s2} - C_{o2}}{C_{s2}} \right). \quad (3)$$

Assuming that community respiration and the gas transfer coefficient are constant over the experimental period, both may be estimated from Equations (2) and (3) (Odum, 1956). Hereafter this will be referred to as Method 1.

Another approach used was to measure planktonic respiration rate (R) in microcosms isolated from the atmosphere (see below), and then solve Equations (2) and (3) for k , from the night D.O. variations in the P-mesocosms. This will be referred to as Method 2. Eight diffusion and eight NPP values were obtained for each mesocosm (seven in the July 1996 campaign) and for the lagoon.

There are several methods for the estimation of the oxygen gas transfer coefficients. These were described and compared by Kosinski (1984). The methods used in our work, however, were chosen because more sophisticated formulations based on night-time regressions or on quasi-continuous oxygen measurements are very demanding in terms of data points. In the present study, dissolved oxygen was measured by Winkler titration and therefore it was not possible to collect a very large number of samples without reducing significantly the mesocosms volume. In fact, the experiments were designed to favour replication, measurement accuracy and precision in stead of sampling frequency.

Data analysis

The results of the mesocosm experiments were analysed by ANOVA and the Kruskal–Wallis test. A Three Way ANOVA Model I was used to test the effects of the independent variables - season, mesocosm type (pelagic or benthopelagic), time of sampling

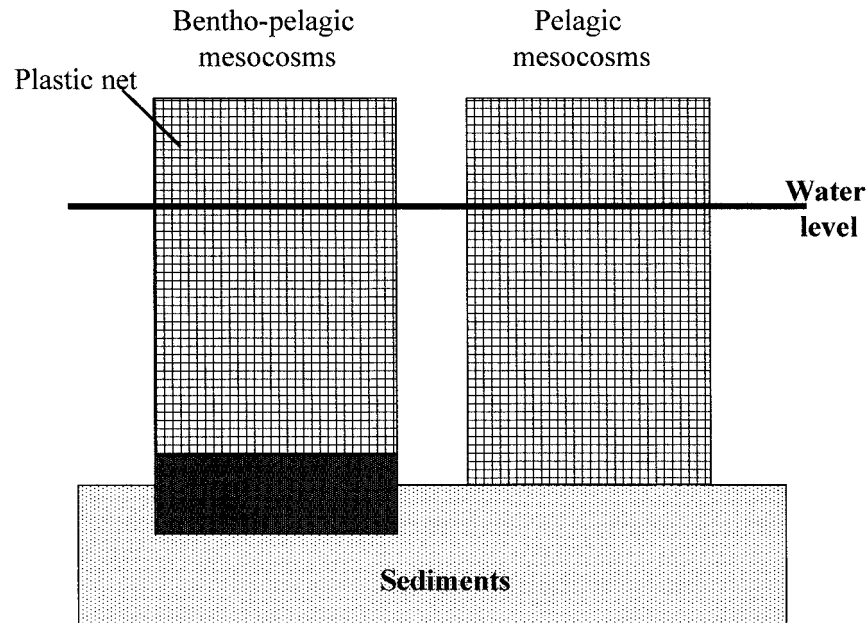


Figure 2. Schematic drawing of Benthic-pelagic (BP) and pelagic (P) mesocosms. The former are partially buried into the sediments. Mesocosms were fixed to the bottom with stakes and their walls reinforced with a plastic net. Their height depended on water depth and varied from ca. 50 to 100 cm.

and their interactions on dissolved oxygen saturation concentration. The post-hoc Newman–Keuls test and the Kruskal–Wallis test were used to contrast different campaigns or treatments.

The data from the lagoon was not included in the statistical tests because there was no replication in it. In spite of the fact that samples from the lagoon were taken in triplicate they were merely subsamples, since they were collected in the same area. Due to logistic constraints it was not possible to sample more stations during the experiments.

Microcosm experiments

Microcosm experiments were carried out in order to measure planktonic and benthic respiration and photosynthesis by the light-dark bottle technique (Vollenweider, 1974). Winkler flasks were used for water column measurements whereas benthic chambers were used in the sediments.

Water column measurements

During all sampling campaigns the oxygen method was used to measure respiration in dark bottles. In the first two campaigns it was also used to measure photosynthesis in transparent bottles. However, since September 1997, photosynthetic rates were measured

by standard ^{14}C techniques (Steemann Nielsen 1962) following the ICES (1996) recommendations. Water samples were placed in 60 ml Winkler bottles and inoculated with 1 ml of $\text{NaH}^{14}\text{CO}_3$ with 10 μCi sodium (Carbon 14 Centralen). A dark bottle was used for the blank determination. Upon removal, samples were filtered through 0.45 μm pore membrane filters. Filters were acidified with HCl and placed in vials with 10 ml scintillation fluid (Insta-Gel Plus, Packard). Radioactivity was then counted in a liquid scintillation analyser (Tri-Carb Model 1600CA). Primary production ($\text{mg C m}^{-3} \text{ h}^{-1}$) was calculated following ICES (1996) and then divided by the phytoplankton biomass to calculate the primary production rate ($\text{mg C mg Chl } a^{-1} \text{ h}^{-1}$). Values obtained were converted into oxygen units assuming a photosynthetic quotient (P.Q.) of 1.00. Respiration incubations were carried out for up to 5 hours, whereas incubations for the measurement of productivity were carried out for periods of 2.5 hours.

From the metabolic rates measured during the short-term incubations, daily values were calculated. Respiration was assumed to have remained constant over a 24-hour period. Regarding photosynthesis, it was necessary to consider sunlight variability. A simple sinusoidal function was used to produce an hourly

time-series of light intensities fitted to the measured values (with a 3-hour interval):

$$I_0 = I_{\max} \sin((\text{Hour} - (\text{SolarNoon} - \text{Photoperiod}/2))/(\text{Photoperiod}/2)), \quad (4)$$

where I_0 , surface light intensity in $\mu\text{E m}^{-2} \text{s}^{-1}$; I_{\max} , light intensity at solar noon in $\mu\text{E m}^{-2} \text{s}^{-1}$.

