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The dynamics of the Adriatic Sea ecosystem. An idealized model study

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Abstract

A biomass-based ecological model is presented here for the Adriatic Sea. The hydrodynamical part is composed of the Princeton Ocean Model, while the European Regional Seas Ecosystem Model describes the biogeochemical processes. An idealized Adriatic basin geometry has been used, with perpetual year seasonal cycle forcing the hydrodynamics and river-borne nutrient input forcing externally the biogeochemical processes. The simulation results highlight the role of the physical processes in determining and maintaining some of the nutrient and phytoplankton biomass distribution and characteristics in the basin. The characteristics of the phytoplankton seasonal cycle have been found to depend, in order of priority, on the river-borne nutrient input and physical horizontal and vertical processes. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The Adriatic Sea basin morphology, characterized by a shallow northern shelf (average depth 35 m) and a deep southern sub-basin (deeper than 1000 m), separated by a central sub-basin of intermediate depth, comprises both a coastal (shelf) and an

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open sea ecosystem, which are closely connected. It is characterized by varying trophic conditions: a productive (potentially eutrophic) shallow northern basin and oligotrophic deeper central and southern basins. The shallow region has a primary production cycle influenced by the riverine discharge of land-derived nutrients (Degobbis and Gilmartin, 1990; Revelante and Gilmartin, 1976,1992; Zavatarelli et al., 1998). The most important riverine source is the Po River, but the whole northern Adriatic coast is bordered by many smaller rivers providing a significant flow of freshwater (Cavazzoni-Galaverni, 1972; Raicich, 1994) and nutrients. In this region the strong, freshwater related, buoyancy input coupled with the nutrient discharges in the coastal water can give rise to local dystrophic events characterized by anoxia of bottom water and consequent mass mortality in the benthic fauna (Stachowisch, 1984; Justic et al., 1987). The shallow depth of the whole northern region also enhances the role of benthic-pelagic interactions, in particular the nutrient recycling due to mineralization of organic matter in the sediment and redistribution into the water column. This is estimated to be a significant source of nutrients in the water column (Giordani et al., 1992).

The middle and southern regions of the Adriatic Sea are characterized by a lower primary productivity, with the continental inputs and the benthic-pelagic interactions being of minor importance in comparison to the northern area. Exceptions are the western coastal areas, which are nutrient enriched by the southward coastal current coming from the northern basin (Artegiani et al., 1997b). Open waters, however, show clearly oligotrophic characteristics (Vilicic et al., 1989), and the nutrient supply to the euphotic zone depends strongly on the vertical stratification/mixing processes. Another source of nutrients in the southern sub-basin is the Mediterranean Levantine Intermediate Water entering the Adriatic from the Ionian Sea through the Otranto Channel (Zavatarelli et al., 1998).

From a hydrological and dynamical point of view, the Adriatic Sea seasonal climatological characteristics have been depicted by Artegiani et al. (1997a,b). The basin shows a seasonal thermal cycle typical of temperate latitude seas, with winter vertical mixing of the water column induced by surface cooling and wind stress. The mixing is particularly strong in the northern basin, where dense waters are formed (Artegiani et al., 1989; Vested et al., 1998). In spring and summer a seasonal thermocline is formed. Its depth ranges from 30 to 75 m. Also, the buoyancy forcing determined by river discharges significantly affects the circulation and is responsible for the dilution characteristics of the Adriatic Sea, as evaporation and precipitation almost cancel each other on a yearly basis (Raicich, 1996).

The general circulation is cyclonic with sub-basin gyres (permanent or seasonal) interconnected by coastal currents and jets (Artegiani et al., 1997b). Of particular interest for the present study is the southward coastal current flowing along the western coast of the basin. Its development results from the combined action of wind stress (more pronounced in winter) and buoyancy forcing. By flowing along almost the entire basin and intercepting the Po river plume, it connects the northern and southern ecosystem regimes described above and can significantly affect the large-scale distribution of the biogeochemical properties.



Fig. 1. Monthly averages of surface chlorophyll-*a* concentration in the northern, central and southern Adriatic Sea computed from the CZCS data.

The close coexistence of coastal-eutrophic and open ocean-oligotrophic conditions implies a north to south trophic gradient, which is one of the most interesting ecological characteristics of the Adriatic Sea.

