

Temporal variations in benthic communities and their response to physicochemical forcing: a numerical approach

G. Triantafyllou, G. Petihakis, C. Dounas,
D. Koutsoubas, C. Arvanitidis, and A. Eleftheriou



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A generic complex ecological model, the European Regional Seas Ecosystem Model (ERSEM), was applied to a shallow lagoon system in the Eastern Mediterranean. Model results depicting the seasonal variation of nutrients and Chl- α in the water column, as well as three benthic functional groups (suspended feeders, deposit feeders, and benthic carnivores), are validated with *in situ* data. The likely effect of a technical intervention (river input) increasing the freshwater nutrient inputs on ecosystem functioning is also investigated. Detailed annual carbon fluxes and benthic fauna biomasses are calculated, before and after the river input. The importance of external physical/chemical forcing on the pelagic system and its subsequent effect on the benthic system are demonstrated. Model experiments indicate the shift of the ecosystem from nitrate limitation to predator control with external inputs. Model experiments also show a significant increase in the amount of carbon entering the benthic system through the activity of filter feeders when river inputs are implemented.

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G. Triantafyllou (corresponding author), G. Petihakis, C. Dounas, D. Koutsoubas, C. Arvanitidis, and A. Eleftheriou: Institute of Marine Biology of Crete, PO Box 2214, 71003 Heraklion, Crete, Greece [E-mail: gt@imbc.gr].

Introduction

Coastal lagoons may be defined as shallow inland water bodies separated from the sea by a barrier, and communicating with the sea by one or more restricted inlets. Currently, lagoon systems are considered distinct from other coastal systems such as estuaries and fjords (Kjerfve, 1994). Gialova, one of the major Greek lagoons, is considered to be of high natural and economic interest. During 1995/1996 a multidisciplinary research programme was carried out to investigate the structure and dynamics of the lagoon and to assess any long-term impacts on the biota caused by an oil spill incident during 1993. An extensive data set of physicochemical and biotic parameters was collected. The ecosystem is dominated by a microbial food web with nutrients being recycled through small phytoplanktonic and zooplanktonic groups, bacteria, and detritus with a strong coupling between pelagic and benthic systems. (Dounas and Koutsoubas, 1996; Koutsoubas *et al.*, 1997a,b).

The application of numerical models on lagoonal systems, which may allow prediction of the direction of future changes caused by natural processes and by man's exploitation, has been suggested as one of the research priorities in this field (Postma, 1994). The extensive, *in situ* collected data set from Gialova Lagoon made simulation of the system possible. Lagoons are characterized by a high degree of ecosystem complexity compared with fully marine systems, and the simulation of their dynamics implies additional difficulties. Therefore, complex models are required. The European Regional Seas Ecosystem Model (ERSEM), a generic complex model developed during the MAST programme, has been successfully applied to open water systems, first in the North Sea (Baretta *et al.*, 1995) and later in the Adriatic (Allen *et al.*, 1997). ERSEM has also been used for simulating the annual cycles of nutrients and phytoplankton in Gialova Lagoon and for reproducing the *in situ* observations in the water column using the best available meteorological forcing functions to establish a validated database (Petihakis *et al.*, 2000).

