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Site Selection Criteria for Off-Shore Mussel Cultivation Use: A Modelling Approach

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Abstract

In the last decade, the Mediterranean mussel production in Italy has been steadily increasing, reaching in 2002 the 7% of the worldwide production. This trend is mainly due to the increase in landings from aquaculture, which in 2002 accounted for about 70% of the country annual production. Despite this growth, the development of off-shore mussel culture activities still encounters a number of constraints concerned with sustainability and environmental impacts. This work presents the development of a mathematical model which aims at describing the impact of farmed mussels on phytoplankton concentration. The model was applied to study the sustainability of mussel culture activities along the western Adriatic coast. Simulation results indicate that, during a critical period of the rearing cycle, phytoplankton concentration could be impacted by the grazing of farmed mussels. Model results were discussed on the basis of considerations on energy requirements to sustain mussel growth. The approach presented can give useful indications related to farms sizes and locations.

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1 Introduction

In the last decade, the Mediterranean mussel (*Mytilus galloprovincialis*) production in Italy has been steadily increasing from approximately 92×10^6 kg in 1994 to 138 x 10^6 in 2002, which represents about 7% of the worldwide production (FAO, fishstat+, *http://www.fao.org/fi/statist/statist.asp*). This trend is mainly due to the increase in cultured mussel landings, which, in 2002, accounted for about 70% of the annual production (Prioli, 2004). As far as the mussel culture production is concerned, the switch from fixed structure to long-line suspended cultures, which took place in the eighties, has certainly contributed to such a trend. In fact, the latter rearing technique allowed one to move mussel farms from sheltered bays and coastal lagoons to off-shore waters, thus leading to a marked increase in the number of culture sites, since areas far from significant sources of pollution became available for mussel culture activities.

As a result, along the western Adriatic coast (Italy), traditional mussel culture sites, such as those once located in the lagoon of Venice and the Sacca di Goro, have been progressively abandoned, while the number of off-shore suspended culture sites has rapidly increased. Despite this growth, the development of off-shore mussel culture activities still encounters a number of constraints concerned with sustainability and environmental impacts (Frankic, 2003). As far as the sustainability is concerned, the optimization of site selection for shellfish aquaculture is the main issue. In fact, a non-optimal location of culture sites may lead to a decrease in the biomass yields in the mid term, eventually calling for a redistribution of existing sites (Hydrores, 2004). Grant (1996) points out that many of the husbandry practices used in the mussel cultivation industry, including the selection of farm sites, have been developed on very empirical bases, i.e., ease of road and boat access, property availability, protection from wave exposure and adequate water depth. On the contrary, less attention has been given to the

actual physiology and growth of the bivalves (the product) and a potential impact on the surrounding environment.

One of the most contentious issues with respect to the development of mariculture throughout the world is the concept of "carrying capacity" (ICES, 2005). Debate on this concept is often fuelled by the lack of a clear and concise definition of the term, which can be given different meaning in different fields, such as physics, biology, economy, and social sciences. From the biological and economic point of view, the production carrying capacity is defined, according to Inglis et al. (2000), as "the attainment of optimum production of the target species and is achieved by modifying the stocking density and yield of the target species". According to Carver and Mallet (1990), Bacher et al. (1998), a series of papers published in special issues of Aquatic Ecology (vol. 31(4), 1998) and the Journal of Experimental Marine Biology and Ecology (vol. 219(1-2), 1998), shellfish carrying capacity depends mainly on natural resources. However, culture techniques and culture site distribution may also play a role (ICES, 2005). In fact, according to Prins et al. (1998), bivalve grazing may result in local food depletion, which may in turn, lead to a decrease in shellfish biomass yield. In raft cultures in Northwest Spain, the phytoplankton concentration at the downstream end of the raft found to be significantly lower than those at the upstream end (Navarro et al., 1991). Depletion of chlorophyll was observed in the Wadden Sea where farmed mussel density was very high (Cadée & Hegeman, 1974), and the findings from a site-specific study conducted in the Northern Adriatic Sea (Martincic, 1998), indicate a local depletion in the phytoplankton concentration in the water column nearby a mussel farm.

The aim of the present work is the development of a mathematical model which aims at describing the impact of farmed mussels on the phytoplankton concentration. The model was applied to the Northern Adriatic coast. In order to study the sustainability of mussel aquaculture at a regional scale, transport processes have been included and parameterized on the basis of site-specific data.

In order to achieve these aims, it was necessary to:

- 1) identify a model of phytoplankton dynamics;
- 2) to calibrate it using site-specific data;
- 3) to estimate the effect of mussel grazing on the phytoplankton dynamics.

Two different temporal scales were investigated:

- a) the annual dynamics of the phytoplankton in the absence of mussel grazing pressure;
- b) a short-term dynamics of the phytoplankton in the presence of mussel farms.

Step a) focuses on testing model ability to reproduce the observed yearly phytoplankton dynamics, while step b) intends to study whether the ration availability exerts a constraint on mussel growth in the period just before harvesting (March-April). Consideration regarding feeding constraints on mussel growth are presented, on the basis of a review of the literature regarding feeding physiology and energy demand of *M. galloprovincialis*.

2 Methods

Model selection

Smaal et al. (1998) point out that, at a regional scale, food availability is a principal factor that constraints the growth of bivalve suspension feeders, depending mainly on transport processes and primary production. Transport processes such as advection and diffusion/dispersion, and biological/chemical conversion processes, which affect primary production, are governed by a set of well-known advection-reaction-diffusion type of equations (see e.g. Orlob et al., 1983). In 3-D, the general equation reads as:

$$\frac{\partial C}{\partial t} + \nabla(vC) = \nabla(K\nabla C) + R(C,\beta), \qquad (1)$$

where:

C = the vector of state variables;

t = time;

v = the current velocity;

K = diffusivity tensor; and

 $R(C,\beta)$ = the vector of rates of change of concentrations due to reaction processes which depends on model parameters β , and on the state vector.

In our study, the two terms on the right of Eq. (1) were specified, taking into consideration the hydrodynamics and ecological features of the northern Adriatic coastal zone.

Transport processes in the Northern Adriatic application

Along the western Adriatic coast, the surface coastal boundary current is called the Western Adriatic Current, WAC. This current is mostly confined to the shallow Italian shelf (where the shelf break is at approximately 20 m) (Cushman-Roisin et al., 2001). This general current pattern is confirmed from the analysis of a set of field data, regarding the current velocity and direction, collected in a site nearby the farming area in which our model was applied, during a three years program by the Central Institute of Applied Marine Research, ICRAM, (*http://www.icram.org*). Data were registered each twenty minutes from November 2000 to August 2002 by means of a current meter moored 2 m above the bottom. As one can see from Fig. 1b, the principal direction of the current is, in this area, between 150 and 200 degrees direction to the North (which in this area is, with a reasonable approximation, parallel to the coastline).



