

## ASSESSING THE POTENTIAL IMPACT OF CLAM REARING IN DYSTROPHIC LAGOONS: AN INTEGRATED OXYGEN BALANCE

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In this work we propose an integrated model to simulate the oxygen balance of a eutrophic lagoon exploited for mollusks farming. The balance is determined by macroalgal primary production and respiration rates plus the oxygen demand by clams and sediment. The aim is to evaluate the impact of intensive clam rearing on the vulnerability of the lagoon ecosystem to anoxic crises. The model is based on field data collected in the Sacca di Goro lagoon (Po River Delta) and has a stochastic formulation accounting for environmental unpredictability. The results show that clams have a considerable impact on the ecosystem, *i.e.* densities of 500 clams m<sup>-2</sup> can cause hypoxic events (DO < 2 mgO<sub>2</sub> L<sup>-1</sup>) in June and September, whilst densities over 1000 clams m<sup>-2</sup> (one half the maximum observed seeding densities) can determine a state of chronic hypoxia during the whole summer period, with minimum DO values lower than 1 mgO<sub>2</sub> L<sup>-1</sup>. The model provides a valuable tool for assessing the sustainability of different rearing policies.

*Keywords:* *Tapes philippinarum*; Lagoon ecosystems; Intensive mollusk rearing; Anoxic crises; Stochastic models; Sustainable densities

### INTRODUCTION

Shallow coastal lagoons are interfaces between land and sea, where nutrient-rich fresh-water mixes with marine water rich in oxygen (Bellan, 1987). They are generally extremely productive environments and are heavily exploited all over Europe for aquaculture activities, in particular for the rearing of filter-feeding mollusks, due to the high availability of suspended organic matter which enhances their growth rates. The most frequently reared species are oysters, mussels and clams. The first two are generally reared in nets or attached to ropes suspended in the water column, whilst clams are seeded in surficial sediments.

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In the latest years, an increasing number of coastal environments has been affected by extensive blooms of opportunistic macroalgae (green tides), due to huge nutrient loading from the washout of cultivated areas (Castel *et al.*, 1996; Jørgensen and Richardson, 1996; Valiela *et al.*, 1997). Massive macroalgal blooms are generally followed by a collapse phase, during which the accumulation of decomposing organic matter in the water column and in the sediment fuels intense microbial respiration (Jørgensen and Richardson, 1996). As a result, the respiratory oxygen demand largely exceeds the oxygen production (Carrada *et al.*, 1987; Sfriso *et al.*, 1992; Ceccherelli *et al.*, 1994), determining hypoxic or even anoxic conditions in the water column and massive mortality of the benthic fauna and causing severe economic losses in aquaculture plants.

Although the major cause of dystrophic crises has long been identified in macroalgal growth and collapse, the impact of high densities of bivalves, such as those observed in intensive rearing areas, on the oxygen balance may be quite important. High densities of filter-feeding bivalves produce indeed a net retention of particulate matter and a huge, localized input of labile organic matter due to the production of faeces and pseudo-faeces (Peterson and Heck, 1999). Mineralization processes in organic matter rich sediments often result in fast consumption of electron acceptors, thus favoring the accumulation of reduced sulphidic compounds (Kaspar *et al.*, 1988; Hall *et al.*, 1992; Holmer and Kristensen, 1992; Karakassis *et al.*, 1998; Sorokin *et al.*, 1999). Furthermore, aquaculture plants in lagoon environments are generally localized in confined stagnant areas which, due to the low water renewal, are more subject to oxygen deficiency.

The study of the interactions between mollusks and the environment has long been limited to mollusk physiology (Dame, 1972; Walne, 1972; Jørgensen, 1996) or the impact of mollusk grazing on phytoplankton availability (Cloern, 1982; Prins *et al.*, 1998; Chapelle *et al.*, 2000; Gangnery *et al.*, 2001). In the last ten years, however, the scientific community has paid attention to a more thorough assessment of the impact of intensive mollusk farming, with the aim of preserving the ecology of coastal lagoons and the economic value associated to mollusk farming (Kaiser *et al.*, 1998). The principal mechanisms that regulate the primary producers succession, trigger macroalgal blooms and build-up reducing conditions in both the sediment and the water column have been clarified. The impact of mollusks farming on water and sediment quality has been studied in terms of animal respiration, organic matter production and induced nutrient release from surficial sediments (Baudinet *et al.*, 1990; Hatcher *et al.*, 1994; Gouilletquer *et al.*, 1999). All these recent works have evidenced that high clam densities can affect oxygen and nutrient dynamics in the lagoon and at the same time stimulate macroalgal growth (Bartoli *et al.*, 2001).

In this paper we propose a comprehensive model describing the oxygen balance in a eutrophic coastal lagoon, the Sacca di Goro. The lagoon's production of the Manila clam *Tapes philippinarum* is one of the largest in Europe. This site has experienced severe dystrophic events following the collapse of macroalgal mats, resulting in extensive death of mollusks and considerable losses for the local economy.

The model includes production rates of micro- and macroalgae, respiration rates of mollusks, macroalgae and sediments; it also considers some of the physical processes that contribute to water column oxygenation. Macroalgae production, mollusks respiration rates and sediment respiration activity have been determined experimentally and linked to seasonal fluctuations of the water temperature. The overall balance produced by the model allows us to predict the effect of different aquaculture practices. In fact, by simulating the model for different clam densities, we can estimate the resulting oxygen concentration in the water column. As the model is stochastic we calculate not only point estimates, but also the probability distribution of the DO concentration over the year, providing estimates of the risk of anoxia associated with different rearing strategies.

## STUDY AREA

The Sacca di Goro (Fig. 1) is a shallow lagoon of the Po River Delta with a mean depth of 1.5 m and an overall area of 26 km<sup>2</sup>. It is characterized by strong anthropogenic eutrophication, due to high nutrient inflow from Burana-Volano and Po watersheds, and, during the summer period, is prone to extensive blooms of macroalgae (mainly *Ulva rigida*), whose biomass can reach 10 kg m<sup>-2</sup> (Viaroli *et al.*, 2001). Intensive rearing of Manila clams (*Tapes philippinarum*) and mussels (*Mytilus galloprovincialis*) is the basis of local economy since the middle of the 1980's, when the alien species *T. philippinarum* was introduced into the lagoon. At present, about one-third of the lagoon surface is farmed, with annual productions of about 10,000 tons and clam densities exceeding, in some areas, 2000 individuals m<sup>-2</sup>. High clam densities, together with sediment resuspension caused by substrate sieving for clam harvesting, have a strong impact on the oxygen and nutrient cycles. A decline in productivity has become apparent in recent years, due to sudden hypoxic and dystrophic events accompanied by diffusion of sulfides from the sediments to the water column, determining high mortality rates of the benthic fauna. Dystrophic events have generally been ascribed to the decomposition of macroalgal beds, but mortalities under hypoxic conditions have been reported also in the absence of macroalgae (Turolla, pers. comm.). In the summer months respiration rates of up to 20 mmol O<sub>2</sub> m<sup>-2</sup> hr<sup>-1</sup> and respiratory quotients (CO<sub>2</sub> flux/O<sub>2</sub> flux) far beyond unity have been measured in the rearing areas (Bartoli *et al.*, 2001). These conditions are