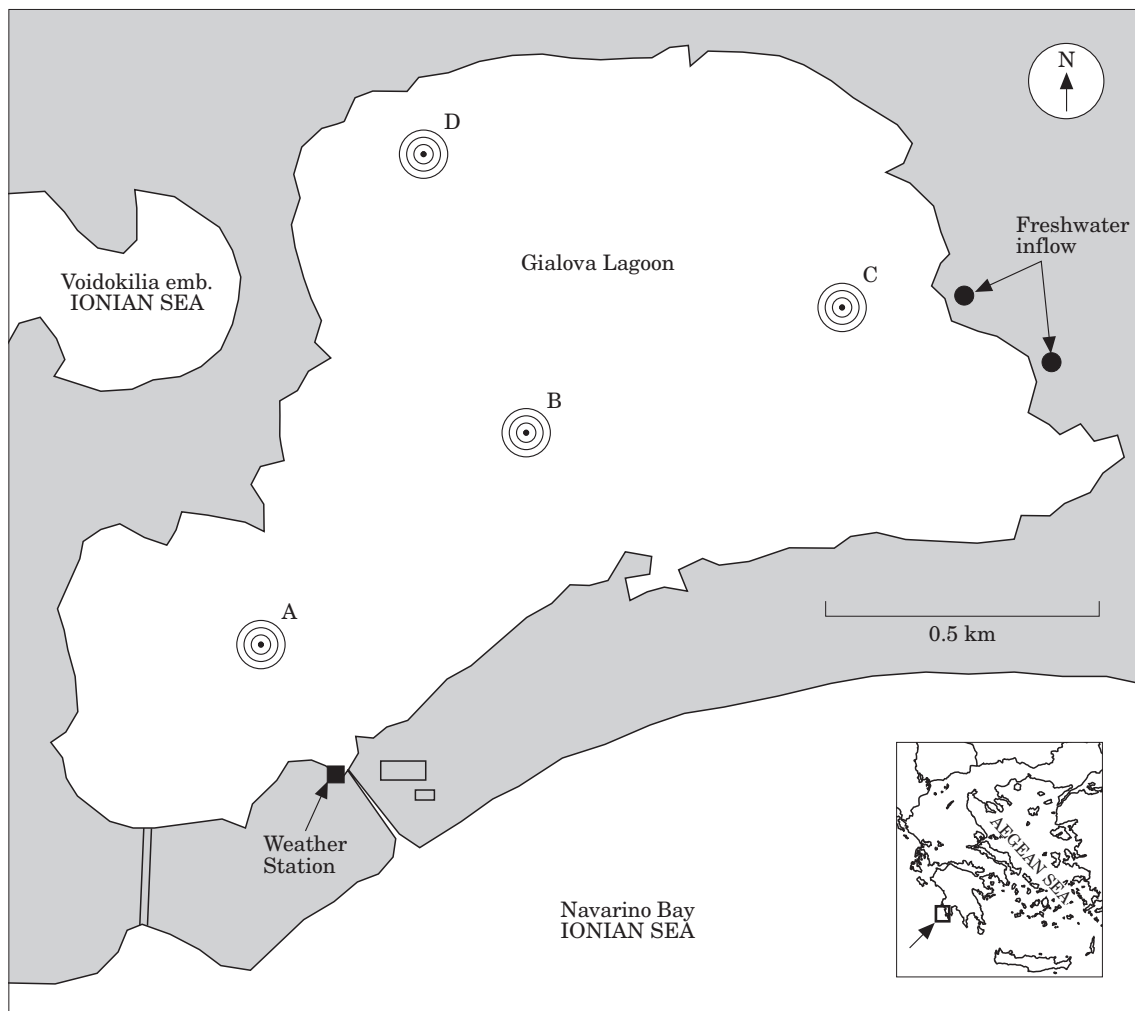


Figure 1. Map of Gialova Lagoon with sampling stations.

We further implemented ERSEM to describe the benthic system in Gialova Lagoon and tested its performance against a coherent data set. The model was also used to explore the behaviour of the system prior to an increase in freshwater nutrient fluxes from the existing small feeder river, a technical intervention under a LIFE-Nature project during 1999. The model was re-run with 0.5 and 1.5-times the river inputs to determine the likely effects on the water column and on the benthos. Detailed carbon fluxes through the benthic biological system, before and after the proposed technical intervention, are estimated and discussed.

Materials and methods

Gialova Lagoon is located in southwestern Greece, adjacent to the Ionian Sea. It has a surface area of

approximately 2.5 km² and a volume of 2 million m³ (Fig. 1). It is a well-mixed water body owing to its shallow depth (0.5–1 m), exhibiting large seasonal fluctuations caused by tides and wind forcing. To the southwest it is connected with Navarino Bay *via* a narrow channel, while to the east two inlets of a small river supply it with fresh water during the winter only.

As described by Dounas and Koutsoubas (1996), biweekly estimates of temperature, salinity, dissolved oxygen, Chl-*a*, phaeopigments, and nutrients (NO₂, NO₃, NH₄, SiO₂ and PO₄) in the water column (300–1000 ml water samples) were made at four stations between June 1995 and June 1996 (Fig. 1). Chl-*a* and phaeopigment concentrations were determined according to the fluorometric method by Yentsch and Menzel (1963). Nutrient concentrations were determined according to standard procedures outlined by Strickland and Parsons (1972), Grasshoff *et al.* (1983), and Parsons

et al. (1984). Major biotic groups in the water column were identified and enumerated. In addition seven stations were seasonally sampled with a spatial distribution covering the entire body of the lagoon. Five replicate samples (total surface area of 0.24 m²) with a hand-operated van Veen grab were taken for macrofaunal analysis at each station in June 1995, September 1995, December 1995, and March 1996. The samples were sieved, through a 0.5-mm mesh and preserved in 5% neutralized formalin. Macrofaunal organisms were identified to species level and meiofaunal organisms to major taxonomical groups. Ash-free biomass of both was measured.