Figure 1 a,b. Current velocity data collected by the Central Institute of Applied Marine Research, ICRAM, in site 1

Based on these findings, the description of transport processes given in Eq. (1) can be simplified for the specific northern Adriatic application. In fact, the advection is much stronger along the direction parallel to the coastline than along the orthogonal one. Furthermore, the vertical transport in this coastal area is much smaller than the horizontal one. Therefore, the transport term can be written as Eq. (2),

$$\frac{\partial C}{\partial t} + v \cdot \frac{\partial C}{\partial x} = k_x \cdot \frac{\partial^2 C}{\partial x^2} + R(C, \beta) , \qquad (2)$$

where x is the coordinate parallel to the coastline, v and k_x are, respectively, the velocity (considered to be constant along the x direction) and the dispersion coefficient in the longitudinal direction. According to Koryavov (1974), this equation can be further simplified if the mean velocity of the current along the principal flow direction is high relative to the longitudinal dispersion. Under this condition, the diffusion term is omitted, and Eq. (2) becomes,

$$\frac{\partial C}{\partial t} + v \cdot \frac{\partial C}{\partial x} = R(C, \beta) \tag{3}$$

Reaction term

The dynamics of phytoplankton in the Northern Adriatic has been the subject of several investigation (see Bernardi Aubry et al., 2004). Recently a simulation model has been proposed (Vichi et al., 1998a,b; Zavatarelli et al., 2000; Vichi et al., 2003a,b) which is based on the ERSEM complex biogeochemical model (Baretta et al., 1995), first applied to the North Sea. The results of this modelling approach are certainly interesting. However, it was decided to adopt a less complex model, since the investigation of biogeochemical cycles is beyond the scope of this study. The conceptual model, representing the relationships between state variables and forcing functions in the reaction term is presented in Fig. 2.



Figure 2. Relationships between state variables (square box) and forcing functions (oval boxes) in the reaction term

Four state variables were considered: diatom concentration, P_1 , phytoflagellate concentration, P_2 , concentration of zooplankton grazing on diatoms, Z_1 , and on phytoflagellates, Z_2 . Phytoplankton dynamics were described by considering two different functional groups. In fact, according to Zoppini et al. (1995), the typical seasonal evolution of phytoplankton biomasses in the Northern Adriatic Sea is characterized by the succession of two groups: diatoms usually blooms in winter time, while phytoflagellates biomass is higher in summer and autumn. This behavior can be explained by an adaptation of each group to different environmental conditions. According to Dippner (1998), we assumed that diatoms out compete the other groups at low temperature, whereas flagellates are dominant at low nutrient concentrations. In the present study nutrient concentrations are considered as forcing function. This approximation is justified by the fact that the nutrient concentration in the coastal zone is rather high, due to the riverine input. Rate equations are reported in Tab. 1. Phytoplankton dynamics include three processes: gross primary production, metabolic losses, due to dark respiration and photorespiration, and mortality, which is the sum of three terms: intrinsic mortality, zooplankton and mussel grazing. The effect of the variations in nutrient concentrations, water temperature, and irradiance level on phytoplankton metabolism is described by equations 1.5-1.16. The nutrient limitation functions are given by a Monod kinetics (Eq. 1.3-1.5). Dissolved inorganic nitrogen is not as a limiting nutrient, as phosphorus is widely recognized to be the principal limiting nutrient in the northern Adriatic ecosystem (Zoppini et al., 1995). For diatoms, silicate is considered as an additional limiting nutrient and a minimum formulation, based on "Liebig's law of the minimum", is used to limit the growth, see Eq. (1.5). The effect of temperature on phytoplankton maximum growth rate was described adopting the formulation by Lassiter and Kearns (1974), see Eq. (1.5), (1.6). This type of functional response, in which the growth rate increases with temperature up to an optimum temperature and then decreases, was considered more appropriate for this kind of environment than a linear or an exponential function (for a complete review on this subject see Bowie et al., 1985), as water temperature during summer may exceeds 26 °C. Growth limitation due to available irradiance follows the formulation by Steele (1962). The available solar radiation, I(z), was computed from the effective solar radiation at the sea surface, I_E , following Lambert-Beer law, see Eq. (1.12). Mass balances for zooplankton consider absorption and mortality processes, see Eq. (1.3-1.4). The description of zooplankton grazing process follows the modification of Parsons et al. (1967) of the formulation of Ivlev (1966), see Eq. (1.15 - 1.16): the grazing goes to saturation with the increasing amount of phytoplankton available, and ceases below a minimal threshold of phytoplankton concentration.

Effect of mussels grazing on phytoplankton in the model, see Eq. (1.1), was computed as the product of the individual clearance rate and mussel density in the farm, M (g dry weight m⁻³). Mussel density was introduced in the model as a forcing function, and its value was obtained from field data of mussel weight and husbandry practices. Clearance, or filtration, rate is the most commonly used measurement of filtering activity and is defined as "that volume of water completely cleaned by particles in a unit of time" (Bayne, 1976). For the short term simulation here presented, we considered a fixed value of clearance rate, see Tab. 3, according with the experimental findings by Denis et al. (1999), Sarà & Mazzola (2004) and Martincic (1998). A characteristic function, χ , was used to distinguish farmed areas, $\chi = 1$ inside a farm and $\chi = 0$ outside.