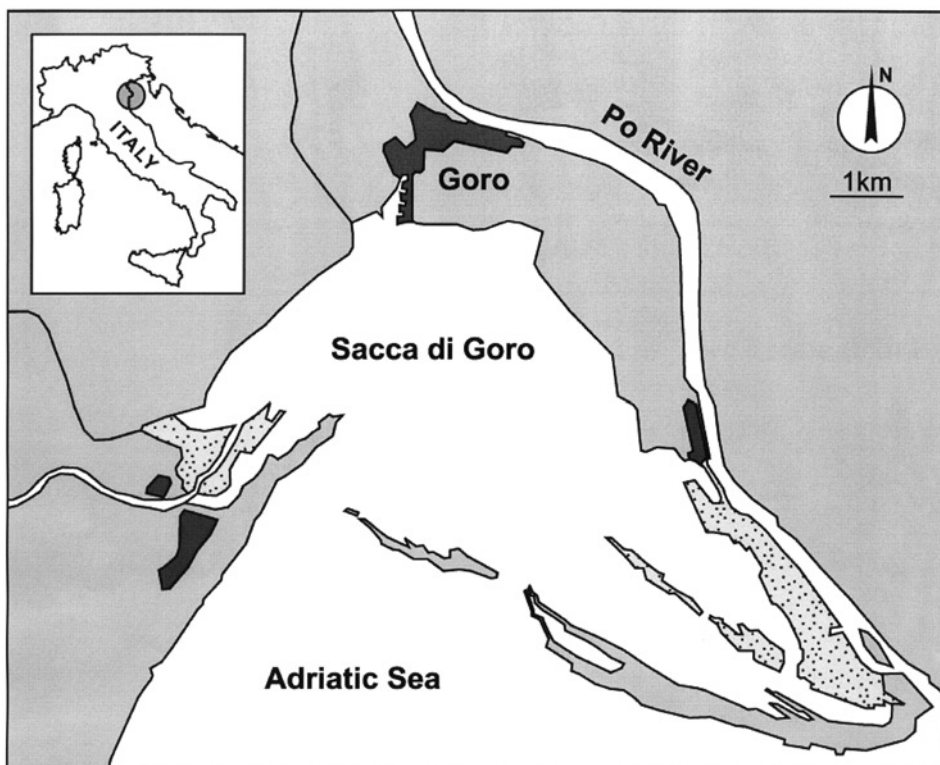


FIGURE 1 The Sacca di Goro lagoon (44°47'–44°50' N, 12°15'–12°20' E).

typical of reducing sediments with a scarce capability of oxidizing the products of anaerobic metabolism.

## AVAILABLE DATA

Sampling was performed in the eastern corner of the Sacca di Goro, where macroalgae beds generally develop, at about 40-day intervals from January 1997 to March 1998. Two different incubation systems were used for flux measurements on bare and on macroalgae-covered sediments (Dalsgaard *et al.*, 2000). Oxygen fluxes on bare sediments were measured in intact sediment cores ( $\varnothing$  8 cm, height 40 cm); stirring of the water column was ensured by a Teflon coated stirring bar rotating at 60 rpm and driven by an external magnet; the bar was placed at about 5 cm above the water–sediment interface. The cores were provided with a floating lid fitted with a valve for water withdrawal.

Oxygen fluxes on sediments covered by *U. rigida* were measured in Plexiglas chambers containing sediment, macroalgal mat and water. The base of the chamber was  $20 \times 20$  cm and the working height 40 cm. Stirring was created by drawing water out through a water dispersal unit placed at one side of the chamber and pumping it back inside at the other side through an identical unit; water was passing almost horizontally over the macroalgal mat simulating *in situ* hydrodynamic conditions. Water was pumped through Tygon tubing by a centrifugal pump at a rate of  $5 \text{ L min}^{-1}$ . During measurements, gas exchange between water and atmosphere on top of the chamber was prevented by a floating transparent lid. Undisturbed sediment with macroalgal mat (when present) was placed in the Plexiglas chambers. The core was obtained with a hand-held box corer which was pushed through the algal mat into the sediment cutting out a block of algal mat and sediment.

In both incubation systems oxygen fluxes were measured in light and darkness as variations of  $\text{O}_2$  concentration in the water with time; dissolved oxygen was determined according to the Winkler method.

Clam respiration rates have been measured in the lab via short incubations of single clam individuals in 100 ml glass beakers filled with filtered lagoon water. Clams were transferred to 100% saturated water and dissolved oxygen evolution was followed via an oxygen micro-sensor inserted in the lid of the beaker; the incubation time was generally less than 1 hour and water mixing was ensured by the clam filtration activity. Clam shells were cleaned before incubation in order to remove epibenthic organisms.

## MODEL FORMULATION

The model developed in this work describes the main processes that determine the oxygen balance of a eutrophic lagoon like Sacca di Goro. It is formulated in terms of four processes that describe: (1) gross oxygen production and respiration by macroalgae; (2) gross oxygen production by microphytoplankton and epibenthic microalgae, planktonic and benthic respiration, mineralization processes both in the water column and in the sediment (microalgae + sediment complex); (3) clam respiration, as an additional term to benthic respiration in intensive rearing areas; and (4) physical reaeration. Respiration and primary production rates are expressed as a function of water temperature. Seasonal temperature fluctuations are described by a stochastic model accounting for environmental unpredictability. The mathematical formulation of the considered processes has been kept as simple as possible to adequately fit the available experimental data.