The photoperiod and the solar noon were calculated from standard formulations described in Brock (1981). I_{\max} was obtained from the light intensity measurements carried out during the experiments to adjust equation 4 to the observed data. Productivity was calculated from light intensity (equation 4) by a depth integrated Michaelis–Menten equation:

$$P = B \int_0^z \frac{P_{\max}}{z} \frac{I_0 e^{-kz}}{I_k + I_0 e^{-kz}} \partial z \quad (5)$$

$$= B \frac{P_{\max}}{kz} \ln \frac{|I_k + I_0|}{|I_k + I_0 e^{-kz}|},$$

where P , gross productivity ($\text{mg C m}^{-3} \text{h}^{-1}$); B , Phytoplankton biomass (mg C m^{-3}); k , light extinction coefficient (m^{-1}); z , depth (m).

The value for P_{\max} was based on the results of the *in situ* incubations. It was assumed that the productivity value measured under full sunlight was a good estimate of P_{\max} . The I_k value was based on laboratory incubations under controlled light intensities and temperatures. These results were discussed elsewhere (Macedo et al., 2001). The hourly productivities calculated from equation 5 were integrated over a day and reported to m^2 . Carbon units were converted to oxygen units assuming a P.Q. of 1.00. The choice of a saturation model for the calculation of productivity, rather than an inhibition model was justified based on laboratory results, from which there was no evidence of light inhibition in phytoplankton samples from St. André lagoon (Macedo et al., 2001).

Benthic chambers

Benthic chambers were 4 l plastic jars with an opened bottom. The area covered by the jars was 0.02 m^2 . A plastic tube was attached to the upper end and the water samples were extracted from the chamber through this tube using a hand pump. Triplicate samples for D.O. were taken at the beginning of the experiments. The lower part of the chambers was buried 5 cm into the sediment. Each incubation lasted 3 hours. Three dark and three transparent chambers were used. Respiration and net production of oxygen were calculated

from the dissolved oxygen changes observed in the dark and in the transparent jars, respectively.

Ruppia cirrhosa contribution to the community metabolism

The contribution of the keystone species *R. cirrhosa* to the community metabolism was calculated similarly to what was described for phytoplankton. *R. cirrhosa* is considered a keystone species because it strongly determines the community structure in the lagoon (cf., Krebs, 1994). Equations (4) and (5) were employed with parameters derived from Menéndez & Peñuelas (1993), Calado (1997) and Calado & Duarte (2000). According to these authors P_{\max} and I_k values for this species may range from 5.50 to 21.04 $\text{mg O}_2 \text{g}^{-1} \text{h}^{-1}$ and 13.20 to 58.36 $\mu\text{E m}^{-2} \text{s}^{-1}$, respectively. In the present case, the median value of each interval was chosen for the calculations. A similar approach was followed for respiration that ranges from 0.56 to 4.80 $\text{mg O}_2 \text{g}^{-1} \text{h}^{-1}$ (Menéndez & Peñuelas, 1993).

Modelling

Modelling was used to evaluate the potential contribution of the macrophyte biomass to thermal stratification and anoxia development. A vertically resolved hydrodynamic model was used to simulate water column stratification. The model was described by (Price & Weller, 1986) and applied by Janowitz & Kamykowski (1991) to Lake Titicaca and by Duarte & Ferreira (1997) to simulate oceanic stratification. It is a one-dimensional vertical exchange model, forced by wind stress at the surface, by solar and long wave radiation and by sensible and latent heat transfer across the surface. Estimation of light intensity and radiation fluxes between the water and the atmosphere – atmospheric long-wave radiation, water leaving radiation, latent and sensible heat transfers - and their influence on water temperature, were based on standard formulations described in Brock (1981) and Portela & Neves (1994). The calculated photosynthetically active radiation (PAR) was used to compute photosynthesis. The number of vertical layers is variable; in the present case 12 layers of 10 cm were used. The model has three phases:

(i) A deterministic phase, which uses wind stress forcing at the atmosphere-water interface in order to calculate the horizontal velocity of the surface water layer. It calculates the density of all the layers based on incident radiation. Although salinity is a state

variable, it is not considered in the density determination because the vertical density structure of the water column is considered to be temperature dependent.

(ii) A convective mixing phase, which looks for vertical instability in the water column. This stage uses a stepwise approach, examining adjacent water layers for densimetric instability, and re-initialising all the layers above with the average values for the horizontal velocity components, temperature, salinity and any other dissolved or particulate properties.

(iii) A dynamic mixing phase, which is responsible for turbulent mixing between layers, based on the shear stress at the interface. This is calculated by means of the Richardson number obtained for each layer. The Richardson number is a nondimensional ratio of the density gradient to the velocity shear and is a measure of the vertical mixing in a fluid (Knauss, 1997).

Model simulations were carried out for periods of over 5 days with a time step of 0.1 hours under summer solar heating, with an average air temperature of 25 °C and with no wind, as to simulate the most likely conditions for the occurrence of stratification. These conditions are frequent in SW Portugal during summer. Therefore, the water was still and dynamic mixing did not occur. Considering that molecular diffusivity of heat is $1.5 \times 10^{-7} \text{ m}^2 \text{ s}^{-1}$ it may be estimated that the time it would take for heat to be transferred over a distance of 10 cm – the spatial scale of the model – is about 18.5 hours (less than the time scale of the model runs). Therefore, molecular diffusion of heat became significant in the present case and was also included in the model.

Model simulations were carried out in order to quantify the time needed for stratification to develop, under the conditions described in the previous paragraph and in the presence of different macrophyte biomasses. The effect of the macrophyte canopy was taken into account by imposing different extinction coefficients over depth, as a function of macrophyte density and canopy height. The extinction coefficient influences light penetration and therefore water heating processes (model phase (i)).