$$\begin{split} \frac{dP}{dt} &= \left[\mu_{1} \cdot \min(f_{3}, f_{6})\right] \cdot P_{1} - \mu_{1} \cdot \left[r_{g} + r_{p} \cdot \min(f_{3}, f_{6})\right] \cdot P_{1} - f_{8} \cdot Z_{1} - \chi \cdot CR \cdot M \cdot P_{1} - m_{p} \cdot P_{1} & (1.1) \\ \frac{dP_{1}}{dt} &= \left[\mu_{2} \cdot \min(f_{3}, f_{7})\right] \cdot P_{2} - \mu_{2} \cdot \left[r_{g} + r_{p} \cdot \min(f_{3}, f_{7})\right] \cdot P_{2} - f_{3} \cdot Z_{2} - \chi \cdot CR \cdot M \cdot P_{2} - m_{p} \cdot P_{2} & (1.2) \\ \frac{dZ_{1}}{dt} &= (1 - \gamma) \cdot f_{8} \cdot Z_{1} - m_{Z} \cdot Z_{1} & (1.3) \\ \frac{dZ_{2}}{dt} &= (1 - \gamma) \cdot f_{9} \cdot Z_{2} - m_{Z} \cdot Z_{2} & (1.4) \\ \mu_{1} &= \mu_{\max 1} \cdot f_{1}(T) & (1.5) \\ \mu_{2} &= \mu_{\max 2} \cdot f_{2}(T) & (1.6) \\ f_{1}(T) &= \left[\frac{T_{m1} - T}{T_{m1} - T_{01}}\right]^{b(T_{m1} - T_{01})} \cdot \exp[b \cdot (T - T_{01})] & (1.7) \\ f_{2}(T) &= \left[\frac{T_{m2} - T}{T_{m2} - T_{02}}\right]^{b(T_{m2} - T_{02})} \cdot \exp[b \cdot (T - T_{02})] & (1.8) \\ f_{3}(P) &= \frac{P}{(P + k_{p})} & (1.9) \\ f_{4}(Si) &= \frac{Si}{(Si + k_{Si})} & (1.10) \\ f_{5}(P, Si) &= \min[f_{1}(P), f_{4}(Si)] & (1.11) \\ l(z) &= I_{E} \cdot \exp[-K \cdot z) & (1.12) \\ f_{0}(I) &= \frac{I}{I_{01}} \exp\left[1 - \frac{I}{I_{02}}\right] & (1.14) \\ f_{3}(P_{1}) &= r_{Z} \cdot \left[1 - \exp(-A \cdot (P_{1} - P_{0}))\right] & (1.15) \\ f_{9}(P_{2}) &= r_{Z} \cdot \left[1 - \exp(-A \cdot (P_{2} - P_{0}))\right] & (1.16) \\ \end{split}$$

Table 1. Rate equations and functional expressions used in the reaction term

Field data

Field data regarding water-quality parameters were downloaded from the Italian Ministry Si.di.Mar. _ of Environment web-based dataset (http://www.minambiente.it). Fortnight measures of temperature, nutrients, and chlorophyll-a from 2001 to 2005 in different stations along the Adriatic coast can be downloaded. Sampling sites are represented as black dots in Fig. 3. Time series of water temperature, phosphate and silicate from May 2002 to June 2003 were used to force the model. Time series of chlorophyll-a, collected at the same time, was used to calibrate the model. Data were collected in a station off-shore Cesenatico near a mussel farm, see Fig.3. Hourly data regarding the solar radiation at the sea surface in this area are available at the website of the Oceanological branch of the National Research Council (http://www.ve.ismar.cnr.it/).



Figure 3. Mussel farming sites in the Northern Adriatic Sea, grey polygons, and location in which were collected the field data used in this study.

Field data regarding off-shore mussel farm location along the Adriatic coast used in this study were collected by the Central Institute for Marine Research, ICRAM, and MARE S.c.a r.l. Data were treated using the G.I.S. software ESRI Arc Gis. Contiguous plants were represented using a single polygon, resulting from the union of the areas interested occupied by single plants (Fig. 3). Husbandry information, regarding the characteristics of the rearing cycle and the structure of a typical farm, see (Tab. 2), were collected by MARE S.c.a r.l. (Prioli, 2003) in a long-line farm 1.5 miles off-shore Cattolica, named in this study as site 2 (Fig. 3). The farm is of the longline type, with mussels being grown on ropes supported in the water column by large floatation drums, as shown in (Fig. 4a,b). Average distance between two consecutive ropes is 0.7 m. The longlines are oriented parallel to the shoreline, approximately 2000 m long and arranged at 30 m intervals. Average height of one rope was of 2.5 m and these are suspended at 4-5 m above the bottom, to protect mussels from storm events.

A time series of length data following the same mussel cohort reared in the farm was available. Length of the shell was measured to the nearest millimiter each month during one rearing cycle, from the end of June to the beginning of May. Average mussels density, g of dry weight m^{-3} , was computed on the basis of the available data regarding rope density in the farm, see Tab. 2. Dry weight of the individual was recalculated from shell length data, using the allometric relationship,

(4)

Dry Weight = $a * length^b$

Different values for the parameters *a* and *b* in Eq. (4) were experimentally observed, depending on the season and type of rearing environment (Ceccherelli & Rossi, 1984; Fernandez-Reiriz et al., 1996; Denis et al., 1999; Barbariol & Razouls, 2000). In the present study, we used allometric model estimated in a Northern Adriatic lagoon during the April-May period (Ceccherelli & Rossi, 1984).

Length	2000 m
Width	1000 m
Average distance between ropes	0.7 m
Average distance between lines	30 m
Average rope height	2.5 m
Average distance from rope to bottom	4 -5 m

Table 2. Husbandry data regarding a typical farm





Figure 4 a,b. Longline type of mussel farm

3 Results

Model calibration

The model described in previous section was calibrated against a one year time series of phytoplankton concentration, setting to 0 the mussel grazing. Two parameters were calibrated, μ_{max1} and μ_{max2} . Values of remaining parameters were set according to literature. Model equations were integrated numerically, using a set of Matlab routines. Partial differential equations were integrated using the characteristic method (Arnold, 1983), while for the integration of ODE system a Runge-Kutta 4th order method was utilized. Model time-step was one hour. Fortnight measures of phytoplankton concentration, expressed in g C m⁻³, were recalculated from chlorophyll-a data, assuming a constant ratio of 50 (Jørgensen, 1983) between phytoplankton and chlorophyll-a concentration, Fig. 5a,b. The set of water quality data used to force the model is reported in Fig. 6a – 6e. Data were interpolated by means of a cubic spline function, using a Spline Matlab routine (de Boor, 1978). The calibration was performed by minimizing the function,

$$\Gamma = \sum_{i=1}^{n} (\hat{y}_i - y_i)^2,$$
(5)

where \hat{y} is the value of phytoplankton concentration predicted by the model, y is its observed value, and n is the total number of observations. As a first attempt to describe the advection process, a constant velocity v equal to 4 cm sec⁻¹ was used in the simulations, according to the experimental data presented in Fig. 1a. Initial condition for phytoplankton concentration was set in accordance with experimental data, while for zooplankton the initial concentration was tentatively set to 1/10 of phytoplankton, due to a lack of experimental informations. Simulation started the first of June and lasts one year.



Figure 5 a,b (read from left to right). Observed Chl-a data and recalculated phytoplankton concentrations (see the text for details).



Figure 6 a,b,c,d,e (read from left to right and from top to bottom). Environmental field data used as forcings in the model. Data sources are cited in the text

The results of the calibration of the model in the absence of mussel grazing pressure are reported in Fig. 7. Model parameters values are reported in Tab. 3. The trajectory of the predicted phytoplankton concentration is represented as the sum of the contributes from the two functional groups described in the model. The black squares represent phytoplankton concentration, recalculated from chlorophyll-a data, which were used in model calibration. As one can see, the big diatom bloom experimentally observed in the Adriatic Sea during winter-time (Zoppini et al, 1995), is reproduced by the model, as well as the summer and early spring small peaks, due respectively to phytoflagellates and diatom blooms.