The existence of such a trophic gradient is illustrated by Fig. 1, where the climatological monthly averages of the surface chlorophyll-*a* concentration in the northern, central and southern Adriatic Sea have been computed from the Coastal Zone Color Scanner, CZCS (Barale and Folving, 1996). The higher average concentrations in the northern Adriatic Sea compared with the central and southern sub-basins are evident. Moreover, Fig. 1 reveals that peak concentrations occur during the winter season (December, January). This seems to be a peculiarity of the Adriatic Sea seasonal phytoplankton cycle, as it looks different from the "classical" cycle typical of temperate waters, which is characterized by a phytoplankton biomass peak in spring and a secondary maximum in autumn. On the contrary, the CZCS data show only one period of sustained primary production related biomass spanning from September to March. However, a slight increase of the chlorophyll-*a* concentrations during May in the northern Adriatic can be noted. We will return to this peculiarity when discussing the phytoplankton seasonal cycle simulated by the model (see Sections 4.1 and 4.3). The maintenance of the trophic gradient is dependent on the interactions between the biogeochemical processes, the circulation processes and the water mass structure of this basin. The evaluation of the extent and the importance of these interactions are explored in this paper, where a complete three-dimensional hydrodynamical model is run together with a complex biogeochemistry representation.

The aim of this ongoing modeling study is to investigate the relations and interactions between physical and biogeochemical processes occurring in the Adriatic marine environment at seasonal time scales. In particular, we focus on the understanding of the role played by the physical forcing on the spatial and temporal evolution and variability of the marine ecosystem in shallow and open sea conditions.

To reach the ultimate objective of this study, the development and application of a fully three-dimensional, multi-parametric ecosystem model, several steps were necessary, which partly have been completed now. First, the capability of an ecosystem model to reproduce the observed seasonal evolution of the lower trophic levels and nutrients in the water column in the Adriatic Sea was tested with a onedimensional vertically resolved model (Allen et al., 1998; Vichi et al., 1998a–c). As these tests could not account for the role of horizontal transport, an idealized three-dimensional model setup was made here with the following objectives: (1) to implement and test a practical procedure for coupling a general circulation model and a complex ecosystem model; (2) to ascertain whether this coupled model in an idealized setup would be able to qualitatively reproduce the salient features of the ecosystem dynamics. This model allows us to do sensitivity experiments on physical and biogeochemical parameters, which will be developed in the second part of this work, to appear later.

2. Model design

The ecosystem model consists of the Princeton Ocean Model, POM (Blumberg and Mellor, 1987), and the European Regional Seas Ecosystem Model, ERSEM (Baretta et al., 1995).

POM is a free surface, primitive equation, finite difference model. It prognostically calculates surface elevation, velocity, temperature, salinity and horizontal and vertical diffusion coefficients; the horizontal diffusion is calculated by a Smagorinsky (1993) formulation, while the vertical diffusion is calculated by a second-order turbulence closure submodel (Mellor and Yamada, 1982). The model can use orthogonal curvilinear grids and in the vertical utilizes a sigma (bottom following) vertical coordinate system.

ERSEM is a generic, biomass-based, ecosystem model, with its first application to the North Sea, describing the biogeochemical processes occurring in the water column and in the sediment, as well as their interactions, in terms of the cycling of carbon, nitrogen, phosphorus and silicon within the marine ecosystem. The biological state variables are aggregated into functional groups according to their trophic level. In some cases the functional groups are subdivided again (e.g. the functional group phytoplankton is subdivided into diatoms, which require also silicate as a nutrient, and flagellates with a higher activity respiration, because of their motility).

The pelagic model prognostically calculates the concentrations in the water column of nutrients, oxygen, phytoplankton, microzooplankton, bacteria, organic detritus and mesozooplankton from the uptake and regeneration fluxes between the functional groups and the abiotic state variables. The benthic submodel prognostically calculates concentrations in the sediment of nutrients, oxygen, bacteria, organic detritus and benthic fauna, again from the calculated fluxes. The trophic relations and the flow of matter between the various functional groups considered by ERSEM are schematized in Fig. 2.

Details of the primary production module can be found in Varela et al. (1995), of the mesozooplankton module in Broekhuizen et al. (1995), of the microbial loop submodel in Baretta-Bekker et al. (1995), of the benthic biology module in Ebenhöh et al. (1995), and of the benthic nutrient dynamics in Ruardij and Van Raaphorst (1995). However, these papers refer to the ERSEM version 5.2, while the model used in the present paper is ERSEM version seven, where some modifications were introduced. The most notable one is the introduction into ERSEM of the Droop (1973,1975) phytoplankton nutrient kinetics, which is modeled according to Nyholm (1977a,b) and has been described for ERSEM version 11 in Baretta-Bekker et al. (1997).