The effect of the macrophyte canopy on light penetration was previously studied by Calado (1997). The light extinction coefficient in the lagoon has values around 1–2 m^{-1} . However, under a macrophyte canopy with a biomass of 400 g DW m^{-2} it may reach 10 m^{-1} . In the model simulations carried out in the present work, a value of 1.6 m^{-1} was used for the light extinction coefficient, in the absence of macrophytes,

based on historical data (Bernardo, 1990). The model computed the extinction coefficient for each layer, using the mentioned value in the absence of macrophytes or a canopy value calculated from Calado (1997):

$$k_{\text{canopy}} = \frac{\text{Biomass}}{227.3 + \text{Biomass}} 16.3, \quad (6)$$

Where k_{canopy} is the canopy light extinction coefficient (m^{-1}) and biomass is in g DW m^{-2} . Equation (6) predicts a linear increase in k_{canopy} with biomass until an asymptotic value of 10 m^{-1} . Whenever the top of the canopy was between the top and the bottom of a layer, light intensity was calculated using the water extinction coefficient from the top of the layer until the top of the canopy, and using the canopy extinction coefficient from the top of the canopy until the bottom of the layer.

Regarding the influence of the macrophytes on the oxygen dynamics, the approach used was the same as described above for the estimation of the role of *R. cirrhosa* on the oxygen budget. The oxygen produced/consumed by the macrophytes at every time-step was added/removed from all the vertical layers occupied by the canopy. The oxygen concentrations in each layer were also exchanged by convective mixing and in the upper layer, by diffusion to/from the atmosphere. Different macrophyte biomasses and canopy heights were tested to evaluate their effects on temperature and oxygen vertical dynamics. The general equations describing the oxygen budget in the model are:

$$\frac{dC_0}{dt} = GP_0 - R_0 + k_{\text{gas}} \left(\frac{C_s - C_o}{C_s} \right) \pm \text{Convection}, \quad (7)$$

$$\frac{dC_i}{dt} = GP_i - R_i \pm \text{Convection}, \quad (8)$$

where GP_i , gross production of oxygen in layer i ; R_i , consumption of oxygen in layer i ; k_{gas} , C_s and C_o as in Equation (1).

The first equation (Equation 7) applies to the upper water layer and it includes a term to represent diffusion with the atmosphere. For the gas transfer coefficient a value of 0.4 $\text{g O}_2 \text{ m}^{-2} \text{ h}^{-1}$ was chosen, according to the value calculated in the present work for a summer situation in September 1997 (Table 3). There was no need to include a term for molecular diffusion between the different layers since its value for oxygen in water ranges from 1.2 to $2.3 \times 10^{-9} \text{ m}^2 \text{ s}^{-1}$ (Libes, 1992), i.e., two orders of magnitude lower than the molecular

Table 2. Mean values for the reference parameters measured in St. André Lagoon during the mesocosm experiments (PAR – Photosynthetically Active Radiation)

Date	July 1996	Nov. 1996	Sept. 1997	Dec. 1997	March 1998	June 1998
Mesocosms depth (m)	1.0	1.0	0.4	1.0	1.0	0.6
Temperature (°C)	26.3	16.6	25.2	14.0	15.5	24.7
Salinity (psu)	13.2	10.0	16.2	3.5	10.0	20.2
pH	9.4	9.6	9.4	8.9	9.4	8.8
Daily average surface PAR ($\mu\text{E m}^{-2} \text{ s}^{-1}$)	113	65	546	34	248	354
Daily average bottom PAR ($\mu\text{E m}^{-2} \text{ s}^{-1}$)	51	3	239	4	40	272
Macrophyte Biomass (g(dw)m^{-2})	49.7	217.5	23.2	–	–	17.4
Chl <i>a</i> (mg m^{-3})	-	–	6.0	42.2	34.7	3.9

Table 3. Gas-transfer coefficients (mean values) calculated for the mesocosm experiments with Method 1 and Method 2 (see text)

Date	Gas transfer coefficients ($\text{g O}_2 \text{ m}^{-2} \text{ h}^{-1}$)	
	Method 1	Method 2
July 1996	1.0	0.2
November 1996	2.6	0.9
September 1997	1.7	0.4

diffusion of heat. Therefore, the time scale for molecular diffusion of oxygen to take an effect is larger than the time-scale of the model runs.

The first two terms in Equations (7) and (8) represent the gains and losses of oxygen through macrophyte gross production and respiration. The last term in both equations corresponds to the gains/losses through convective mixing, which occurs mainly during overnight cooling of the surface layer.

The model was implemented using the modelling software EcoWin (Ferreira, 1995). EcoWin uses Object Oriented Programming (OOP) to relate a set of ‘ecological’ objects by means of a server, or shell, which allows these to interact with each other, and displays the results of their interaction. Both the EcoWin shell and the different objects have been implemented in C++ for Windows™.

Results and discussion

Mesocosm experiments

In Table 2 the reference parameters measured in the lagoon during the experiments are presented. Data on oxygen dynamics obtained during the mesocosm experiments, are shown in Figure 3. Some of the oxygen curves exhibit a ‘normal’ behaviour (e.g., July 1996, November 1996 and September 1997), with a clear decrease in dissolved oxygen during the night and a clear increase during the day, whereas others show less clear patterns (December 1997, March 1998 and June 1998). These patterns are difficult to justify when there are positive oxygen variations during the night that can not be explained by diffusion, as is the case when oxygen concentrations are above saturation. A possible explanation for these ‘abnormal’ results could be the bubble air injection of oxygen by the wind (Emerson et al., 1993) and/or rain in the case of the December 1997 campaign.

In Table 3 the gas transfer coefficients estimated with Methods 1 and 2 are shown. In Table 4 the daily integrated production, respiration and diffusion for the mesocosms and for the lagoon (neglecting advection), computed with Methods 1 and 2, are presented.

Tables 3 and 4 include only the results of the first three campaigns because in the other experiments a ‘normal’ oxygen curve was not observed (Figure 3), reason why it was not possible to obtain reliable estimates of oxygen net production and diffusion. This could be explained by a dominance in physical processes over the biological ones with high rates of oxygen diffusion and bubble air injection.