Figure 7. Simulated phytoplankton dynamics outside the farm. Different colours represent the two functional groups described in the model. Field data are reported as black points

Parameter	Description	Value	Unit	Reference
μ_{maxl}	Maximum growth rate for diatoms	0.35	[day ⁻¹]	calibration
μ_{max2}	Maximum growth rate for phytoflagellates	0.45	[day ⁻¹]	calibration
K_p	Half saturation constant for phosphate	0.06	[mmol P m ⁻³]	(Dippner, 1998)
K_{Si}	Half saturation constant for silicate	0.5	[mmol Si m ⁻³]	(Dippner, 1998)
<i>I</i> ₀₁	Optimum light intensity for photosynthesis for diatoms	47	[W m ⁻²]	(Dippner, 1993)
I ₀₂	Optimum light intensity for photosynthesis for phytoflagellates	83	[W m ⁻²]	(Dippner, 1993)
K	Light extinction coefficient	0.1	$[m^{-1}]$	(Dippner, 1993)
r _B	Dark respiration	0.1		(Dippner, 1993)
r_P	Photorespiration	0.05		(Dippner, 1993)
r_Z	Maximum herbivore ingestion rate	1	[day ⁻¹]	(Dippner, 1993)
Λ	Ivlev constant for herbivore grazing	0.57	$[(g C m^{-3})^{-1}]$	(Dippner, 1993)
P_0	Threshold phytoplankton concentration	0.04	[g C m ⁻³]	(Dippner, 1993)
m_P	Mortality rate of phytoplankton	0.05	[day ⁻¹]	(Dippner, 1993)
mz	Mortality rate of zooplankton	0.05	[day ⁻¹]	(Dippner, 1993)
γ	Unassimilated fraction of herbivore grazing	0.3		(Dippner, 1993)
b	Lassiter-Kearns constant	0.1157		(Lassiter & Kearns, 1974)
T_{ml}	Temperature inhibition threshold for growth for diatoms	16	[°C]	(Solidoro et al., 1995; Si.di.Mar. data)
<i>T_{m2}</i>	Temperature inhibition threshold for growth for phytoflagellates	35	[°C]	(Solidoro et al., 1995; Si.di.Mar. data)
T _{ol}	Optimal temperature for growth for diatoms	12	[°C]	(Solidoro et al., 1995; Si.di.Mar. data)
<i>T</i> _{<i>o</i>2}	Optimal temperature for growth for phytoflagellates	31	[°C]	(Solidoro et al., 1995; Si.di.Mar. data)
CR	Clearance rate of mussels	0.0025	$[m^3 h^{-1}gDW^{-1}]$	Denis et al. (1999)
v	Current velocity module	4	$[\text{cm sec}^{-1}]$	ICRAM data
\mathcal{E}_p	Average energetic content for			Platt & Irwin
	рпуюртанкюн	4.7	[joule µg chl-a ⁻¹]	(17/3)

Table 3. Parameters used	l in	the	model
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Model application

The model was then applied to simulate the short term impact of mussel grazing on phytoplankton density. The simulation was run during March-April, according to field data presented in this work, which indicate that during this period phytoplankton availability is scarce while mussels, having reached commercial size, require a large amount of energy for fattening. Distribution of the plants along the northern Adriatic was conceptually represented as described by Fig. 8, where *n* consecutive plants are located along the direction *x*, which represents the horizontal direction of the principal current flow. Farm length, L, was set to 2000 m according to farm description reported in Tab. 2, and between consecutive farms a distance D=2000 m was assumed.



Figure 8. Conceptual representation of a succession of farms along the coast

Results from the simulation of weekly dynamics of phytoplankton concentration crossing a set of consecutive mussel farms are reported in Fig. 9. Black dotted lines represent phytoplankton concentration inside the farming area at five different times during the end of March-April period. Distance, in m, is referenced to the beginning of the first mussel farm. The results show a big mussel grazing pressure, causing a huge depletion of phytoplankton stock. Phytoplankton concentration increases after the farm in only two cases, April 11 and 21. In the remaining cases, phytoplankton does not recover after the plant due to physical forcing and/or high zooplankton grazing.



Figure 9. Phytoplankton concentration inside the farming area during the March-April period. Distance, in m, is referenced to the beginning of the first farm

4 Discussion

Model calibration

The model calibrated in this work reproduces the main features of the yearly dynamics of phytoplankton concentration recalculated from chlorophyll-a data. Furthermore, the succession of phytoplankton groups simulated by the model agree with the one observed experimentally by Zoppini et al. (1995). The order of magnitude of the calibrated μ_{max1} and μ_{max2} parameters, the maximum growth rates for each phytoplankton group, is in accordance with the experimental observations by Montagnes & Franklin (2001). Results from a long term simulation show that after the first year the model solution has a periodic behaviour. The stability analysis performed along one time period indicates that the found solution has a stable behaviour around its limit cycle. Details regarding the different methodologies applied in these analyses are

reported in appendix A. A local sensitivity analysis with respect to most uncertain parameters was performed, see appendix A. This analysis shows that optimal temperatures for phytoflagellates growth is the most sensitive parameter. This result can be related to the hypothesis that diatoms growth is mainly controlled by nutrients, while phytoflagellates growth strongly relates to temperature. Further step to improve sensitivity analysis would be to apply a Monte Carlo method to study the global sensitivity of the model with respect to the whole set of parameters. Furthermore, in order to assess its robustness, a validation of the model would be performed on a time series of field data collected in the same site during a different year.

Model application

The effect of bivalve grazing on phytoplankton stock in coastal embayments was recently modelled by Dowd (2005). The author assumed a steady state biomass, considering that mussel density and size is controlled by farmers through stocking and harvesting activities. In our study, mussel density is treated as a forcing function. As a first step in the development of an integrated model (see Smaal et al., 1998), including a bioenergetics deterministic model of the mussel, this approximation provides a more realistic description of the system with respect to the steady state assumption. The simulation which studies the impact of mussel grazing on phytoplankton stock, was applied during a critical period of the rearing cycle, according to the indications given in Incze et al. (1981). The result of our short-term simulation indicates that, even after a single plant, phytoplankton concentration is strongly reduced. This behaviour is in accordance with the observations made in the Spanish Rias by Navarro et al. (1991), but does not have any field corroboration along the Western Adriatic coast. It should be stressed here that the simulation was performed under a "worst case scenario", in which no diffusion, that can provide a phytoplankton source for the farming area, was included in the model. The introduction of a diffusion term in Eq. (3) would lead to an overall increase in the phytoplankton density along the farm and increasing its renewal rate between two consecutive farms.