## Macroalgae

Primary production in the Sacca di Goro lagoon is mainly due to photosynthesis by macroalgae, in particular *U. rigida* (Naldi, 1994). Oxygen production by microalgae is largely negligible for the most part of the year except during the summer months, when, after the macroalgal collapse, microalgal production can represent the main endogenous oxygen source (Naldi, 1994). As the macroalgal biomass is subject to huge fluctuations through the year, a mathematical description of the demography of *U. rigida* is necessary to describe the contribution of macroalgae to the oxygen balance. The problem of describing *U. rigida* demography in Adriatic lagoons has been tackled in several works (Bendoricchio *et al.*, 1994; Coffaro and Sfriso, 1997; Solidoro *et al.*, 1995; 1997a,b; Viaroli *et al.*, 1992; 2001). However, the key factors regulating *U. rigida* dynamics, and particularly the mechanisms triggering the sudden summer collapse, have not been fully understood yet. Here we use a simplified model, providing only a phenomenological, approximate description of its biomass dynamics. We describe both the growth phase and the summer collapse of the algae by exponential curves:

$$B_A(t) = \begin{cases} B_{A \max} \exp(\eta_2(t - t_2 + 365)) & 0 \leq t < t_1 \\ B_{A \min} \exp(\eta_1(t - t_1)) & t_1 \leq t < t_2 \\ B_{A \max} \exp(\eta_2(t - t_2)) & t_2 \leq t < 365 \end{cases} \quad (1)$$

where  $B_A$  ( $\text{gdw m}^{-2}$ ) is the dry biomass of *U. rigida* per unit area,  $B_{A \min}$  and  $B_{A \max}$  ( $\text{gdw m}^{-2}$ ) are the minimum and the maximum values of the biomass over the year,  $\eta_1 (>0)$  and  $\eta_2 (<0)$  are the growth rates ( $\text{day}^{-1}$ ) during the growth and the collapse phase, respectively, and  $t_1$  and  $t_2$  are the days at which  $B_A$  equals  $B_{A \max}$  and  $B_{A \min}$  respectively.  $t_1$  and  $t_2$  are set *a priori* to June 15th and August 15th.

To describe the dependency of *U. rigida* gross production and respiration upon water temperature, we use a Lassiter and Kearns (1967) formulation. Photosynthetic productivity  $p_A$  ( $\text{mgO}_2 \text{ hr}^{-1} \text{gdw}^{-1}$ ) is given by

$$p_A = p_{A \max} \left( \frac{T_{A \max} - T}{T_{A \max} - T_{A \text{opt}}} \right)^{\gamma_A (T_{A \max} - T_{A \text{opt}})} \exp(\gamma_A (T - T_{A \text{opt}})), \quad (2)$$

where  $p_{A \max}$  ( $\text{mgO}_2 \text{ hr}^{-1} \text{gdw}^{-1}$ ) represents the maximum value of the hourly gross production per dry biomass unit,  $T_{A \text{opt}}$  ( $^{\circ}\text{C}$ ) is the optimal temperature for *U. rigida* photosynthetic production (*i.e.*, at which  $p_A$  attains its maximum),  $T_{A \max}$  ( $^{\circ}\text{C}$ ) is the temperature at which production vanishes, and  $\gamma_A$  ( $^{\circ}\text{C}^{-1}$ ) is a shape parameter.

Similarly, we express oxygen consumption  $r_A$  as

$$r_A = r_{A \max} \left( \frac{T_{A \max} - T}{T_{A \max} - T_{A \text{opt}}} \right)^{\beta_A (T_{A \max} - T_{A \text{opt}})} \exp(\beta_A (T - T_{A \text{opt}})), \quad (3)$$

where  $r_{A \max}$  ( $\text{mgO}_2 \text{ hr}^{-1} \text{gdw}^{-1}$ ) is the maximum respiration rate per dry biomass unit and  $\beta_A$  ( $^{\circ}\text{C}^{-1}$ ) is a shape parameter. The reference temperatures of the respiration curve  $T_{A \text{opt}}$  and  $T_{A \max}$  are assumed to be the same as in the gross production curve (Eq. (2)).

The daily net production by macroalgae ( $\text{mgO}_2 \text{ day}^{-1}$ ) can then be written as

$$\text{NP}_A(t) = [F(t)p_A - 24r_A]B_A A, \quad (4)$$

where  $F(t)$  is the photoperiod length ( $\text{hr day}^{-1}$ ),  $p_A$  and  $r_A$  are given by Eqs. (2) and (3) respectively, algal biomass  $B_A$  is given by Eq. (1), and  $A$  is the water column cross section area. Notice that a complete description of the photosynthetic activity of *U. rigida* – considering, *e.g.*, photoinhibition and self-shading effects – would require data on the vertical stratification of macroalgal beds and a detailed description of macroalgal demography. For this reason, we consider only the effect of seasonal fluctuations of the photoperiod on *U. rigida* contribution to the oxygen balance.

### Microalgae + Sediment

Primary production by microalgae is largely negligible for the most part of the year when compared with macroalgal production. During the summer months, however, after *U. rigida* density has collapsed, microalgal production can represent the main endogenous oxygen source (Naldi, 1994). As no data were available to build up a model of planktonic and benthic microalgae dynamics, we only provide a rudimentary model linking the average gross production of the whole microalgal compartment with water temperature. According to Chapelle *et al.* (2000), the relationship linking phytoplankton production and respiration with temperature can be modeled by means of an exponential function. Therefore, we write the gross production per unit area ( $\text{mgO}_2 \text{hr}^{-1} \text{m}^{-2}$ ) as

$$p_a = p_{a0} \exp(\delta_a T), \quad (5)$$

where  $p_{a0}$  ( $\text{mgO}_2 \text{hr}^{-1} \text{m}^{-2}$ ) is the hourly gross production per unit area at  $0^\circ\text{C}$  and  $\delta_a$  is expressed in  $^\circ\text{C}^{-1}$ .

The daily oxygen consumption caused by mineralization processes (both in the water column and at the sediment level) and the respiration of microalgae and benthic fauna has been aggregated due to the lack of precise data. The overall effect of these processes can also be represented by means of an exponential curve, describing the oxygen consumption per unit area ( $\text{mgO}_2 \text{hr}^{-1} \text{m}^{-2}$ ) as

$$r_a = r_{a0} \exp(\zeta_a T), \quad (6)$$

where  $r_{a0}$  ( $\text{mgO}_2 \text{hr}^{-1} \text{m}^{-2}$ ) is the hourly oxygen consumption per unit area at  $0^\circ\text{C}$  and  $\zeta_a$  is expressed in  $^\circ\text{C}^{-1}$ .

The net contribution of the whole microalgal and benthic compartment to the oxygen balance ( $\text{mgO}_2 \text{day}^{-1}$ ) can then be written as

$$\text{NP}_a(t) = [F(t)p_a - 24r_a]A, \quad (7)$$

where  $F(t)$  is the photoperiod length ( $\text{hr day}^{-1}$ ),  $p_a$  and  $r_a$  are given by Eqs. (5) and (6), respectively, and  $A$  is the water column cross section area.