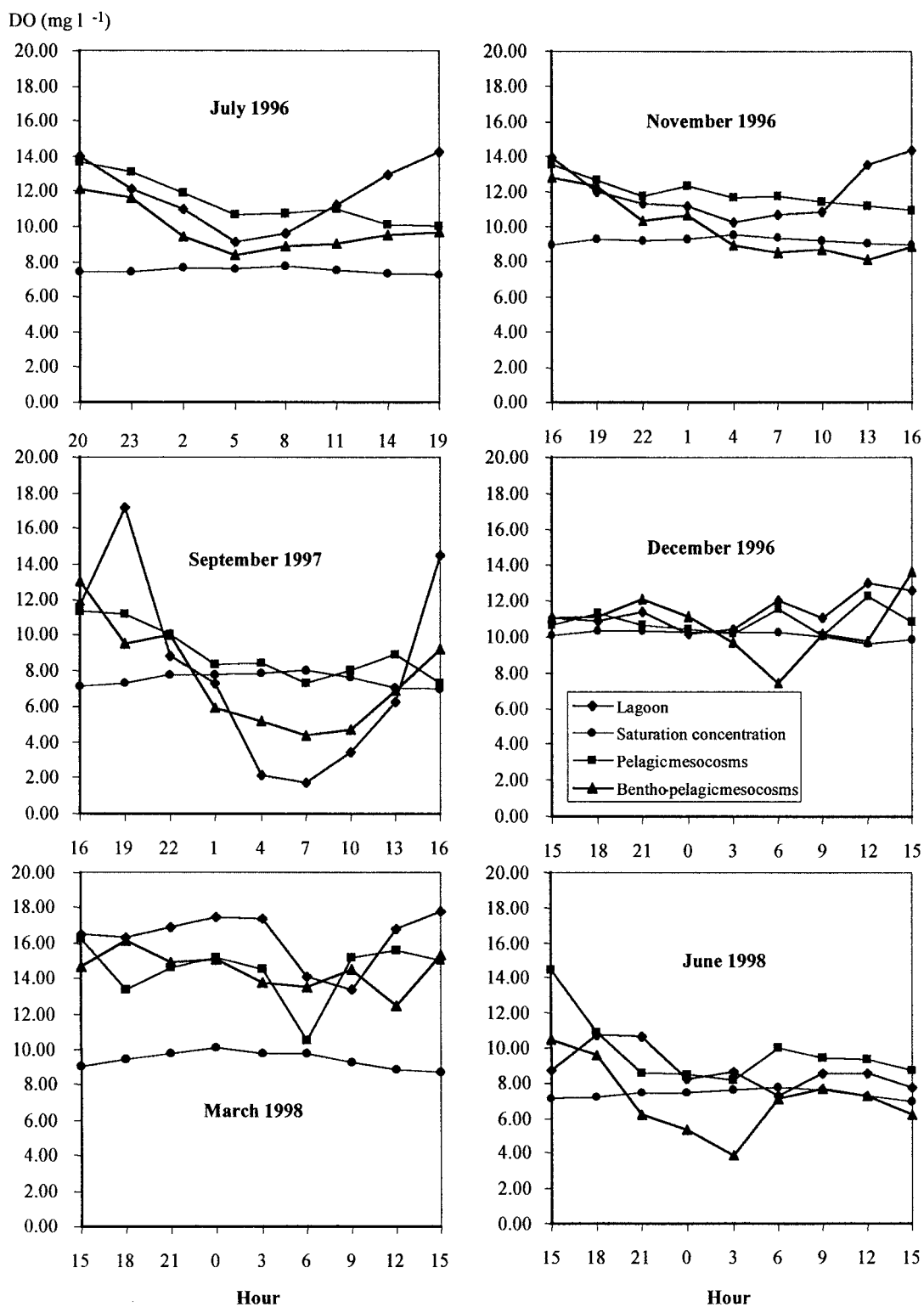


Figure 3. Dissolved oxygen (DO) concentrations (mean values) in the lagoon, in the pelagic and benthic-pelagic mesocosms and saturation concentration.

Table 4. Summary of metabolism measurements ($\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$) in the lagoon and in the mesocosms (mesocosms values are means of three replicates) calculated with Methods 1 and 2 (see text). D - Diffusion, GPP - Gross Primary Production, R - Respiration and NPP - Net Primary Production

Date		Lagoon		Pelagic mesocosms		Benthic-pelagic mesocosms	
		Method 1	Method 2	Method 1	Method 2	Method 1	Method 2
July 1996	D	-8.0	-2.8	-10.8	-2.9	-7.9	-1.6
	GPP	12.4	12.5	7.6	4.9	7.1	8.1
	R	4.0	9.3	5.8	7.5	3.8	10.2
	NPP	8.4	3.2	1.8	-2.6	3.3	-2.1
November 1996	D	-	-5.8	-	-5.5	-2.3	-1.1
	GPP	-	9.1	-	2.4	3.0	3.8
	R	-	6.9	-	2.4	9.3	10.4
	NPP	-	2.2	-	0.0	-6.6	-6.6
September 1997	D	-0.2	-0.1	-4.3	-0.9	0.7	1.5
	GPP	15.6	14.5	5.1	5.6	12.6	6.2
	R	14.3	13.3	3.2	10.0	15.1	12.3
	NPP	1.3	1.2	1.9	-4.4	-2.5	-6.1

tion across the air-water interface (Kemp & Boynton, 1980; Emerson et al., 1993). In Table 4, the results regarding the lagoon and the P-mesocosms of the November campaign calculated with Method 1, are not shown because overnight oxygen net production gave positive results. This is probably a consequence of underestimating respiration or overestimating diffusion, or both, and it is more likely to occur when the oxygen curve does not have a very clear dusk maximum and dawn minimum. Another problem with the data from Table 4 is the higher respiration rate, calculated with Method 1, in the P-mesocosms than that of the BP-mesocosms of the July 1996 campaign.

The gas transfer coefficients reported in Table 3 are well within the values obtained by other authors (e.g., Odum, 1956; Hornberger & Kelly, 1975; Kemp & Boynton, 1980; Reyes & Merino, 1991). Diffusion rates are generally negative (Table 4) as a result of the oversaturated D.O. concentrations commonly observed in the lagoon and in the mesocosms, the unique exception being the BP-mesocosms in September 1997, when night D.O. values were well below saturation (Figure 3).