The model applied uses a functional group approach to describe the ecosystem. Biota are grouped according to their trophic level and subdivided according to size class or feeding method. State variables were chosen to keep the model relatively simple without omitting any component exerting a significant influence upon the energy balance of the system. The ecosystem is considered to be a series of interacting complex physical, chemical, and biological processes, which together exhibit coherent system behaviour. Biological functional growth dynamics are described by both physiological (ingestion, respiration, excretion, egestion, etc.) and population processes (growth, migration, and mortality). The biological variables are phytoplankton, functional groups related to the microbial loop, zooplankton, and benthic fauna (Baretta-Bekker *et al.*, 1995; Blackford and Radford, 1995; Broekhuizen *et al.*, 1995; Ebenhoh *et al.*, 1995; Varela *et al.*, 1995). Biologically driven carbon dynamics are coupled to the chemical dynamics of nitrogen, phosphate, silicate, and oxygen. Mineralization of organic matter, coupled to diagenetic nutrient processes in the sediments, is included (Ruardij and van Raaphost, 1995). The phytoplankton pool is described by four functional groups based on size and ecological properties. The microbial loop contains bacteria, heterotrophic flagellates, and microzooplankton, each with dynamically varying C:N:P ratios. The benthic–pelagic coupling is described by the settling of organic detritus onto the benthos and diffusional nutrient fluxes into and out of the sediment after mineralization and diagenesis. The benthic sub-model contains a food web that describes nutrient and carbon cycling *via* aerobic and anaerobic bacterial pathways, bioturbation/bioirrigation, and the vertical transport of particulate matter in the sediment owing to the activity of benthic biota. Benthic nutrient dynamics are described separately. In the model, the vertical positions of the sediment oxygen and sulphide horizons, nutrient profiles, and the resultant flux to/or from the sediment are determined. These processes are strongly dependent on benthic community structure and activity.

Because the lagoon is shallow, the model is constructed as a one-dimensional, one-box model. It is

structured on a modified food web to account for the different ecosystem functioning compared with the standard North Sea model. The initial temperature, salinity, and pelagic biogeochemical values in the model were taken from the standard Gialova Lagoon 4-box model, as described by Petihakis *et al.* (1999). The data set used to force the model for the perpetual year includes meteorological records of the area as well as physico-chemical parameters of the water column. A meteorological data set was obtained by the AANDERAA automatic weather station installed in the area (air temperature, wind speed, sunshine duration, rainfall, humidity, and heat flux) for the period April 1995 to June 1996, and monthly mean wind stresses were calculated as described by Petihakis *et al.* (1999). Incident sea surface solar radiation was calculated from the latitude and modified by monthly averaged cloud cover data from the Comprehensive Ocean Atmosphere Data Set (COADS). Original benthic biomass data were used to initialize the benthic module. Although the shallow pelagic system exhibits significant variations in time, the benthic processes are much slower and require long integration times (Ruardij and van Raaphost, 1995). In an attempt to accommodate both these time scales, a 10-year model integration period was chosen. The model was run for 10 years to a quasi-steady state and re-run for another year, initialized with the values of the state variables on the last day of year 10.

All sampling measurements within the lagoon are treated as replicates and averaged. Range bars are used to indicate spatial variability (minimum and maximum values) at each sampling period. Those values are plotted against computed data of the last simulation year.

Results and discussion

Standard run

Computed values of phosphate were in close agreement with the validation data, with the exception of the sustained simulated high summer levels (Fig. 2a). High summer concentrations are a common characteristic of many lagoons, associated with an increased release from the sediment caused by high temperatures and the development of anoxic conditions (Postma, 1981; Taft and Taylor, 1976). However, similar patterns have also been found in closed and well-oxygenated lagoons, which were attributed to the increased amounts of remineralized detritus at high summer temperatures (Nixon, 1982).