POM and ERSEM were run together "on line" through the development of an interface between the two models and inserted into the SESAME (Ruardij et al., 1995) simulation environment.

The exchange of variables between POM and ERSEM is schematized in Fig. 3. Such exchange occurs every time step of the POM model, and ERSEM receives from POM information about the temperature (T), velocity (u, v, w), and horizontal (A) and vertical (k) diffusion coefficient fields (see the appendix). The temperature is used to calculate the metabolic response of the different biota, and the velocity and diffusion coefficient fields are used to compute the advective/diffusive rate of change of the biogeochemical state variables. This is added to the rate of change of the pelagic variables dependent on the different biogeochemical processes. The benthic biogeochemical model considers only diffusion of dissolved nutrients to/from the pore waters to the water column, so that it is in fact decoupled from the physical model. Bottom stress and turbulent diffusion do not resuspend the particulate organic matter. The addition of such coupling is a further step in model development.

The model runs at the internal time step required by POM, but ERSEM maintains the possibility of dynamical time step cutting. When ERSEM requires such cutting (as in the case of a phytoplankton bloom or bloom decay), the physical fields remain constant and the ecological variables are integrated for a number of time steps until the integrated time interval matches the time step of POM. The final results of these integrations are calculated and adopted as the values corresponding in time to the physical variables calculated by POM.

In this version of the model, there is as yet no feedback from the ecology to the physics. Potentially significant feedback from ecology to physics include the effect of biogenic material in modifying the penetration depth of solar radiation and changes in the bottom roughness at high densities of benthic organisms and at high rates of



Fig. 2. Schematic overview of the trophic relations among the functional groups considered by ERSEM. After Baretta et al. (1995).

particulate matter resuspension. These issues will be addressed in a future version of the model.

The idealized Adriatic basin setup for the simulations is shown in Fig. 4a. It is a rectangular basin (without open boundaries) having approximately the same size



Fig. 3. Schematic representation of the POM-ERSEM coupling. See text and the appendix for explanation of the symbols. Dashed lines represent potential feedback of the ecological model on the physical model, which are not yet implemented.

and the same geographical location as the "real" Adriatic. A coarse grid having a horizontal resolution of about 25-km covers the model domain. The bottom geometry (Fig. 4b) consists of a sloping bottom with a minimum depth of 50 m in the north and a maximum depth of 500 m in the south. In the vertical the model has 10 sigma layers.

The model domain has been subdivided into three parts (whose boundaries are shown in Fig. 4a) over which hydrological and biogeochemical properties hav e been spatially and seasonally averaged for data comparison purposes. It has to be mentioned that the northern section of the model domain excludes the two northernmost grid point rows and is referred as the "deep" northern Adriatic, in order to carry out a proper comparison with the climatological seasonal profiles elaborated by Zavatarelli et al. (1998). They divided the northern Adriatic into two subregions: the "shallow" northern Adriatic (bottom depth < 40 m, truly coastal, strongly influenced by river runoff), and the "deep" northern Adriatic (bottom depth > 40 m). Since the minimum depth in our idealized model domain is 50 m, we limit most of the comparison with data to the "deep" northern Adriatic.

3. Initial conditions and forcing functions

The initial temperature and salinity fields were obtained from the ATOS II (Adriatic Temperature, Salinity and Oxygen, version 2) hydrological data set



Fig. 4. The idealized Adriatic Sea model domain. (a) The model grid is overlaid on the realistic bottom topography and the coastline geometry. The subdivision of the model domain into the northern, middle and southern Adriatic regions is given for reference to the other figures. Points 1, 2 are the grid points corresponding with the northern and central time series mentioned in Figs. 9 and 11. (b) The model bottom geometry and the distribution of the sigma layers.

(Artegiani et al., 1997a,b) through an objective analysis procedure (Carter and Robinson, 1987) carried out directly on the model grid. The initial hydrological fields refer to the winter season, where winter is defined, according to Artegiani et al. (1997a,b), as the four-month period from January to April.

Pelagic biogeochemical initial fields were defined as horizontally and vertically uniform profiles, approximately consistent with the climatological winter vertical profiles relative to the northern and middle Adriatic Sea obtained from the analysis of the ABCD II (Adriatic BiogeoChemical Data set version 2 data set, Zavatarelli et al., 1998).