Feeding constraints

Consideration regarding feeding constraints on mussel growth can be introduced in the model on the basis of literature information regarding mussel energy requirements. Navarro et al. (1991), Navarro et al. (1996), Labarta et al. (1997), Babarro et al. (2000), Gardner (2000) and Gardner (2002) pointed out that phytoplankton concentration quantifies only a component of the food available, while seston concentration, overestimates the true ration, including a fraction of non-utilisable organic detritus. Therefore, to obtain a correct estimate of the food available for mussel growth one should know both seston concentration and composition, in terms of phytoplankton and detrital organics. Since this data are not available for the Northern Adriatic area where the present model was applied, the estimation of the overall 'energy density' available in the water column requires some hypothesis on the amount of energy that can be provided by the digestion of non-phytoplanktonic particles. Three different available diets were hypotized here (Tab. 4). In diet A, the detritus component is extremely low, and the 80% of energy is provided by phytoplankton. Differently, energy provided by phytoplankton in diets B and C is respectively 50% and 20% of the energy of the overall ration.

The critical threshold for phytoplankton concentration, under which maintenance ration for mussel is not guarantee, was obtained on the basis of the concept of Scope for Growth, SfG (Bayne, 1976). This quantity is positive when surplus energy is available for growth and reproduction. When the SfG is negative an organism must utilize its own energy storage for self-maintenance and, therefore, looses weight. The Scope for Growth, therefore, provides an index of energy balance without distinction between somatic growth and gamete production. Growth is regarded as the net increase in energy content of the animal per unity time. In an ecological context, growth relationships of this sort are described as efficiencies. As pointed out by Paloheimo & Dickie (1965, 1966a,b) growth efficiency, GE, is an increasing function of ration until an inflection to negative slope is reached. In Mytilus edulis growth efficiency is negative at a very low ration level, but small increases in quantity of food ingested result in greatly improved GE. When the energy ingested equals the total energy metabolized GE is zero, and the quantity of food ingested is a measure of the maintenance ration, C_m , see Fig. 10. Further increase in ingested food leads to greater values of GE until an inflection to negative slopes occurs. The optimum ration, C_{opt} (see Fig. 10), at which growth is most efficient, is an increasing function of weight, reflecting the greater energy input required to offset the total metabolism of a larger animal. At low absolute ration levels smaller animals are more efficient in converting food into body tissue, although the ration is

large in relation to body weight. Thompson & Bayne (1974) observed an optimal gross growth efficiency between 170 and 250 cal d^{-1} for 1000 mg, and between 185 and 265 cal d^{-1} for 2000 mg *Mytilus edulis* individuals. The maintenance ration for mussels of 1000 mg was of 130 cal d^{-1} , while for the bigger mussels measured GE in a range of ingested ration between 0 and 400 cal d^{-1} , was always less than 0. As far as we know, *M. galloprovincialis* GE was not measured, therefore in this preliminary attempt to compare model results with mussel energy requirements, we decided to use growth efficiency estimated for *M. edulis*:

- 1) the maintenance ration, C_m , was fixed on the basis of actual mussel weight;
- 2) the average energy content for phytoplankton in the model was fixed in accordance with Platt & Irwin (1973);
- 3) the phytoplankton concentration threshold under which maintenance requirements are not matched was calculated for each diet composition hypotized, see Tab. 4.

diet	% of energy income by phytoplankton	phytoplankton threshold for mussel maintenance
А	80	0.23
В	50	0.14
С	20	0.06

Table 4. Simulated diets and relative critical thresholds for phytoplankton



Figure 10. Generalized curve for growth efficiency, from Bayne (1976). C_m and C_{opt} are respectively the maintenance and optimal rations.

In Fig. 11 are represented the simulated values of phytoplankton concentration at increasing distance from the first farm, named according to the day in which the water column gets across the first farm. Horizontal crossed-line in the figure represent the threshold under which the ingested ration cannot sustain energy requirements for mussel maintenance, referring to the three different diets reported in Tab. 3. Even referring to diet C, in which phytoplankton accounts only for the 20% of the total available energy, after the third consecutive farm phytoplankton concentration falls under the critical threshold.



Figure 11. Phytoplankton concentration along the farming area and critical energy thresholds for the three different diets (grey areas are occupied by mussel farms).

Model checking

The numerical solutions of the model was compared with the analytical solution which is obtained by simplifying the reaction term in Eq. (3) as follows. Let P^* be the concentration of one of the two phytoplankton functional groups described in the model, Z^* the concentration of the zooplankton grazing on it, and P^*_0 the Ivlev's threshold phytoplankton concentration (Eq. (1.15), (1.16)). Assuming that $P^* \approx P_0^*$ meanwhile the water column gets across the *n* consecutive farms, the grazing rate of zooplankton, $f_8(P^*)$, becomes approximately $r_z^*P^*$, with constant $r_z^* \approx r_z \Lambda$, thus obtaining:

$$\frac{dP^*}{dt} = \mu^*(T, N, I) \cdot P^* - r_z^* \cdot P^* \cdot Z^* - \chi \cdot CR \cdot M \cdot P^*, \qquad (6)$$

where μ^* is the net phytoplankton growth rate at the beginning of the first farm, including losses due to respiration and mortality, and χ is the characteristic function, $\chi = 1$ inside a farm and $\chi = 0$ outside. Taking into account that in our case study the duration of crossing by water column of one farm (of the length of 2 *km* approximately) together with the distance between farms (also of the length of 2 *km* approximately) is about 28 hours it may be assumed that during the crossing of a few farms all coefficients and zooplankton density Z^* are approximatively constant. The approximate solution of Eq. (6) becomes,

$$\begin{cases} P^* = P_0^* \cdot exp[(\mu^* - CR \cdot M - r_z^* \cdot Z^*) \cdot t] &, \text{ inside the farm } (\chi = 1) \\ P^* = P_0^* \cdot exp[(\mu^* - r_z^* \cdot Z^*) \cdot t] &, \text{ outside the farm } (\chi = 0) \end{cases}$$
(7)

where t is time and P_0^* is the initial condition for phytoplankton concentration. Knowing the average current velocity, v, the value of phytoplankton concentration at the beginning of the second plant, P_1^* , can be calculated as follows:

$$P_1^* = P_0^* \cdot exp\left[\left(\mu^* - CR \cdot M - r_z^* \cdot Z^*\right) \cdot \left(\frac{L}{v}\right)\right] \cdot exp\left[\left(\mu^* - r_z^* \cdot Z^*\right) \cdot \left(\frac{D}{v}\right)\right], (8)$$