The range of measured nitrate concentrations was very high (0.01–18.28 mmol m⁻³), and model results deviate significantly from the high values observed in winter (Fig. 2b). Measured ammonium concentrations also exhibit wide fluctuations (0.07–34.93 mmol m⁻³)

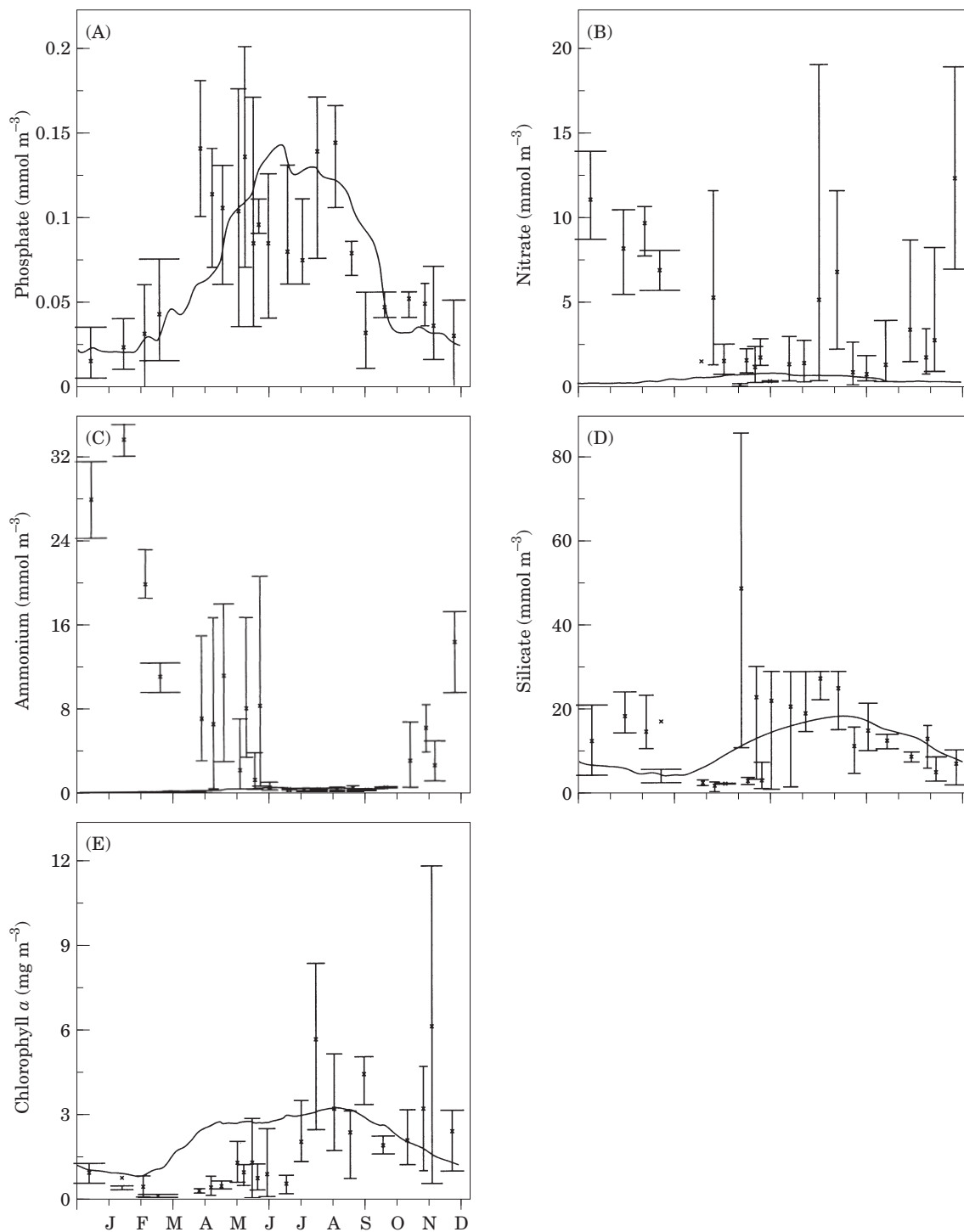


Figure 2. Results of the simulations compared with *in situ* data: (a) phosphate; (b) nitrate; (c) ammonium; (d) silicate and (e) Chl-*a*.

with a significant increase in winter, while simulated concentrations were much lower (Fig. 2c). The high nitrogen concentrations observed during winter are

probably caused by leaching of nitrogen-based fertilizers from the surrounding farmland that enter the lagoon via the river because high values of these nutrients coincide

with heavy rainfall. Since measurements of external fluxes into the lagoon were not performed during the initial study, such effects could not have been simulated correctly and the concentrations must be considered unpredictable.