### Clams

Solidoro *et al.* (2000) describe the respiration process of *T. philippinarum* with a Lassiter and Kearns (1967) model, assuming the oxygen consumption to be independent of DO concentration. However, it seems reasonable to consider that the oxygen uptake from the water column will become more difficult as the oxygen concentration decreases. Therefore, we assume that the amount of oxygen removed by a single clam per time unit is proportional

to the DO concentration in the water column. Furthermore, the increase of oxygen consumption as a function of the clam dry weight is also included through an allometric relationship. Hence, the variation of the oxygen mass per unit time in a water volume  $V$  (L) may be written as

$$\frac{VdC}{dt} = -r_v C w^\alpha, \quad (8)$$

where  $C$  represents the DO concentration ( $\text{mgO}_2 \text{L}^{-1}$ ),  $t$  is time (hr),  $w$  is the average dry weight of a clam (g),  $\alpha$  is an allometric coefficient (dimensionless), and  $r_v$  is the respiration rate. Although  $\alpha$  can vary through the life cycle of an organism and depends upon the environmental conditions, 0.7 is considered to be a standard value for several organisms, including mollusks (Bayne, 1976). Therefore,  $r_v$  is expressed in  $\text{L g}^{-0.7} \text{hr}^{-1}$ . Integrating Eq. (8) over a time interval of duration  $\Delta t$ , and solving for  $r_v$ , we can obtain

$$r_v = \frac{V}{w^\alpha \Delta t} \ln\left(\frac{C_0}{C_f}\right) \quad (9)$$

where  $C_0$  and  $C_f$  are the initial and final oxygen concentrations. By means of Eq. (9)  $r_v$  can be calculated from our experimental data. To model the dependence of  $r_v$  upon water temperature, we use the relationship proposed by Solidoro *et al.* (2000) for *T. philippinarum* in Northern Adriatic lagoons:

$$r_v = r_{v \max} \left( \frac{T_{v \max} - T}{T_{v \max} - T_{v \text{opt}}} \right)^{\beta_v (T_{v \max} - T_{v \text{opt}})} \exp(\beta_v (T - T_{v \text{opt}})), \quad (10)$$

where  $T$  is temperature ( $^\circ\text{C}$ ),  $r_{v \max}$  is the maximum value of the respiration rate at the temperature  $T_{v \text{opt}}$ ,  $T_{v \max}$  is the temperature at which respiration becomes zero and  $\beta_v$  ( $^\circ\text{C}^{-1}$ ) is a shape parameter. For a given clam weight  $w$  and a given clam density, the daily oxygen consumption by clam respiration can be written as

$$R_v(t) = 24 r_v C(t) w^\alpha N(t) A, \quad (11)$$

where  $R_v$  is measured in  $\text{mgO}_2 \text{day}^{-1}$ ,  $r_v$  is given by Eq. (10),  $C$  is the DO concentration ( $\text{mgO}_2 \text{L}^{-1}$ ),  $N(t)$  is the density of clams per unit area ( $\text{individuals m}^{-2}$ ),  $A$  is the cross section area of the water column ( $\text{m}^2$ ).

### Physical Reaeration

In the absence of detailed data describing the hydrodynamic regime and its influence on the reaeration process, the oxygen flux  $\rho$  ( $\text{mgO}_2 \text{day}^{-1}$ ) at the air–water interface can be described by the following simple equation:

$$\rho = k(C - C_{\text{sat}})V, \quad (12)$$

where  $k$  is the oxygen exchange coefficient (assumed to be equal to  $0.0458 \times 24 \text{day}^{-1}$ ; cfr. Pastres *et al.*, 2001),  $C$  is the DO concentration ( $\text{mgO}_2 \text{L}^{-1}$ ) in the water column,  $C_{\text{sat}}$  is the oxygen concentration at saturation ( $\text{mgO}_2 \text{L}^{-1}$ ) and  $V$  is the volume of the water column (L).

$C_{\text{sat}}$  is a function of both water temperature  $T$  and salinity  $S$  (which we consider here to be constant and equal to 30‰), and can be calculated as (APHA, 1989)

$$C_{\text{sat}} = 14.6244 - 0.367134T + 0.0044972T^2 - 0.0966S + 0.00205TS + 0.0002739S^2. \quad (13)$$

### Temperature

Seasonal temperature fluctuations, which regulate both respiration and production rates and represent one of the most important sources of unpredictability in the system, are described by a sinusoidal curve plus an autoregressive, stochastic term:

$$T(t) = \hat{T}(t) + \phi(T(t-1) - \hat{T}(t-1)) + \varepsilon(t), \quad (14)$$

where  $\hat{T}(t) = 9.76\sin((2\pi/365)(t - 114.74)) + 16.35$  (Melià *et al.*, 2000),  $\phi = 0.92$  and  $\varepsilon$  is a Gaussian random term with mean zero and standard deviation  $0.57^\circ\text{C}$  (Melià, 2001).

### Overall Oxygen Balance

The overall oxygen balance in the water column is given by the algebraic sum of the contributions of the different trophic compartments: production and respiration of macroalgae (Eq. (4)), production and respiration of the microalgae + sediment complex (Eq. (7)), clam respiration (Eq. (11)) and physical reaeration (Eq. (12)). All terms of the oxygen balance depend upon temperature, whose dynamics are stochastically described by Eq. (14). The time unit variation of the DO concentration ( $\text{mgO}_2 \text{L}^{-1} \text{day}^{-1}$ ) is then given by

$$\frac{dC}{dt} = \frac{1}{V}(\text{NP}_A + \text{NP}_a - R_v + \rho). \quad (15)$$

Notice that, for the sake of simplicity, clam density  $N(t)$  (Eq. (11)) is supposed here to be a constant. Equation (15) thus provides a tool to calculate, for any given day of the year and given initial conditions, the DO concentration associated to a given density of clams, as determined by the interaction of the main compartments of the lagoon ecosystem. Running model (15) an adequate number of times over an yearly horizon, we can obtain the mean annual path of the oxygen balance and the probability distribution of the estimated DO concentration in any given day of the year and for a given clam density.

### Model Calibration

The calibration of the model has been performed by minimizing the following cost functions:

$$J_k(\theta_{k1}, \dots, \theta_{kn}) = \sum_i [y_{k \text{ obs},i} - y_{k \text{ est},i}]^2, \quad (16)$$

where  $J_k$  is the cost function for the  $k$ th sub-model (clam respiration, production and respiration of macroalgae, production and respiration of the microalgae + sediment complex),  $\theta_{k1}, \dots, \theta_{kn}$  are the  $n$  parameters of the sub-model,  $y_{k \text{ obs},i}$  is the  $i$ th experimental datum referring to the  $k$ th sub-model and  $y_{k \text{ est},i}$  is the corresponding estimate obtained with the same

sub-model. The parameter values that minimize  $J_k$  have been calculated by using the Nelder–Mead Simplex algorithm (Nelder and Mead, 1965), which is suitable for problems that are roughly nonlinear or have a number of discontinuities.

In order to avoid overparameterization, the reference temperatures of the production and respiration curves for macroalgae and clams (Eqs. (2), (3), and (10)) are imposed *a priori*, by setting them to values taken from the literature. We assume  $T_{A\text{opt}} = 17.5^\circ\text{C}$  (the average value of the optimal range reported by Coffaro and Sfriso, 1997) and  $T_{A\text{max}} = 27^\circ\text{C}$  (Coffaro and Sfriso, 1997) for macroalgae,  $T_{v\text{opt}} = 20.5^\circ\text{C}$  (Bensch *et al.*, 1992) and  $T_{v\text{max}} = 35^\circ\text{C}$  (Pellizzato, 1990) for clams.