The lowest oxygen values were measured in September 1997, when the water level was very low, ca. 60 cm, the water temperature high, 25.2 °C, and the bottom of the lagoon covered with macrophytes, mainly *Ruppia cirrhosa*. During summer months, the oxygen dynamics observed in the BP-mesocosms

was closer to the results obtained in the lagoon and quite different from the results observed in the P-mesocosms. These differences are less important in the other months, when the lagoon is generally deeper due to rainfall, and physical processes become more important as suggested by the absence of a typical oxygen curve.

The fact that oxygen levels were predominantly above saturation, suggests that the P/R ratio of the lagoon was greater than one. However, during the hot season, dissolved oxygen values during the night may approach zero leading to anoxia. Generally, the initial D.O. values in the BP-mesocosms were higher than the final ones whereas in the lagoon the initial and final values were quite similar. One of the reasons for this difference may be the lower light intensities in the mesocosms than in the lagoon (about 60–80% of the lagoon values) due to light absorption by the mesocosm walls. Besides that, the isolation of the water in the mesocosms might lead to nutrient depletion and limitation of phytoplankton photosynthesis. Nutrient limitation of benthic photosynthesis is less likely to occur since rooted aquatic macrophytes usually take up nutrients both from the sediments and from the water column (Short & McRoy, 1984; Thursby & Harlin, 1984; Harlin, 1995), transferring them through different parts of the plant (Brix & Lyngby, 1985). The predominantly negative net oxygen productions are a

result of the negative differences between the final and the initial D.O. values in the mesocosms.

The assumptions of the applied three way ANOVA were checked prior to analysis. There were no significant correlations between the means and the variances. However, there was a significant heterogeneity of variances among samples ($p < 10^{-5}$ with the Cochran test). This heterogeneity could not be removed by any of the transformations indicated for percentage data (Underwood, 1981, 1997) and it was probably a result of the different relative behaviour of the replicate mesocosms in different campaigns. This is to be expected in a highly heterogeneous environment, where for example the macrophyte biomasses enclosed in the three replicate BP-mesocosms in different campaigns can differ significantly, leading to different variances. Therefore, any results leading to the rejection of the null hypothesis must be taken with care in spite of the robustness of the ANOVA to the heterogeneity of variances (Underwood, 1997). The ANOVA results revealed significant differences for all the independent effects – campaign, treatment (Pelagic vs. Benthic-pelagic) and time of sampling – for a probability level ($p < 10^{-10}$) several orders of magnitude lower than the one leading to the rejection of variance homogeneity, confirming the reliability of the rejection of the null hypothesis (Underwood, 1981). These results were confirmed by planned comparisons contrasting treatments and campaigns, *post-hoc* comparisons with the Newman–Keuls test and the non parametric Kruskal–Wallis ANOVA by ranks. The mean D.O. saturation value of the P-mesocosms, 129%, was significantly higher than that of the BP-mesocosms, 110.0%. Analysis of Figure 3 supports the results of the statistical tests, with most of the D.O. concentration values of the P-mesocosms, being higher than those of the BP-mesocosms. These differences could be partially attributed to sediment resuspension caused by the placing of the BP-mesocosms at the bottom of the lagoon. This phenomenon could induce high oxygen consumption leading to lower oxygen levels in the BP-mesocosms. However, analysis of Figure 3 does not reveal any systematic differences between the initial D.O. values in both treatments. Therefore, from the results obtained, it may be inferred that in the BP-mesocosms the higher respiration rates are compensated by their higher gross productions in relation to the P-mesocosms. This increase in the relative importance of community respiration led generally to lower net productions, lower saturation D.O. levels and lower diffusive fluxes from the water

to the atmosphere in the BP-mesocosms then in the P-mesocosms. The interaction effect – campaign *versus* treatment – was also significant but at a higher probability level ($p < 2 \times 10^{-4}$). From this it can be inferred that the differences between the treatments changed significantly with the campaign factor. This result may be explained by the changing relative importance of planktonic and benthic metabolism.

Analysis of the data presented in Table 4 suggests that the pelagic contribution to community respiration may be between ca. 20 and 80% of total respiration. These results are in good agreement with similar estimates for other *Ruppia* dominated communities (Murray & Wetzel, 1987). The high contribution of plankton to total respiration may result from high dissolved organic matter (DOM) levels and bacterial activity. In the literature there seems to be no information regarding the exudation rates of the dominant macrophyte species found in St. André lagoon. However, considering the high exudation rates reported for macroalgae, that may be above 15% of gross production (Khailov & Burlakova, 1969), it seems plausible to hypothesise that macrophytes may also contribute with large amounts of DOM. In this case, the macrophyte release of DOM could serve as a major pathway to link benthic primary production to pelagic food webs and secondary production, similarly to what is described by Khailov & Burlakova (1969) for coastal ecosystems.

The lagoon metabolism is predominantly autotrophic according to the results of Table 4, which is in agreement with the generally observed oxygen oversaturation. However, it must be remembered that advection was not considered in the lagoon calculations and this may influence the results, specially on windy days, when the water may be advected from more/less productive sites of the lagoon influencing the dissolved oxygen dynamics at the study site. Comparison of the two summer campaigns (July 1996 and September 1997) shows two different situations of oxygen dynamics. In the July 1996 campaign, oxygen levels were always above saturation, whereas in the September 1997 campaign undersaturated overnight values were observed in all treatments (Figure 3). The shallower depth in the latter campaign may justify by itself greater differences between day (when P/R > 1) and night (when P/R < 1) oxygen values. This is because the initial oxygen concentrations were similar in both campaigns. Therefore, there was a smaller quantity of oxygen per unit of area in the latter campaign. The results of Table 4 (Method 2) indicate higher rates

of benthic and pelagic respiration on an areal basis in the September 1997 experiment.

The results of the mesocosm experiments may be useful to understand the relative importance of the pelagic and benthic contributions to community metabolism. Method 2 gave more reliable results than Method 1, with the former giving net oxygen production during the night (see above), although the assumption of a constant gas transfer coefficient and respiration rate is probably not very adequate. In fact, the high gross productions calculated for the pelagic mesocosms with Method 2 (Table 4) are probably a result of overestimating the diffusion rates, specially during the September 1997 experiment (see below).