The silicate observations (Fig. 2d) once again showed a wide range of concentrations (from 0.38–85.42 mmol m⁻³). The simulation results were satisfactory, except in winter when the model fails to reproduce the high values observed.

Measured Chl-*a* concentrations exhibit a wide range (0.08–11.7 mg m⁻³), but modelled results are in rather good agreement with the validation data, exhibiting a peak during late summer–autumn (Fig. 2e), a common feature of lagoons (Boynton *et al.*, 1996). However, the model produces an increase during spring, which is inconsistent with the observations. This might be attributed to inefficient forcing. Lagoons appear to be based on a fairly predictable energetic basis, despite the different plant communities that contribute to primary production, with long-lasting particulate debris as well as living phytoplankton cells forming the dominant food resource for the consumer community (Newell, 1982). Simulations indicate that primary production is limited during spring by nitrate concentrations (Fig. 3), as expected from the low nitrate simulated concentrations. This model result is not expected to be a representation of the real system because of the excess influx of nitrogen not included in the simulations.

The benthic community is characterized by a wide range of biomass values varying among stations and seasons. Environmental stress reduces the community to a smaller number of species that can tolerate a wide range of conditions, reproduce rapidly when conditions are favourable and exhibit marked fluctuations in biomass and community structure from year to year (Mann, 1980). Two types of population fluctuations may be distinguished in lagoons: (a) unpredictable fluctuations within or between years attributable to the environment, and (b) predictable seasonal fluctuations due to influx and emigration (Barnes, 1980).

In Gialova Lagoon, 87 species were found, with annelids, crustaceans, and molluscs being the most abundant taxa accounting for 39%, 28%, and 26% of the total number of the species, respectively, and with the highest number occurring during summer (Dounas and Koutsoubas, 1996). The *in situ* biomass of suspension feeders exhibits a wide range (0–550 mg C m⁻²) among stations, while the simulated values are more or less constant within this range with the only exception of September (Fig. 4a). Deposit feeders exhibit a similar variability (0–540 mg C m⁻²), with simulated values being close to the average seasonal values (Fig. 4b). Finally, also the simulated values for benthic carnivores are in good agreement with the *in situ* values (Fig. 4c).

Annual budget

Figure 5a shows the overall results of the standard run for the benthic community, after integration of the carbon fluxes calculated by the model over the year. Several values deserve additional comment. Suspension feeders have a clear preference for pelagic detrital material (69%) with a small contribution from diatoms (19%) and to a lesser extent from nanoplankton (5%) and benthic detritus (7%). Deposit feeders take most of their carbon from benthic detritus (61%), followed by meiobenthos (35%) and benthic bacteria (4%). Clearly, detritus recycling is important in the benthic system with most of the carbon being recycled through meiobenthos, the major detritus consumer. Benthic detritus is a significant food source for meiobenthos (68%), with bacteria contributing 5% and with a large amount of carbon recycling through cannibalism (27%). Benthic carnivores mainly feed on deposit feeders (60%) and to a lesser extent on meiobenthos (38%). Cannibalism does not seem to be important in benthic carnivores (3%).

The major flux from the water column to the benthos occurred during summer, following the pelagic spring bloom. The carbon budgets indicate that there is a strong benthic-pelagic coupling with the water column supplying the necessary carbon in the form of detrital material rich in nutrients. Most of the model input to the benthos is *via* sedimentation (99%) and only the remaining 1% is mediated *via* suspension feeders.

Environmental management and sensitivity analysis

Numerical ecosystem models, as operational tools, may directly apply to problems of environmental management, predicting the response of natural systems to perturbations and modifications of various kinds. Since nutrient dynamics are described in some detail, the model may provide insight into the role of nutrient input in influencing plankton and benthic dynamics in the system. Thus, the Gialova Lagoon model can be used to begin to explore aspects of management activity. One area of increasing concern involves the input of fresh water from the nearby river and drainage channels into the lagoon to enrich the water with nutrients (Dounas and Koutsoubas, 1996).