## RESULTS

The results of the calibration of each single sub-model (Eqs. (1)–(3), (5), (6) and (10)) are reported in Table I. The fitting of the clam respiration sub-model is shown in Figure 2, whereas Figure 3 displays the dynamics of *U. rigida* and the sub-models describing gross macroalgal production and respiration, respectively. Figure 4 shows the fit to data of the microphytobenthos gross production and the respiration sub-model for the microphytobenthos + sediment complex, respectively.

Figure 5 evidences the effect of the different ecological compartments on the DO balance, as simulated by Eq. (15). Figure 5(a) shows the DO dynamics in the absence of both clams and macroalgae. Sediment respiration keeps the DO concentration below saturation along the whole year, the most critical months being July and August, when

TABLE I Results of the Calibration of the Different Sub-models.

<i>Sub-model</i>	<i>Exp. Var.</i>	<i>Parameter</i>	<i>Units</i>	<i>Value</i>
Macroalgal demography	78%	$B_{A\text{min}}$	$\text{gdw m}^{-2}$	6.0
		$B_{A\text{max}}$	$\text{gdw m}^{-2}$	244.8
		$\eta_1$	$\text{day}^{-1}$	0.0122
		$\eta_2$	$\text{day}^{-1}$	-0.0608
		$t_1$	days	166 (June 15th)
		$t_2$	days	227 (August 15th)
Macroalgal gross production	52%	$p_{A\text{max}}$	$\text{mgO}_2 \text{ hr}^{-1} \text{gdw}^{-1}$	14.03
		$\gamma_A$	$^\circ\text{C}^{-1}$	0.636
		$T_{A\text{opt}}$	$^\circ\text{C}$	17.5
		$T_{A\text{max}}$	$^\circ\text{C}$	27.0
Macroalgal respiration	8%	$r_{A\text{max}}$	$\text{mgO}_2 \text{ hr}^{-1} \text{gdw}^{-1}$	2.10
		$\beta_A$	$^\circ\text{C}^{-1}$	0.303
Microalgal gross production	14%	$p_{a0}$	$\text{mgO}_2 \text{ hr}^{-1} \text{m}^{-2}$	16.46
		$\delta_a$	$^\circ\text{C}^{-1}$	0.062
Microalgal + sediment respiration	33%	$r_{a0}$	$\text{mgO}_2 \text{ hr}^{-1} \text{m}^{-2}$	38.86
		$\zeta_a$	$^\circ\text{C}^{-1}$	0.047
Clam respiration	86%	$r_{v\text{max}}$	$\text{g}^{-0.7} \text{hr}^{-1} \text{L}$	0.236
		$\beta_v$	$^\circ\text{C}^{-1}$	0.652
		$T_{v\text{opt}}$	$^\circ\text{C}$	20.5
		$T_{v\text{max}}$	$^\circ\text{C}$	35.0
		$\alpha$	–	0.7
Physical reaeration	–	$k$	$\text{day}^{-1}$	1.099
Temperature	–	$\phi$	–	0.92
		$\varepsilon$	$^\circ\text{C}$	$\sim N(0, 0.57)$

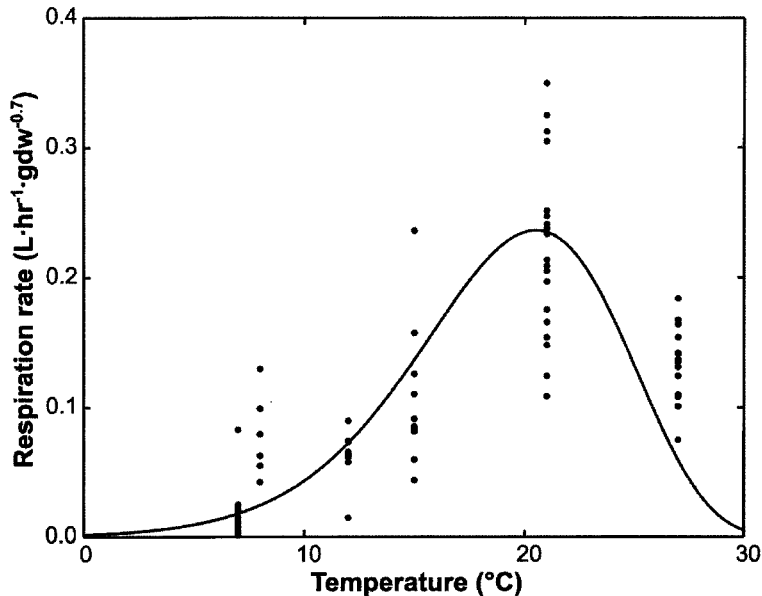


FIGURE 2 Respiration rate of *T. philippinarum* as a function of water temperature. Dots identify experimental data, while the solid line is the fitting provided by Eq. (10).

the DO concentration declines to  $4.7 \text{ mgO}_2 \text{ L}^{-1}$ . To evaluate the ecosystem health level, we define a hypoxic threshold as 20% of the DO concentration at saturation. As can be noted from Figure 5(a), hypoxic conditions are never reached in the absence of clams and macroalgae, not even during the most critical months (the minimum DO concentration is 58% of the saturation level).

The presence of macroalgae determines a spring peak of DO concentration (Fig. 5(b)), as the macroalgal bloom (see Fig. 3(a)) determines supersaturated conditions in the water column. During this phase, the model is likely to overestimate DO concentration in the absence of clams, since values above  $20\text{--}25 \text{ mgO}_2 \text{ L}^{-1}$  have never been recorded *in situ*. In fact, above saturation dissolved oxygen tends to form bubbles and escape from the water column to reach the atmosphere; quite often *U. rigida* mats float and drift due to the presence of oxygen entrapped within the thalli. In summer the DO concentration decreases, due to the combined effect of the reduction of photosynthetic activity and the increase of respiration rates at high temperatures, suddenly dropping to  $4.3 \text{ mgO}_2 \text{ L}^{-1}$  (52% of the saturation level) in June. The presence of *U. rigida* determines a huge oxygen increase, but only in spring; in summer, by contrast, the system is exposed to the risk of hypoxia, and the introduction of clams can have a strong impact on the ecosystem health, as exemplified in Figure 5(c). If we assume clams to have an average dry weight  $w$  of  $0.4 \text{ g}$ , corresponding to a fresh weight of about  $8 \text{ g}$  and a shell length of about  $30 \text{ mm}$  (medium-sized clams), a density of ‘only’  $1000 \text{ clams m}^{-2}$  determines a drop of the DO concentration to  $0.9 \text{ mgO}_2 \text{ L}^{-1}$  (11% of the saturation level) in September and June. Figure 6(a) shows the impact of different clam densities on the annual dynamics of the DO balance. Even relatively low densities –  $500$  individuals per square meter, approximately corresponding to  $4 \text{ kg m}^{-2}$  of fresh biomass – can result in an oxygen consumption which is sufficient to determine hypoxic conditions in summer (with minima of  $1.6 \text{ mgO}_2 \text{ L}^{-1}$  at the end of July and in September). Higher densities progressively increase the risk of hypoxia; Figure 6(b) shows the number of days in which the average DO