where L and D are respectively the length of one farm and the distance between two consecutive farms. If we assume a fixed value for L and D, the phytoplankton concentration at the beginning of the third farm will be,

$$P_2^* = P_0^* \cdot exp \left\{ 2 \cdot \left[\left(\mu^* - r_z^* \cdot Z^* \right) \cdot \left(\frac{L+D}{v} \right) - \left(CR \cdot M \right) \cdot \left(\frac{L}{v} \right) \right] \right\}$$
(9)

and the phytoplankton concentration after the *n* consecutive plants, P_n ,

$$P_n^* = P_0^* \cdot exp \left\{ n \cdot \left[\left(\mu^* - r_z^* \cdot Z^* \right) \cdot \left(\frac{L+D}{v} \right) - \left(CR \cdot M \right) \cdot \left(\frac{L}{v} \right) \right] - \left(\mu^* - r_z^* \cdot Z^* \right) \cdot \left(\frac{D}{v} \right) \right\}$$
(10)

The net phytoplankton photosynthesis rate at the beginning of the first farm, μ^* , was calculated for the day 27 March. The maximum photosynthesis rate, μ_{max} , was limited using the actual values of *T*, *P*, *Si* and *I* and subtracting the losses due to respiration and mortality, in accordance to equations reported in Tab. 1. The values of the parameters used in the calculations are reported in Tab. 5. Before the third plant (after two farms and two breaks) phytoplankton concentration is 0.031 gC m⁻³, that is in good accordance with the result of the numerical simulations, 0.033 gC m⁻³, reported in Fig. 9, blue line.

Incze et al. (1981) studied the carrying capacity for bivalve molluscs by applying a simple analytical model, based on maintaining critical levels of particle flow trough culture areas. The analytical simplification of the model here presented, based on similar considerations, improves this approach by allowing one to reproduce both the competition between cultured mussel and zooplankton for food and the environmental constraints which affect the primary production.

Parameter	Description	Value	Unit
μ^*	Net photosynthesis rate	0.0063	h^{-1}
r_z^*	Maximum herbivore ingestion rate	0.024	h^{-1}
Z^*	Zooplankton concentration	0.1	gC m ⁻³
М	Mussel density	40	individuals m ⁻³
P_{0}	Phytoplankton concentration	0.065	gC m ⁻³
CR	Clearance rate	0.00085	m ³ h ⁻¹ individuals ⁻¹
L	Farm length	2000	m
D	Distance between two consecutive farms	2000	m
v	Current velocity module	144	$m h^{-1}$

Table 5. Values of the parameters used for Eq (10)

5 Conclusions

A mathematical model which describes the impact of farmed mussels on phytoplankton concentration was developed. Physico-chemical and water quality parameters, as well as data concerning mussel growth and rearing practices, have been acquired for the study site. The model was calibrated against a one year time series of phytoplankton concentration, recalculated from site-specific chlorophyll-a data. The model was applied to study the sustainability of mussel culture activities along the western Adriatic coast. Simulation results indicates that phytoplankton concentration can be strongly reduced by the grazing of farmed mussels. Model results were discussed on the basis of considerations on energy requirements to sustain mussel growth. The hypotized scenarios indicate that mussel growth can be reduced by food scarcity during a critical period of the rearing cycle. The good accordance of the numerical solution of the short-term simulation with the analytical solution obtained by simplifying the reaction term indicates the possibility of applying a simple analytical model as a first step when assessing the impacts of mussel farming on phytoplankton stocks. The approach presented in this work can give useful indications related to farm size and location, and helps in reducing the lack of tools developed for this purpose.

References

- Arnold V.I., 1983. Geometrical Methods in the Theory of Ordinary Differential Equations (Grundlehren der mathematischen Wissenschaften), Springer 334 pp.
- Babarro, J.M.F., Fernández-Reiriz, M.J., Labarta, U., 2000. Feeding behavior of seed mussel Mytilus galloprovincialis: environmental parameters and seed origin. J. Shellfish. Res. 19, 195-201.
- Bacher, C., Duarte, P., Ferreira, J.G., Heral, M., and Raillard, O. 1998. Assessment and comparison of the Marennes-Oleron Bay (France) and Carlingford Lough (Ireland) carrying capacity with ecosystem models. Aquat. Ecol. 31, 379–394.
- Barbariol, V., Razouls, S., 2000. Experimental studies on the respiratory metabolism of *Mytilus galloprovincialis* (Mollusca Bival-via) from the Mediterranean Sea (Gulf of Lion). Vie Milieu 50, 87-92.
- Baretta JW, Ebenhöh W, Ruardij P, 1995. The European Regional Seas Ecosystem Model, a complex marine ecosystem model. Neth. J. Sea. Res. 33(3/4), 233–246.
- Bayne, B.L., 1976. Marine Mussels: Their Ecology and Physiology. Cambridge Univ. Press, Cambridge, 506 pp.
- Bernardi Aubry, F, Berton, A, Bastianini, M, Socal, G, Acri, F, 2004. Phytoplankton succession in a coastal area of the NW Adriatic, over a 10-year sampling period (1990–1999). Cont. Shelf. Res. 24, 97–115.
- Bowie, G.L., Mills, W.B., Porcella, D.B., Campbell, C.L., Pagenkopf, J.R., Rupp, G.L., Johnson, K.M., Chan, W.H., Gherini, S.A., 1985. Rates, constants, and kinetics formulations in surface water quality modelling (second edition). U.S. Environmental Protection Agency, EPA/600/3-85/040.