To assess the effect of river inputs into the system, fresh water and land-derived nutrients have been implemented in the model as an external source. In an attempt to estimate the appropriate nutrient flux levels and because of the lack of *in situ* data, the differences in nutrient concentration between station C (close to the fresh water input) and station B (centre of lagoon) were calculated. The river can supply the lagoon with an average of 50 m³ day⁻¹ (Dounas and Koutsoubas, 1996). To simulate the river discharge into the lagoon

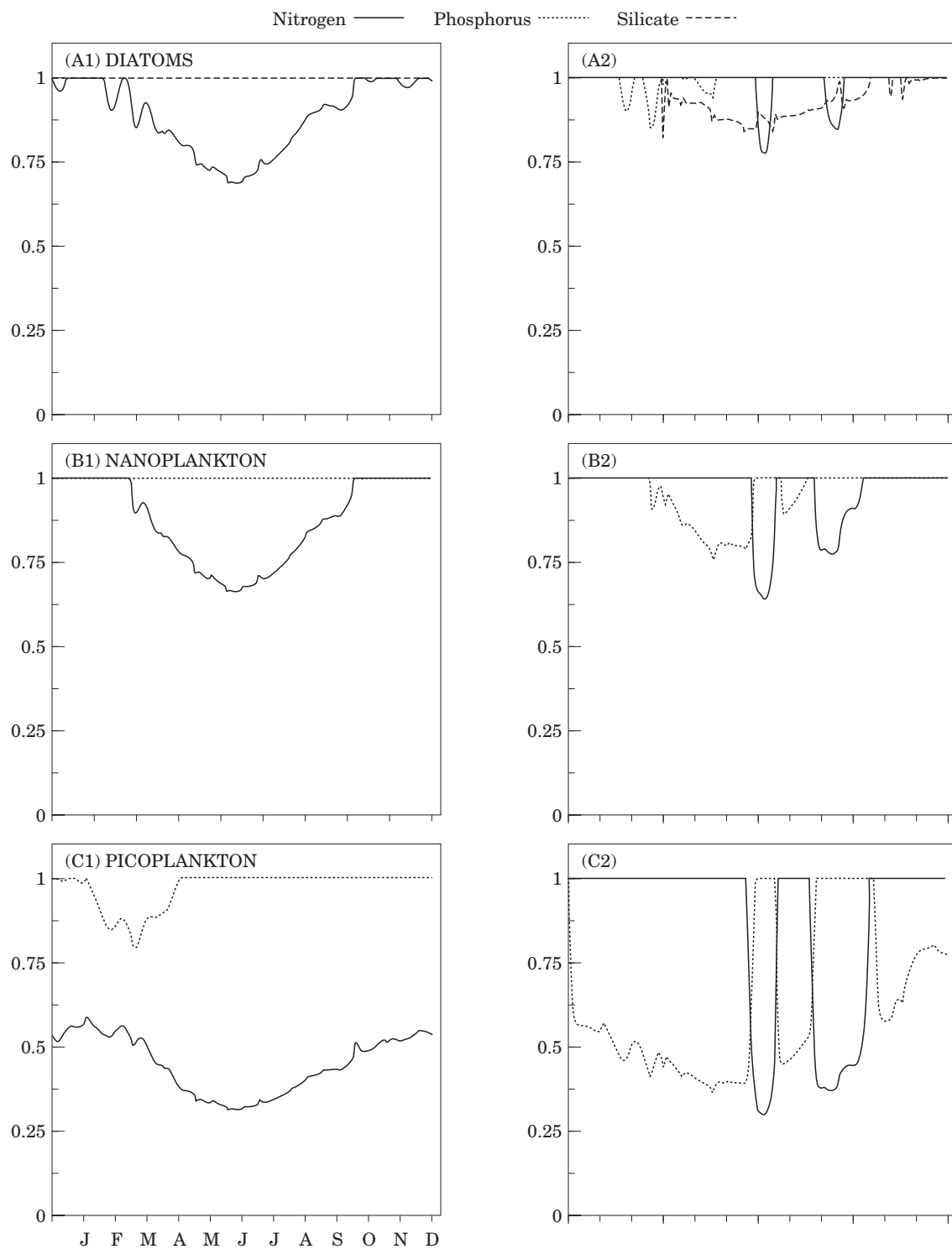


Figure 3. Limitation of phytoplankton by different nutrients (left: standard run; right: run with river inputs): (a) diatoms; (b) nanoplankton; (c) picoplankton.

realistically, the outflow (Q) is represented by a sinusoidal function (Kremer and Nixon, 1978) reaching a maximum of $50 \text{ m}^3 \text{ day}^{-1}$:

$$Q(\text{m}^3 \text{ day}^{-1}) = 50 + 50 \times \cos(2\pi(\text{day}-60)/365)$$

During late summer, the flow is truncated reaching a minimum value of $0.009 \text{ m}^3 \text{ day}^{-1}$. The model was run for another 10 years to a quasi-steady state including river forcing.