Because of lack of data, benthic biogeochemical initial fields were defined as concentrations decreasing linearly as a function of depth, starting from initial values for the detrital organic matter in the sediments and the benthic organisms that were taken from the North Sea ERSEM box corresponding to the English Channel. This box includes the Rhine estuary and therefore represents a situation characterized by strong external inputs, like the northern Adriatic. The initial concentration of porewater nutrients, was defined equal to the concentration in the water immediately overlying the bottom to avoid strong initial diffusive adjustment at the sedimentwater interface during model spin up.

The external forcing functions of POM and ERSEM are schematized in Fig. 3. POM is forced by wind stress, heat and freshwater fluxes. River inputs of dissolved and particulate matter and nutrients are also considered by ERSEM. The solar radiation is provided to the ERSEM primary production submodel as photosynthetically available radiation (PAR: 40% of the short-wave solar radiation reaching the sea surface; see Apel, 1987).

Solar radiation penetrates the water column, and (in ERSEM) the extinction of light depends upon vertical extinction coefficients calculated at each time step from the concentrations of phytoplankton, detritus, bacteria and inorganic suspended matter (taken here as a constant concentration value of 1 mg/m³). In POM the extinction of the short-wave radiation depends upon a constant vertical extinction coefficient (reported in appendix) taken from Jerlov (1976).

The atmospheric surface forcing was taken from the May (1982,1986) Mediterranean Sea 1°X1° monthly climatologies for wind stress and heat fluxes. The data pertinent to the Adriatic Sea were interpolated into the model grid. Salinity forcing was not used in the form (E-P-R), the balance between evaporation, precipitation and river runoff, but was parameterized by imposing seasonal means of surface salinity from the ATOS II data set. The explicit volume forcing from the rivers on the hydrology (low salinity waters imposed at a lateral boundary point) has been neglected since the surface salinity field mimics this contribution. The surface salinity field in fact contains the river run-off signal as a narrow band of low salinity on the western side of the Adriatic basin.

Only the Po river discharge, in terms of nutrients, was introduced into the model by defining a constant in time (in terms of nutrient concentration) source of nutrients at a grid point that covers the Po delta. The nutrient concentrations in the river were taken from Degobbis and Gilmartin (1990), who estimate the annual Po nutrient discharge into the northern Adriatic Sea, corresponding to a nitrate, phosphate,

ammonium and silicate annual input of 7347, 230, 1056 and 5990 (10^6 mol/yr) respectively. This input constitutes about 50 to 60% of the estimated total river-borne nutrient input to the Adriatic. The Po freshwater discharge was set equal to its long-term annual average ($1600 \text{ m}^3 \text{ s}^{-1}$). This approach excludes from the simulation the seasonal variability of the Po river nutrient input, but the poor information available about this did not allow for the specification of a seasonal cycle. The choice to exclude the nutrient input contribution from other sources was dictated by the poor definition of the specific nutrient contributions of the other rivers, since specific information is available only for the Po river contribution. The effect of the underestimated riverine nutrient input into the basin on the simulated phytoplankton biomass concentration will be discussed later.

POM was run alone (without ERSEM) in a perpetual year mode, i.e., the monthly varying surface forcing is repeated each year of integration, for two years. Two years are considered the minimum amount of time for the model to spin-up to the seasonal cycle. At the end of the two years, the resulting hydrodynamical fields were used as initial conditions for the on-line ecosystem simulations. The coupled model was integrated for a further two years, and the results shown here were extracted from the last year of model integration. Continued integration for a third year showed no appreciable differences in the seasonal cycle, except for a tendency for the concentration of the biogeochemical state variables to increase and for the average temperature of the basin to decrease, effects due to the lack of open boundaries and the inclusion in the model setup of an external nutrient source that determines accumulation of mass.

4. Results and discussion

4.1. The phytoplankton seasonal cycle

An immediate test for a coupled model is its ability to correctly simulate the seasonal variations in the autotrophic components of the marine food web, to determine whether or not the simulated ecosystem structure reacts appropriately to variations in the external physical forcing. Fig. 5 illustrates the simulated phytoplankton annual cycle as time series of the surface averaged concentrations of diatoms and flagellates (carbon content) and the corresponding surface averaged chlorophyll-*a* concentration, to be compared with Fig. 1. Chlorophyll-*a* (Fig. 5a) was calculated from the diatom and flagellate carbon biomass (Fig. 5b and c, respectively), with the conversion formula of Varela et al. (1995). The surface area-averaged concentrations were calculated separately for the "deep" northern, central and southern portions of the idealized model domain (Fig. 4a).