Microcosm experiments

The results of the microcosm experiments and phytoplankton productivity estimates are summarised in Table 5. During the first two campaigns it was not possible to estimate pelagic primary production, because the difference between the final and the initial oxygen values both in the dark and in the transparent bottles was always negative. This and the negative pelagic net productivities of Table 5, clearly suggest that pelagic metabolism was mainly heterotrophic.

Assuming a photosynthetic quotient (P.Q.)¹ of 1.00, the values presented in Table 5 correspond to a range of 37 to 337 mg C m⁻² d⁻¹. The upper limit of this range is well within the phytoplankton productivity values reported for fertile inland waters (Likens, 1975) and within the range of values measured in e.g., the Lagoon of Venice (Marcomini et al., 1995). The comparison of the P-mesocosm gross productivity of September 1997, shown in Table 4 (Method 2), with the value presented in Table 5, calculated from short-term incubations, shows an order of magnitude difference between both results. If it is assumed that net production is around 40% of gross production (Likens, 1975), the 0.2 g O₂ m⁻² d⁻¹ of Table 5 would correspond to a gross production of 0.5 g O₂ m⁻² d⁻¹, whereas the value from Table 4 (Method 2) is 5.6 g O₂ m⁻² d⁻¹. Considering that chlorophyll concentrations in the St. André lagoon may reach values of over 150 mg Chl *a* m⁻³ (Bernardo, 1990), the latter gross production value is theoretically possible. However, it was very unlikely to occur in the September 1997 campaign when chlorophyll concentration was 6 mg m⁻³ (Table 2).

¹The molar ratio between oxygen production and carbon dioxide fixation by photosynthesis (Vollenweider, 1974).

These higher metabolic estimates based on open-water techniques seem to be a common result (Kemp & Boynton, 1980). Another possible explanation may be taken from Oviatt et al. (1986) who estimated P.Q. values as high as 5.00 from dawn-dusk dissolved oxygen and inorganic carbon measurements in mesocosms. According to these authors, higher or lower than 'normal' (i.e., close to 1.00) P.Q. values may result from e.g. denitrification, sulphate reduction/oxidation and calcium carbonate solution. A P.Q. value of 5 would result in a gross production of 2.5 g O₂ m⁻² d⁻¹. This is the same order of magnitude of the 5.6 g O₂ m⁻² d⁻¹ calculated from the mesocosms. The difference between these last two values could easily be explained by a chlorophyll concentration closer to the one measured in the mesocosms. It could be hypothesised that the value of 6 mg m⁻³ measured at the end of the experiment was lower than the average concentration during the experiment.

In the benthic chamber experiments, the differences between the initial and the final oxygen concentrations were generally negative even under full sun-light. The respiration rates measured in the dark chambers were generally of the order of a few 0–10 g day⁻¹ m⁻², i.e., of the same order of magnitude as the respiration rates obtained for the BP-mesocosms. However, the obtained values had a large error variance, reason why they were not considered in any calculations. In some occasions, the results obtained in the transparent chambers could give positive net oxygen productions in some replicates and negative in other replicates. The reason for the large error variance might be a patchy distribution of organic matter, autotrophic and heterotrophic activity within the sediments.

The estimated contribution of *R. cirrhosa* to the community metabolism during the field experiments is summarised in Table 6. From the results shown in Table 5 it is apparent that the contribution of *R. cirrhosa* to the oxygen budget is positive, except in the November 1996 campaign. The order of magnitude of its respiration rates is comparable to the water column values (Table 4, Method 2), but the production values are much higher than those of Table 4.

Considering the results presented so far it seems clear that both the plankton and the sediment are net consumers of oxygen and therefore predominantly heterotrophic. The positive net oxygen production of *R. cirrhosa*, seems to compensate for the mentioned

Table 5. Summary of pelagic net productivity and respiration integrated over one day

Date	Pelagic net productivity (g O ₂ m ⁻² d ⁻¹)	Pelagic total respiration (g O ₂ m ⁻² d ⁻¹)
July 1996	–	7.5
November 1996	–	2.4
September 1997	–9.8	10.0
December 1997	–1.6	1.7
March 1998	–2.4	3.3
June 1998	–1.1	1.2

Table 6. Summary of *Ruppia cirrhosa* net productivity and respiration estimates (see text). There are no estimates for the December 1997 and March 1998 campaigns, because there were no macrophytes at the study site

Date	<i>R. cirrhosa</i> net productivity (g O ₂ m ⁻² d ⁻¹)	<i>R. cirrhosa</i> respiration (g O ₂ m ⁻² d ⁻¹)
July 1996	4.2	3.2
November 1996	–1.8	14.1
September 1997	1.8	1.6
December 1997	–	–
March 1998	–	–
June 1998	2.1	1.1

heterotrophy and possibly has a determinant role in keeping lagoon metabolism autotrophic.

Model simulations

The results from the model simulations are summarised in Figures 4 and 5. Figure 4 corresponds to a simulation without macrophytes, whereas Figure 5 corresponds to simulations with a macrophyte biomass of 400 g DW m⁻² and two different canopy heights – 0.4 and 1 m. The results obtained with other biomass values are not shown since they would not add any further qualitative information.

In the absence of macrophytes (see Figure 4) the time scale for thermal stratification to develop is about half a day. However, during the night (24 hours after the beginning of the model run), due to night cooling, convective mixing and heat diffusion, stratification remains only at the bottom layer. Finally, after 48 hours, water column temperature becomes vertically homogeneous. Regarding oxygen saturation, the verti-

cal pattern is correlated to that of temperature since this simulation did not include any biogeochemical processes.