A noticeable feature is the significant improvement in the simulated nitrate and ammonium concentrations once external fluxes are implemented (Fig. 6a,b). Figure 6c shows Chl- α results of the tenth simulation year against standard run results and validation data. Since the system is always vertically mixed, nutrients brought in by the river can enter sediments either directly or after passing through an algal phase, and can be resuspended due to wind mixing. The inflow of river waters leads to increased primary production because there is no light temperature limitation and, consequently this leads to an increased benthic production. The picoplankton cells appear to have a clear advantage (doubling their biomass) when river inputs are modelled (Table 1), while diatom biomass shows a small increase (6%). In contrast, the nanoplankton exhibits a significant decrease (37%) in biomass. The results indicate a fast response of diatoms and small cell phytoplankton to increased nutrients.

An interesting feature of river inputs is that the diatom and nanoplankton populations are controlled by the grazing pressure exerted by suspension feeders (Fig. 4) rather than by nutrient limitation (Fig. 3). In contrast, picoplankton production is phosphate limited during spring/early summer switching to nitrogen limitation during summer to early winter (Fig. 3).

Apparently, small amounts of nitrogen are enough to boost primary production (Fig. 6c). Suspension feeders (Fig. 4a) exhibit a significant increase in biomass throughout the year. Maximum values occur during late summer following the phytoplankton bloom and the increase in pelagic detritus, indicating the preference of suspension feeders for diatoms and small cell phytoplankton. Deposit feeders (Fig. 4b) and benthic carnivores (Fig. 4c) also exhibit an increase in biomass, because of the increased carbon inputs from the water column into benthos.

Scrutiny of the annual budget (Fig. 5b) reveals, apart from the general increase in biomass of all state variables, an increase in the uptake of diatoms by the suspension feeders compared with the standard run. The main increase among the functional benthos groups occurred in the suspension feeders, followed by benthic carnivores, deposit feeders, bacteria, and meiobenthos (Table 1). This result was anticipated because suspension feeders are most tightly coupled to the pelagic