- Cadée, G.C. and Hegeman, J., 1974. Primary production of phytoplankton in the Wadden sea. Neth. J. Sea. Res. 8, 240-259.
- Carver, C.E.A., and Mallet, AL. 1990. Estimating the carrying capacity of a coastal inlet for mussel culture. Aquaculture 88, 39–53.
- Ceccherelli, V.U., Rossi, R., 1984. Settlement, growth and production of the mussel Mytilus galloprovincialis. Mar. Ecol. Prog. Ser. 16, 173-184.
- Cushman-Roisin, B., Gačić, M., Poulain, P. M. and Artegiani, A. (eds). Physical oceanography of the Adriatic Sea. Kluwer Academic Publishers, 2001. 304 pp.
- de Boor, C., A Practical Guide to Splines, Springer-Verlag, 1978.
- Denis, L., Alliot, E., Grzebyk, D., 1999. Clearance rate responses of Mediterranean mussels, *Mytilus galloprovincialis*, to variations in the flow, water temperature, food quality and quantity. Aquat. Living Resour. 12, 279-288.
- Dippner, J.W., 1993. A lagrangian model of phytoplankton growth dynamics for the northern Adriatic Sea. Cont. Shelf Res. 13, 331–355.
- Dippner, J.W., 1998. Competition between different groups of phytoplankton for nutrients in the southern North Sea. J. .Mar. Syst. 14, 181-198.
- Dowd, M., 2005. A biophysical coastal ecosystem model for assessing environmental effects of marine bivalve aquaculture. Ecol. Model. 183, 323-346.
- Fernández-Reiriz, M.J., Labarta, U., Babarro, J.M.F., 1996. Comparative allometries in growth and chemical composition of mussel (*Mytilus galloprovincialis* Lmk) cultured in two zones in the Ria Sada (Galicia, NW Spain). J. Shellfish Res. 15, 349-353.
- Frankic, A., 2003. Integrated Coastal Management & sustainable aquaculture development in the Adriatic Sea, Republic of Croatia. Project Report, Ministry for Agricolture, Forestry and Fisheries, government of Croatia.
- Gardner, J.P.A., 2000. Where are the mussels on Cook Strait (New Zealand) shores ? Low seston quality as a possible factor limiting multi-species distributions. Mar. Ecol. Prog. Ser. 194, 123-132.
- Gardner, J.P.A., 2002. Effects of seston variability on the clearance rate and absorption efficiency of the mussels Aulacomya maoriana, Mytilus galloprovincialis and *Perna canaliculus* from New Zealand. J. Exp. Mar. Biol. Ecol. 268, 83-101.
- Grant, J. 1996. The relationship of bioenergetics and the environment to the field growth of cultured bivalves. J. Exp. Mar. Biol. Ecol. 200, 239-256.
- Hale, J. and Koçak, H., 1991. Dynamics and bifurcations. Springer-Verlag, 568 pp.
- Hydrores, 2004. Presentazione del progetto di riorganizzazione delle mitilicolture della costiera triestina nell'ambito del piano di sviluppo integrato della fascia costiera del golfo di Trieste. Hydrores anno XXI-26: 53-58.
- ICES-WGEIM, 2005. Report of the working group on environmental interactions of mariculture, ICES.
- Incze, L.S., Lutz, R.A. and True, E., 1981. Modelling carrying capacities for bivalve mollusks in open, suspended culture systems. J. World Maricult. Soc. 12, 143-155.
- Inglis, G.J., Hayden, B.J., and Ross, A.H. 2000. An overview of factors affecting the carrying capacity of coastal embayments for mussel culture. National Institute of Water & Atmospheric Research Ltd, Christchurch.
- Ivlev, V.S., 1966. The biological productivity of waters (translated by W.E. Ricker). J. Fish. Res. Board Can. 23, 1717-1759.
- Jørgensen, S.E., 1983. Modelling the ecological processes. In mathematical modelling of water quality: streams, lakes and reservoirs. G.T. Orlob editor. Wiley IIASA, ch. 4.
- Koryavov, P., 1974. A way of describing pollution propagation in rivers using the network flow approach and other extensions. IIASA working paper WP-74-48.

- Labarta, U., Fernández-Reiriz, M.J., Babarro, J.M.F., 1997. Differences in physiological energetics between intertidal and raft cultivated mussels *Mytilus galloprovincialis*. Mar. Ecol. Prog. Ser. 152, 167-173.
- Lassiter, R.R., Kearns, D.K., 1974. Phytoplankton population changes and nutrient fluctuations in a simple aquatic ecosystem model. In: Middlebrooks, E.J., Falkenberg, D.H., Maloney, T.E. (Eds.), Modelling the Eutrophication Process. Ann Arbor Science, Ann Arbor, MI, pp. 131–138.
- Martincic, 1998. Modello di Carrying Capacity applicato alle mitilicolture in sospensione. Tesi di dottorato in acquacoltura, Università di Firenze, Pisa ed Udine.
- Montagnes, D.J.S. & Franklin, D.J, 2001. Effect of temperature on diatom volume, growth rate, and carbon and nitrogen content: Reconsidering some paradigms. Limnol. Oceanogr. 46(8), 2008-2018.
- Navarro, E., Iglesias, J.I.P., Camacho, A.P., Labarta, U., Beiras, R., 1991. The physiological energetics of mussels (Mytilus galloprovincialis Lmk) from different cultivation rafts in the Ria de Arosa (galicia, N.W. Spain). Aquaculture 94, 197-212.
- Navarro, E., Iglesias, J.I.P., Pérez Camacho, A., Labarta, U., 1996. The effect of diets of phytoplankton and suspended bottom material on feeding and absorption of raft mussels (*Mytilus galloprovincialis* Lmk). J. Exp. Mar. Biol. Ecol. 198, 175-189.
- Orlob, G.T., 1983. Mathematical modelling of water quality: streams, lakes and reservoirs. Wiley IIASA, 518 pp.
- Paloheimo J.E. and Dikie L.M., 1965. Food and growth of fishes. I. A growth curve derived from experimental data. J. Fish. Res. Board Can. 22, 521-542.
- Paloheimo J.E. and Dikie L.M., 1966a. food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Bd. Canada 23, 869-908.
- Paloheimo J.E. and Dikie L.M., 1966b. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Board Can. 23, 1209-1248.
- Parsons, T.R., Lebrasseur, R.J. and Fulton, J.D., 1967. Some observations on the cell size and concentration of phytoplankton blooms. J. Oceanol. Soc. Japan 23, 10-17.
- Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D., Dejak, C., 2001. Managing the rearing of Tapes phillipinarum in the lagoon of Venice: a decision support system. Ecol. Model. 138, 231–245.
- Platt, T., Irwin, B., 1973. Caloric content of phytoplankton. Limnol. Oceanogr. 18, 306-309.
- Prins, T.C., Smaal, A.C., Dame, R.F., 1998. A review of the feedbacks between bivalve grazing and ecosystem processes. Aquat. Ecol. 31, 349-359.
- Prioli, G., 2003. Utilizzo a scopo produttivo di nuove metodiche nell'allevamento di *Mytilus* galloprovincialis. M.a.r.e. S.c.a r.l.
- Prioli, G., 2004. Studi ed indagini rivolti al miglioramento della mitilicoltura in E.Romagna. M.a.r.e. S.c.a r.l.
- Saltelli, A., Tarantola, S., Campolongo, F., Ratto, M., 2004. Sensitivity Analysis in Practice. John Wiley and Sons, 219 pp.
- Sarà, G., Mazzola, A., 2004. The carrying capacity for Mediterranean bivalve suspension feeders: evidence from analysis of food availability and hydrodynamics and their integration into a local model. Ecol. Model. 179(3), 281-296.
- Smaal, A. C., Prins, T. C., Dankers, N., Ball, B., 1998. Minimum requirements for modelling bivalve carrying capacity. Aquat. Ecol. 31, 423-428.
- Solidoro, C., C. Dejak, D. Franco, R. Pastres, and G. Pecenik, 1995. A model for macroalgae and phytoplankton growth in the Venice lagoon. Environ. Int. 21, 619-626.
- Steele, J.H., 1962. Environmental control of photosynthesis in the sea. Limnol. Oceanogr. 7, 137-150.
- Thompson, R. J. and Bayne, B. L., 1974. Some relationships between growth, metabolism and food in the mussel *Mytilus edulis*. Mar. Biol. 27, 317-326.