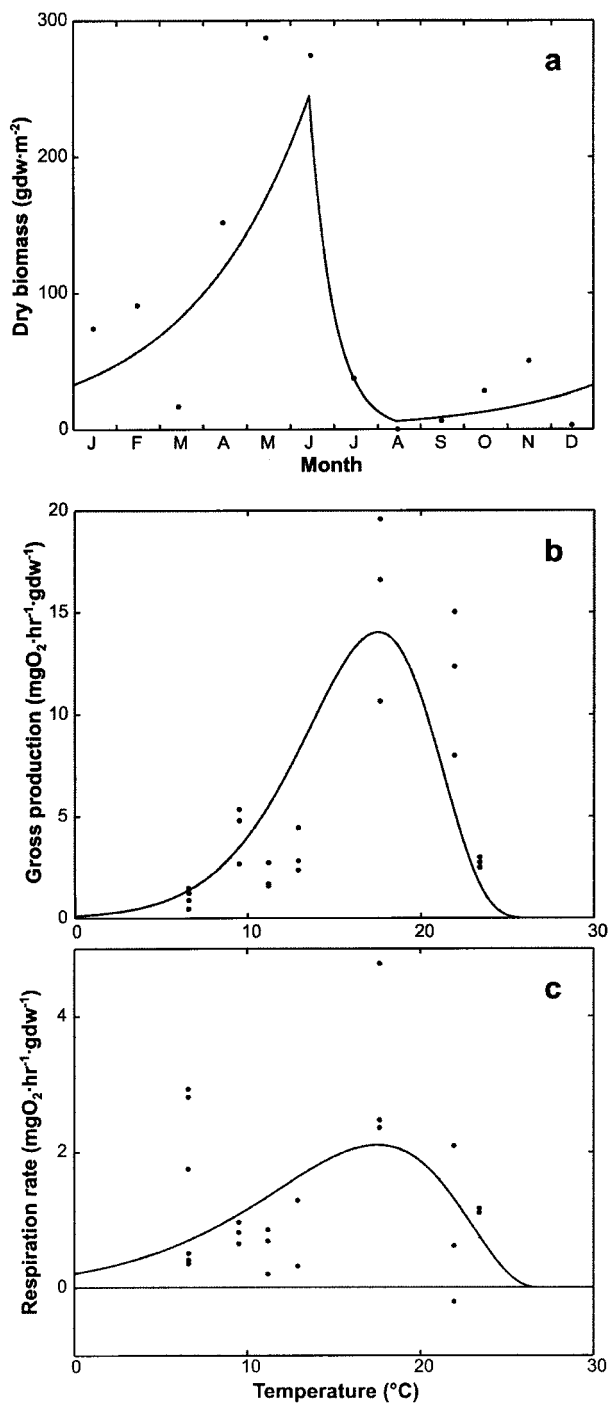


FIGURE 3 Demography of *U. rigida* and its contribution to the oxygen balance. Biomass dynamics over the year (a); gross oxygen production (b) and respiration rate (c) per dry weight unit as a function of water temperature. Dots identify experimental data, while solid lines are the fittings provided by Eqs. (1), (2) and (3), respectively.

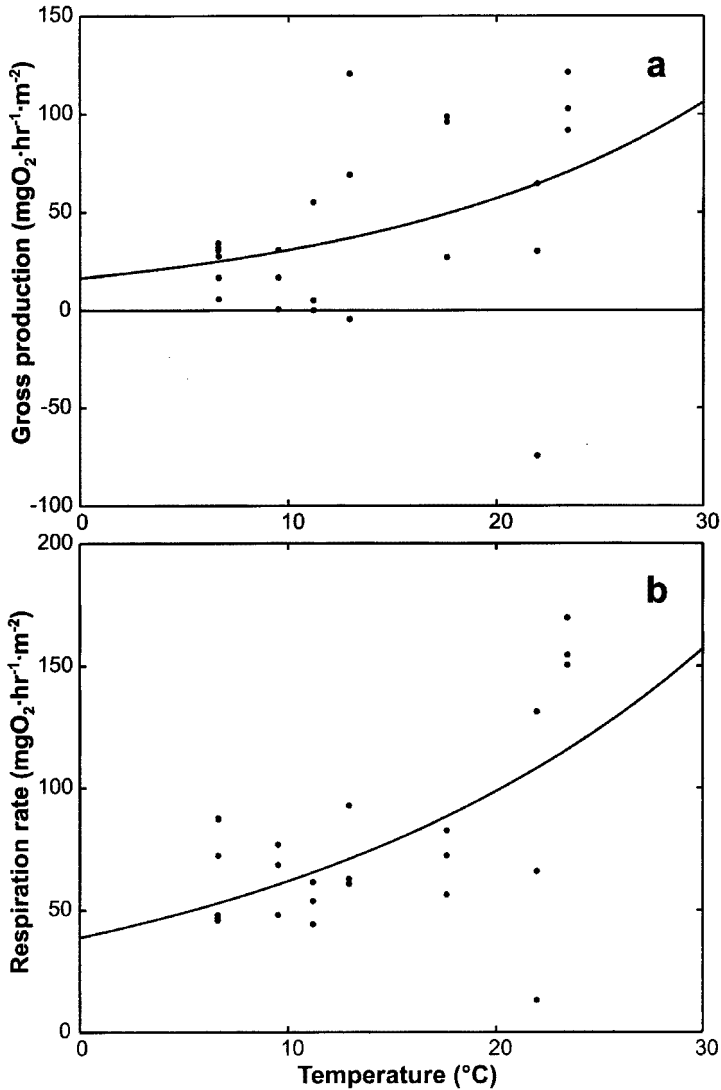


FIGURE 4 Production and respiration of the microalgae + sediment compartment. Gross oxygen production of microalgae (a) and respiration rate of microalgae and sediment (b) per unit area as a function of water temperature. Dots identify experimental data, while solid lines are the fittings provided by Eqs. (5) and (6), respectively.

concentration falls below the hypoxic threshold as a function of clam density. Densities beyond 500 clams  $m^{-2}$  determine one or two progressively longer hypoxic events in June and August–September, whilst at densities beyond 900 clams  $m^{-2}$  the water column can become hypoxic along the whole period from June to October.