Figure 5 shows that the presence of macrophytes may produce a much stronger thermal stratification than that predicted in their absence, specially when the canopy height is 1 m. The observed temperature difference between the surface and the bottom layers was 0.7 °C, in the model run without macrophytes, after 12 hours of simulation. In the model runs with macrophytes, however, the difference was 6.0 °C, under a canopy height of 1 m, but only 1.5 °C under a canopy height of 0.4 m. In the simulations with macrophytes, the thermocline was situated higher during the day, and lower during the night due to convective mixing and heat diffusion. Regarding oxygen dynamics two different situations were found. Under a canopy height of 1 m (Figure 5a) bottom D.O. was always lower than in the top layers, whereas under a canopy height of 0.4 m (Figure 5b), bottom D.O. was higher than in the surface layers during the day, and lower during the night. The former result is a consequence of the shading effect of the higher fraction of the canopy over the lower one, reducing bottom photosynthesis. After a period of ca. 5 days, oxygen levels remained stable in all simulations, with night minima reaching zero in both simulations with macrophytes (not shown). These sharp oxygen gradients were also observed in other shallow water ecosystems (D'Avanzo & Kremer, 1994).

In Table 7, some historical oxygen, temperature and macrophyte biomass data obtained in St. André lagoon are presented. As can be seen, the temperature difference between surface and bottom may be as high as 4.7 °C over a vertical distance of 0.5 m with a macrophyte biomass of 332.1 g (DW) m⁻². This is in good agreement with model results, where

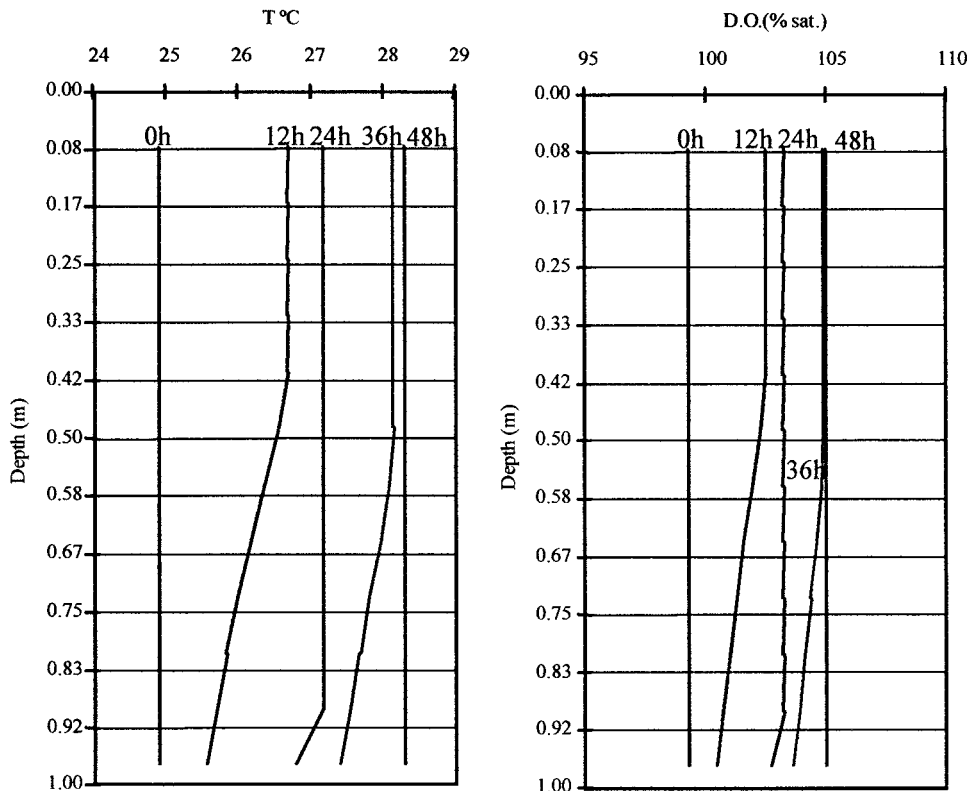


Figure 4. Model results: Temperature and dissolved oxygen distribution across the 12 model layers after 12, 24, 36 and 48 hours since the beginning of the simulation. These results were obtained without macrophytes.

temperature differences of 8.9°C were calculated over a vertical distance of 1 m, giving a similar temperature gradient. This corresponds roughly to a difference of 3 sigma-t units, similar to values reported by D'Avanzo & Kremer (1994) in Waquoit Bay. The data presented in Table 7 show the two types of situations predicted by the model, regarding oxygen saturation concentration: Bottom minimal (e.g., Station 3) and bottom maximal values (e.g., Station 5).

The results presented in Table 7, however, are not directly comparable to model predictions because there is no data available on canopy height. These results give some empirical evidence of a causal relationship between macrophyte biomass loads and thermocline or oxycline development. The model results demonstrate a strong dependence of water column stratification on macrophyte biomass and canopy height. The general agreement between the model results and the empirical data in Table 7 suggest the realism of the model.

Macrophyte harvest may therefore present an important contribution to the sustainable management of

St. André lagoon, in the sense that it may help to stabilise the ecosystem preventing further eutrophication, by reducing the accumulation of organic matter and nutrients, the probability of thermal stratification and overnight anoxia.

Considering that the macrophytes give an important autotrophic contribution to the ecosystem, their biomass should not be totally removed, otherwise the lagoon may become predominantly heterotrophic. The model results presented by Calado & Duarte (2000) suggest that a sustainable macrophyte harvest of up to 25% of available biomass, may be carried out in the summer of alternate years, without affecting macrophyte net production. According to these authors, such a biomass removal may decrease intraspecific competition for light, therefore increasing productivity. Harvest may be combined with agricultural activities, where macrophyte biomass may be used as fertiliser. In fact, this was the situation two decades ago, when farmers used to harvest macrophytes from the lagoon on a regular basis, and according to local people dystrophic crises did not seem to occur.