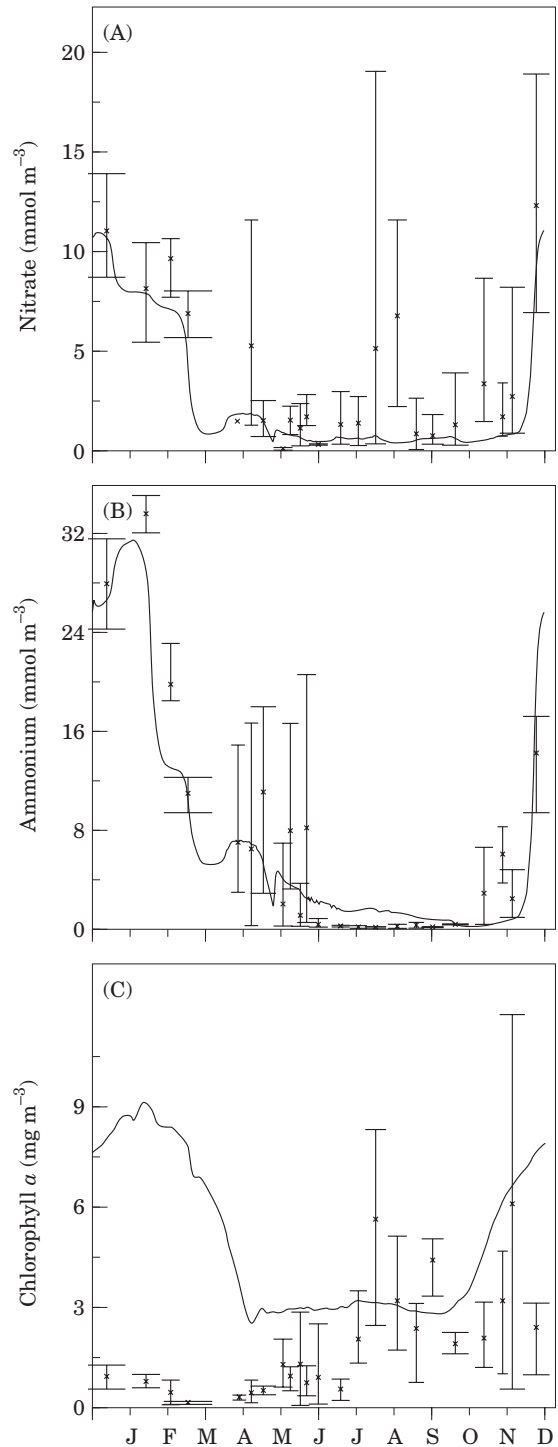


Figure 6. Results of the simulations with river inputs compared with *in situ* data: (a) nitrate; (b) ammonium; (c) Chl- α .

dynamics. A marked difference from the standard run is the increased input of carbon into the benthos *via* filter feeders (26%), with the rest entering as detritus (74%).

Table 1. Net annual pelagic ($\text{g C m}^{-3} \text{y}^{-1}$) and benthic ($\text{g C m}^{-2} \text{y}^{-1}$) production of the main functional groups for the standard run (SR) and for runs with silt input (SI), river inputs (RI), 0.5 and 1.5-times the river inputs.

	SR	SI	RI	0.5 × RI	1.5 × RI
Diatoms	26	27	28	27	28
Nanoplankton	8.4	3.2	5.3	5.4	5.2
Picoplankton	12	24	27	26	29
Pelagic bacteria	51	51	55	54	55
Heterotrophic bacteria	38	41	50	49	51
Deposit feeders	8.2	9.9	12	12	127
Suspension feeders	4.5	203	227	209	244
Meiobenthos	128	140	158	155	160
Benthic carnivores	2.8	11	16	15	17
Benthic bacteria	35	43	51	49	53

This suggests that river inputs create a more favourable environment.

The food supply and the number of suspension feeding benthic animals in lagoons appear to fluctuate more widely than those of deposit feeders. The food supply for suspension feeders (phytoplankton and suspended particulate organic matter) varies seasonally or even from day to day, whereas the food supply for deposit feeders (benthic algae or detritus and microbes growing on these) varies less throughout the year (McLusky, 1989).

To ascertain the short-term effect of changes in land-derived inputs upon the primary production in the area close to the river inlet (10% of the total area) the model has been rerun with freshwater nitrogen, phosphorus, and silica inputs of 0.5 and 1.5-times the input fluxes. Since river input is often associated with the transport of suspended material, silt concentration was also increased proportional to the input fluxes.

The increased silt concentration results in a decrease in pelagic and benthic production, since it increases the extinction coefficient and thereby affects photosynthetic activity. If the model is run with river nutrient inputs halved or doubled, the primary effect in the adjacent area appears in the density of the phytoplankton bloom (Table 1). When inputs are 50% lower, all macrofaunal groups decrease with deposit feeders losing 5%, suspension feeders 8%, and benthic carnivores 5%. Conversely, by increasing input by 50%, the different groups respond by approximately the same percentages. This sensitivity analysis suggests that benthic biomass changes proportionally to river inputs, indicating that the system operates under the same limitation factors.

Conclusions

The simple one-dimensional model anticipates the beginning of the spring–summer bloom rather earlier than the observations indicate. This might be attributed to lack of high-frequency forcing data, which is very

important, particularly in shallow water bodies because of intense vertical mixing. The model uses the COADS cloud cover data, which is spatially coarse (lon 20–22°E, lat 36–38°N) compared with the small area of Gialova Lagoon (2.5 km²). The external nutrient fluxes for nitrate and ammonium represent another important data set. Their forcing is probably as important as the meteorological one in obtaining the seasonal cycle of primary production. Further simulations might clarify this point.

Two important features emerge from the study: (a) the shift of the ecosystem from nitrate limitation to grazing control for diatoms and nanoplankton, and phosphate to nitrogen limitation for picoplankton, once external inputs are implemented; and (b) the increased input of carbon to the benthic system *via* filter feeders. Nevertheless, the simulations proved that for diagnostic purposes *in situ* data of input fluxes are indispensable.

The sensitivity analysis performed on model responses to different river nutrient fluxes and silt concentrations has highlighted the potential utility of the model as an operational tool to support environmental management decisions. No matter how realistic is the model, the results of simulation do not necessarily suggest the best management strategy, but at least they point to the significance of river input in lagoonal ecosystem functioning.

Acknowledgements

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