The risk of excessive clam rearing for the ecosystem is summarized in Figure 7. It shows the probability of hypoxia along the year as a function of clam density. Even densities as low as 500 clams  $m^{-2}$  can cause a long period in September to be characterized by a high hypoxic risk (with a probability of hypoxia exceeding 50%); a density of 1000 clams  $m^{-2}$  extends the 50% risk to the whole period from June to November, whilst the whole month of September has a 100% probability of hypoxia.

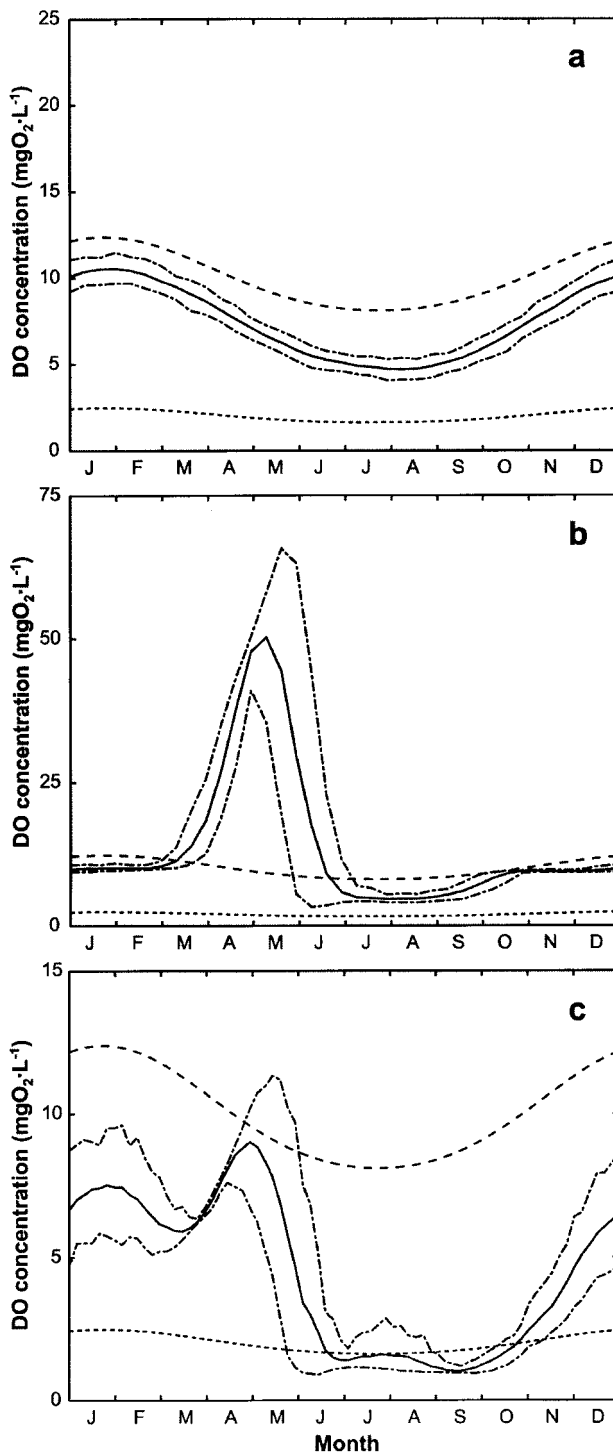


FIGURE 5 DO concentration in the water column along the year as provided by stochastic simulation (100 iterations) in different trophic conditions. Solid lines: average DO concentration; dash-dot lines: confidence intervals (5th and 95th percentile); dashed lines: DO concentration at saturation (long dashes) and hypoxic threshold (short dashes). (a) Without macroalgae and clams. (b) With macroalgae, without clams. (c) With macroalgae and clams (density:  $1000 \text{ individuals m}^{-2}$ ).

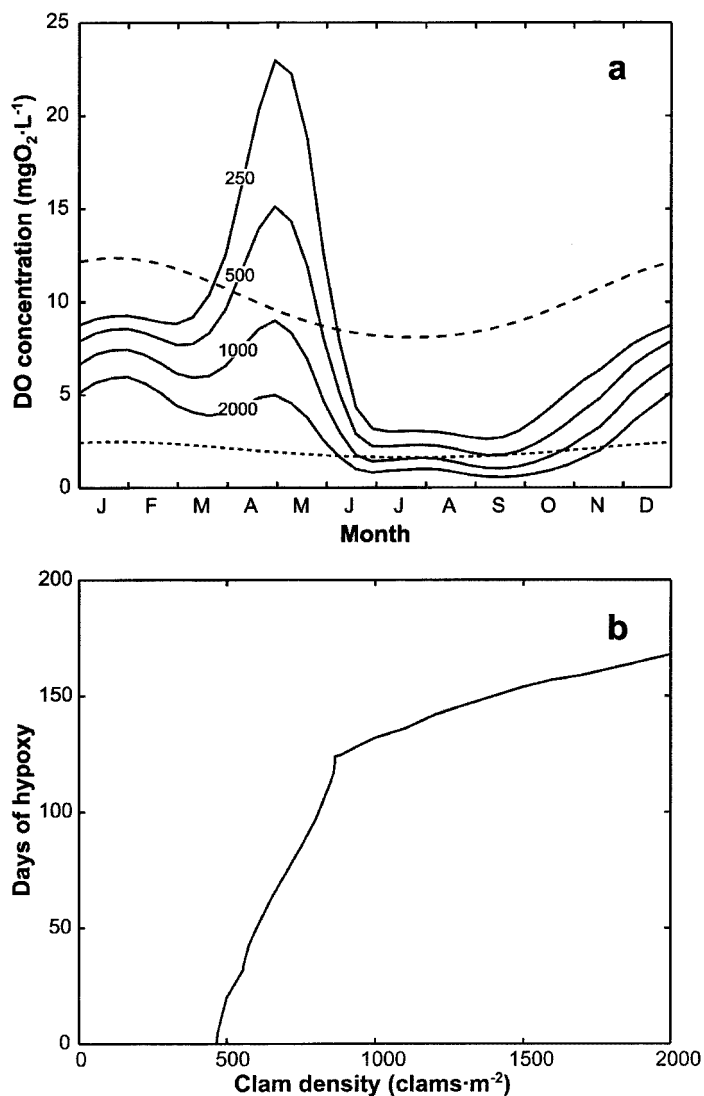


FIGURE 6 Effect of different clam densities on the DO balance. (a) DO concentration in the water column as determined by different clam densities. Solid lines: average DO concentration (as by stochastic simulation, 100 iterations); dashed lines: DO concentration at saturation (long dashes) and hypoxic threshold (short dashes). (b) Number of days in which the DO concentration falls below the hypoxic threshold as a function of clam density.