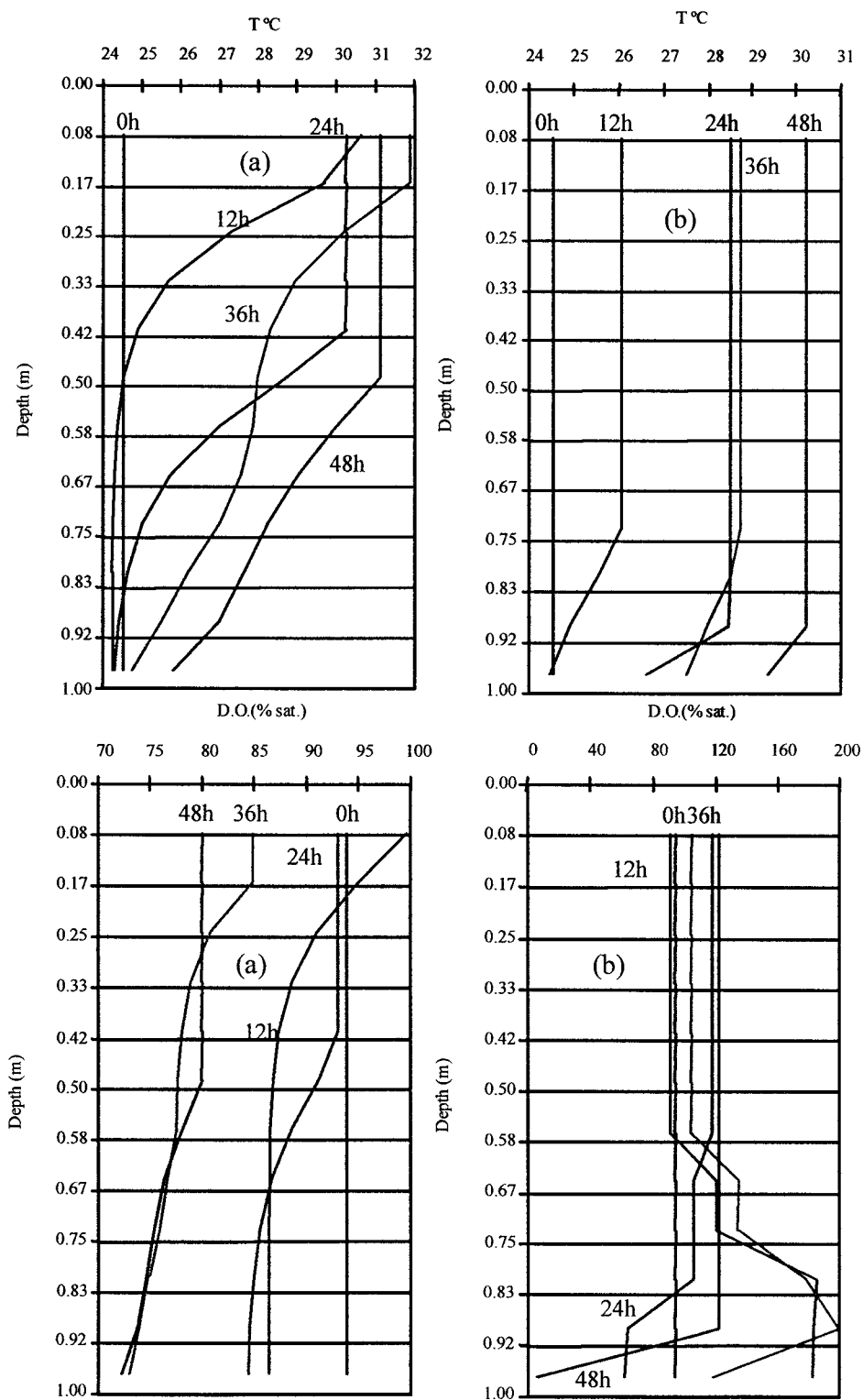


Figure 5. Model results: Temperature and dissolved oxygen distribution across the 12 model layers after 12, 24, 36 and 48 hours since the beginning of the simulation. These results were obtained with a *Ruppia cirrhosa* biomass density of 400 g DW m^{-2} and a canopy height of 1 m in (a) and 0.4 m in (b).

Table 7. Summer thermal stratification under different macrophyte stands (stations shown in Figure 1) (data from Cancela da Fonseca (1989) and Bernardo (1990))

Station	Date	Hour	Depth (m)	Dissolved oxygen (% sat)	Temp °C	Macrophyte biomass g(DW) m ⁻²
Sta 8	30/8/1984	–	0.1	263.7	27.0	104.4
		–	0.5	260.9	25.0	
Sta 3	26/9/1984	16 ^h 30 ^m	0.1	196.6	23.0	332.1
		16 ^h 30 ^m	0.6	49.1	18.3	
Sta 5	26/9/1984	–	0.1	138.4	22.6	223.9
		–	0.5	227.1	22.4	
Sta 4	24/8/1985	17 ^h 30 ^m	0.1	139.3	26.3	181.2
		17 ^h 30 ^m	1.1	203.3	25.6	
Sta 2	28/9/1985	18 ^h 00 ^m	0.1	146.3	25.4	217.4
		18 ^h 00 ^m	1.2	117.4	24.4	
Sta 4	28/9/1985	17 ^h 50 ^m	0.1	133.2	26.0	174.6
		17 ^h 50 ^m	1.0	89.0	23.5	

Conclusions

Regarding the issue of the relative contribution of the different autotrophic compartments to the lagoon metabolism, the results obtained indicate that in terms of net contribution and at the time scales examined, the macrophytes are the most important group. Under summer conditions, in the absence of wind, a thermocline may develop in about half a day. Both empirical and model results indicate that macrophytes may influence thermocline and oxycline development to a great deal. These plants contribute significantly to bottom cooling and depending on their biomass and canopy height they may contribute to an increase or a decrease in bottom oxygen during the day. High canopy heights lead to stronger thermoclines. Lower macrophyte heights lead to weaker thermoclines and positive D.O. gradients towards the bottom during the day, due to higher plant biomass in the bottom layers. The same high biomass explains the opposite trends observed during the night. From these results it follows that lower canopy heights induce greater oscillations in D.O. saturation concentration than higher canopy heights while everything else being equal. Bottom cooling induced by the shading effect of the macrophyte canopy has the disadvantage of creating stratification and therefore reducing vertical mixing. Macrophyte harvest may help to prevent thermal stratification and night anoxia contributing to stabilise the lagoon's ecosystem.

ification and night anoxia contributing to stabilise the lagoon's ecosystem.

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