- Vichi M, Pinardi N, Zavatarelli M, Matteucci G, Marcaccio M, Bergamini MC, Frascari F, 1998a. Onedimensional ecosystem model tests in the Po Prodelta Area (northern Adriatic Sea). Environ. Model. Soft. 13, 471–481.
- Vichi M, Zavatarelli M, Pinardi N, 1998b. Seasonal modulation of microbial-mediated carbon fluxes in the northern Adriatic Sea. Fish. Oceanogr. 7, 182–190
- Vichi M, Oddo P, Zavatarelli M, Coluccelli A, Coppini G, Celio M, Fonda Umani S, Pinardi N, 2003. Calibration and validation of a one-dimensional complex marine biogeochemical fluxes model in different areas of the northern Adriatic shelf. Ann. Geophys. 21, 413–436
- Vichi, M., May, W., Navarra, A., 2003. Response of a complex ecosystem model of the northern Adriatic Sea to a regional climate change scenario. Clim. Res. 24, 141-158.
- Zavatarelli, M., Baretta, J.W., Baretta-Bekker, J.G., Pinardi, N., 2000. The dynamics of the Adriatic Sea ecosystem. An idealized model study. Deep-Sea Res. I 47, 937-970.
- Zoppini, A., Pettine, M., Totti, C., Puddu, A., Artegiani, A. and P a g n o t t a, R., 1995. Nutrients, Standing Crop and primary Production in Western Coastal Waters of the Adriatic Sea. Est. Coast.. Shelf Sci. 41,493-513.

APPENDIX A

Long term simulation

Simulation started on June 1 and the model was forced for 4 consecutive years with the same yearly time series of data of environmental forcings. Model parameters are reported in Tab. 3, while initial conditions are the same as reported in the text. After the first year, the dynamics of phytoplankton concentration show a periodic behavior, see Fig. A1. The different trajectory obtained in the first year of simulation can be related to model dependence on initial conditions and to the period of time necessary for the stabilization on some periodic solution.



Figure A1. Long-term phytoplankton dynamics outside the farm, from model simulation

Stability analysis

The behaviour of solution near a periodic orbit was investigated in terms of the dynamics of the Poincaré map (Hale & Koçak, 1991). If x(t) is the periodic solution of

the equation $\dot{x} = v(x,t)$ on the interval $[t_0, t_1]$, where t_1 - t_0 equals to one period, then the analysis involves the following steps:

1) to solve the variational equation $\dot{X} = A(t) \cdot X$, where X is a dim $x \times \text{dim } x$ square matrix and $A(t) = v_x(x(t),t)$ is the Jacobian matrix. The unit matrix, *E*, has to be taken as initial condition, $X(t_0) = E$;

2) to calculate the module of the eigenvalues of the matrix obtained after integrating the equation for one period, at $t=t_1$;

The cycle is stable if all the modules are less than one.

In the present application, $t_0=2$ years and $t_1=3$ years were taken. The stability of the model which reproduces the annual phytoplankton dynamics was tested, i.e. no mussel grazing was taken into account in the simulation. After integrating the variational equation along one period, the matrix $X(t_1)$ was obtained,

$$X(t_1) = \begin{vmatrix} 6.04 \cdot 10^{-1} & 0 & 6.68 \cdot 10^{-7} & 0 \\ 0 & 4.82 \cdot 10^{-1} & 0 & 2.1 \cdot 10^{-12} \\ 1.12 & 0 & 7.86 \cdot 10^{-10} & 0 \\ 0 & 1.05 & 0 & 5.7 \cdot 10^{-6} \end{vmatrix}$$

By transposing the second and third rows and columns of this block type matrix one can calculate the respective eigenvalues, which have values $\lambda_1 = 0.64$, $\lambda_2 \cong 0$, $\lambda_3 = 0.48$, $\lambda_4 \cong 0$.

Local sensitivity with respect to parameters

A first attempt to study local sensitivity with respect to model parameters was performed by means of the brute force method (Saltelli et al., 2004). The effect of the variation of parameters on the trajectory of the system, x(t), is investigated by perturbing one parameter a time. For small perturbations of the general parameter *j* from its nominal value, the relatively sensitivity coefficient, S_{ij} , of variable *i* with respect to the perturbed parameter, can be written as:

$$S_{i,j} = \frac{x_i(\beta,t) - x_i(\beta_0,t)}{(\beta_j - \beta_{j0})} \cdot \frac{\beta_{j0}}{x_i(\beta,t)}$$

were β_{j0} and β_j represent, respectively, the nominal and the perturbed value of the *j* parameter.

In this work the analysis was focused on four different parameters: the maximum photosyntesis rates and the optimal temperatures for the two phytoplanktonic groups, namely μ_{max1} , μ_{max2} , T_{o1} and T_{o2} . These parameters were selected as they were the ones with the highest range of variation in literature. The numerical experiment was performed by repeatedly integrating the system. The parameters were augmented of a 1% on their nominal values.

Relative Sensitivity coefficients for the state variables describing the two phytoplanktonic groups were calculated at each day for one year, the results are reported in Fig. A2. A rank of model parameters with respect to their sensitivity is attempted in Tab. A1, in which the mean square values of relative sensitivity coefficients with respect to each studied parameter is reported. The sensitivities were calculated with respect to parameters specifying the maximum photosyntesis rate μ_{max1} , μ_{max2} , and the optimal temperatures T_{o1} and T_{o2} . The results show that the augmented maximum photosynesis rate reflects on small change in model trajectory, and low relative sensitivity values. Differently, the positive increase of optimal temperature parameter causes a very pronounced negative shift of model trajectory in the case of state variable *P2*, namely phytoflagellates group.



Figure A2. Relative Sensitivity coefficients for the state variables describing the two phytoplanktonic groups

Parameter	$\sum_{day=1}^{365} \frac{S_{i,j}^{2}}{365}$
T_{o2}	1074.611
μ_{max2}	0.707932
T_{ol}	0.563751
μ_{max1}	0.094222

 Table A1. Mean square values of relative sensitivity coefficients with respect to each studied parameter