## DISCUSSION

The model proposed in this work accounts for the contribution of the main trophic compartments determining the seasonal oxygen balance in a eutrophic lagoon subject to intensive mollusk rearing: macro- and microalgae, sediment and bivalves. The sub-models have been calibrated on the basis of experimental data from both field and laboratory and provide a satisfactory description of the analyzed phenomena, although fitting performances vary considerably from one sub-model to another (Tab. I). In particular, the sub-models describing macroalgal respiration (Fig. 3(c)), microalgal production (Fig. 4(a)) and microalgal + sediment respiration (Fig. 4(b)) are characterized by low levels of

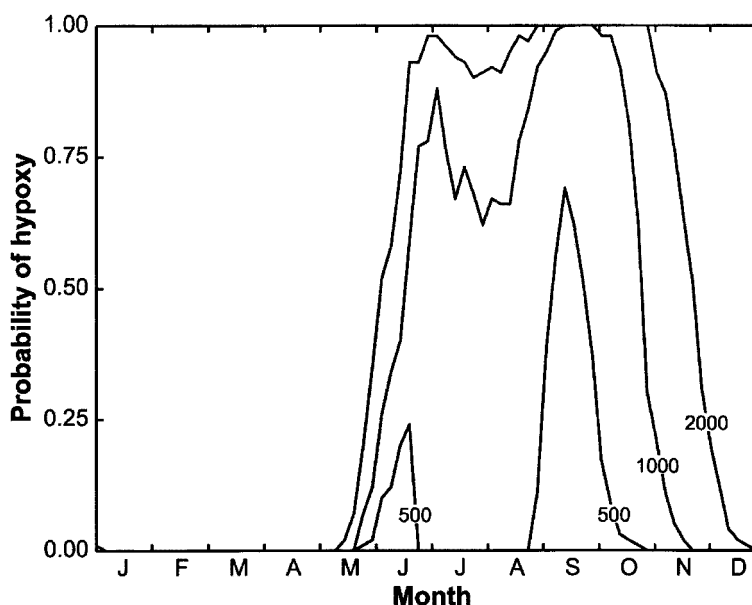


FIGURE 7 Hypoxic risk over the year as a function of clam density.

explained variance. However, the best-fitting curves seem to capture the main features of experimental data.

The integration of the respiration and production sub-models within a unique, flexible model provides a tool for simulating the oxygen balance of a lagoon under different scenarios, such as the presence or absence of macroalgae and clam seeding at different densities. The model provides valuable information to assess the sustainability of mollusk rearing in eutrophic lagoons. Although the effects of excessively low DO concentrations on clam survival are not known in detail, hypoxic or anoxic conditions can undoubtedly induce, especially if protracted in time, high mortalities. Furthermore, they will induce major alterations of the redox equilibria at the sediment level. The consequent release of sulfides from the sediment to the water column can also increase the mortality rates of the benthic fauna, with serious consequences for both the ecosystem health and the profit of the fishermen. Clam densities of up to 500 individuals  $m^{-2}$  (approximately corresponding to 4  $kg m^{-2}$  of medium-sized clams) are likely to keep the average DO concentration above the hypoxic threshold along the whole year, whilst higher densities can endanger the health status of the rearing areas, by progressively increasing the probability of hypoxia.

It is worth stressing that the model presented here does not account for additional negative terms in the oxygen balance. First, during the collapse of *U. rigida* beds, the decomposition of dead macroalgae generates an oxygen demand in addition to algal and benthic respiration, further worsening the hypoxic conditions within the water column. Biodeposition due to the filtering activity of bivalves also contributes negatively to the oxygen balance, as it enriches the sediment with extremely labile pellets, thus stimulating microbial respiration and enhancing sulfide production (Sorokin *et al.*, 1999). Moreover, Eq. (12) provides only a rudimentary description of the physical reaeration process, which is only valid for average weather conditions. Oxygen exchanges between air and the water column can in fact be enhanced by wind and tidal circulation. To evaluate how much our conclusions are affected by the assumption of a constant oxygen exchange

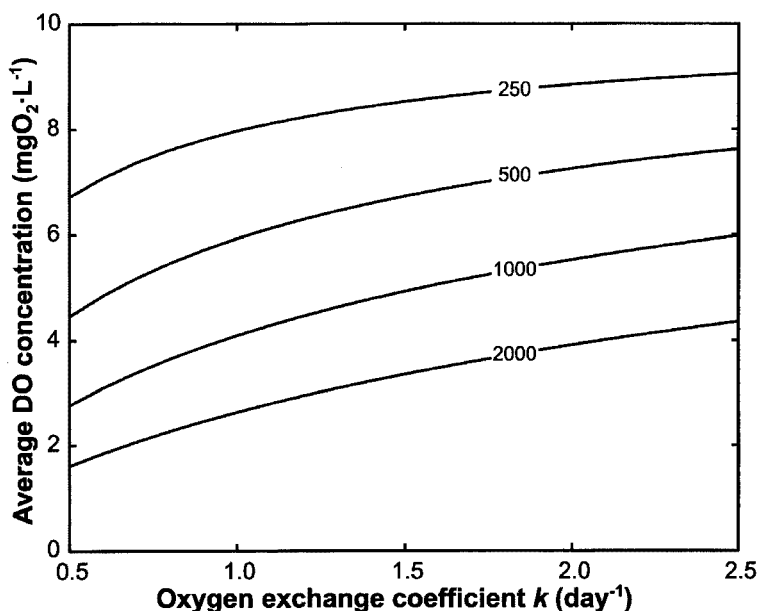


FIGURE 8 Average DO concentration along the year as a function of the oxygen exchange coefficient  $k$  (see Eq. (12)) at different clam densities.

coefficient  $k$ , we have run a sensitivity analysis. A range for  $k$  has been identified using the equation reported by Riley and Stefan (1988), which links the exchange coefficient to the wind speed  $w$  ( $\text{m s}^{-1}$ ) and the thickness  $d$  (m) of the first water layer as  $k = (0.641 + 0.00512w)/d$ . A realistic range for a shallow lagoon like the Sacca di Goro when wind speed is low ( $<10 \text{ m s}^{-1}$ ) is  $0.5 \leq k \leq 2.5 \text{ day}^{-1}$ . Figure 8 shows the average DO concentration along the year as a function of  $k$  within this range and the density of clams. Oxygen availability is much more affected by clam density than by the value of the exchange coefficient, although very small values of  $k$  (which are representative of stagnant water conditions) can determine an even worse oxygenation of the water column. For all these reasons, the results provided by our model should be considered as optimistic estimates of the maximum sustainable clam density.

Although the model can certainly be improved, its predictions are consistent with DO series recorded in the rearing areas (Viaroli *et al.*, 2001). Extensive hypoxic events, followed in most cases by dystrophic crises, have been recorded in June–July and September. Further effort will be necessary to completely understand the oxygen cycling in lagoon ecosystems where intense bivalve rearing takes place. A more detailed knowledge of the phenomenon would help decision makers in formulating management policies that are sustainable from both the ecological and the socio-economic viewpoints.

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