The chlorophyll-*a* annual cycle shows that the simulated surface phytoplankton evolves in time according to a seasonal cycle characterized by high values of surface phytoplankton biomass during autumn-winter and by low values during springsummer. In the "deep" northern Adriatic, concentrations begin to increase in late summer and keep increasing up to mid-winter, to remain at relatively constant values up to early spring. In the middle and southern Adriatic, the biomass increase



Fig. 5. The modeled phytoplankton annual cycle. Surface averaged concentrations for the northern, middle and southern areas indicated in Fig. 4a: (a) chlorophyll-*a* (mg chl-*a* m⁻³); (b) diatoms (mg C m⁻³); (c) flagellates (mg C m⁻³).

begins in autumn; it decreases slightly during winter, to grow again in February-March. From the comparison of the model phytoplankton cycle with the CZCS data (Fig. 1), a qualitative agreement exists between the observed and the modeled surface phytoplankton cycle in the northern Adriatic, where the biomass concentration remains high throughout winter. The decreasing trend occurring from March to May is somewhat slowed down during April-May in correspondence with the slight concentration increase shown in the CZCS data. In the middle and southern Adriatic the modeled cycle differs from the one depicted by the CZCS data, since the data do not show a large spring biomass growth. However, the biomass is peaking in December both in the model and in the observations.

The phytoplankton biomass is formed mostly by the diatom functional group of the model (Fig. 5b), with a minor contribution by flagellates (Fig. 5c). During summer the phytoplankton surface concentrations are low everywhere in the basin, as expected; in fact, under the influence of the stratification of the water column and the resulting nutrient depletion, the production processes occur deeper in the water column (see Section 4.2). The temporal succession in the development of the phytoplanktonic populations is satisfactorily reproduced by the model, since Fig. 5b and c show a time shift of about one month between the diatom and the flagellate spring biomass peaks (Revelante and Gilmartin, 1983).

However, large discrepancies persist in the magnitude of the phytoplankton biomass compared to the CZCS standing stock. To understand this deficiency we need a comparison of the simulated primary production rates with the observed ones and an analysis of the role of the initial conditions and the external nutrient input. In the following, we analyse these three factors in isolation.

The annual cycle of the surface potential (gross) primary production rate in the northern Adriatic Sea has been described by Smodlaka (1986) on the basis of a multiyear sampling program covering the surface waters of the entire northern Adriatic. He found an annual average value of $6.6 \text{ mg C m}^{-3} \text{ h}^{-1}$ and single station values varying, with season and location, between a minimum of 0.1 and a maximum of 143 mg C m⁻³ h⁻¹. The seasonal cycle is characterized by three distinct peaks occurring in February, June and September. In Fig. 6 we show the model seasonal cycle of the surface potential primary production for the "deep" northern Adriatic Sea and (despite the almost complete lack of observations) for the middle and southern Adriatic. The annual average value for the northern Adriatic is 13 mg C m⁻³ h⁻¹, and single grid point values range between a minimum of almost 0 and a maximum of 111 mg C m⁻³ h⁻¹. Therefore, it appears that the simulated values are of the same order of magnitude as the observations, and the observed range of variability is reproduced. However, the three peaks, occurring in February, August and November, are different from the observations. By examining these surface potential primary production rates with the seasonal cycle of the surface phytoplankton biomass (Fig. 5) it can be noted that the biomass peaks occurring at the end and at the beginning of the year are matched by the increase of the potential primary production rates. On the other hand, the increase of the potential production rates occurring in summer does not result in any biomass increase. This indicates that during summer grazing controls the model surface phytoplankton.



Fig. 6. The modeled surface potential primary production rates. Surface averaged values for the northern, middle and southern areas indicated in Fig. 4a. Units are mg C m⁻³ h⁻¹.

In the middle and southern Adriatic Sea the annual average of the simulated surface potential primary production rate is 3 and 5 mg C m⁻³ h⁻¹, respectively, but unfortunately no data are available for comparison. The seasonal production cycles entirely match the biomass seasonality, with enhanced potential primary production rates matching the increase of the phytoplankton biomass.

A study of the seasonal cycle of the net primary production rate (integrated over the depth of the euphotic zone) was carried out by Poniz et al. (1996) at a coastal station in the northern Adriatic Sea. They found a seasonal cycle ranging between a minimum of 197 (November) and a maximum of 2023 (June) mg C m⁻² d⁻¹. The model net primary production rates, computed at a grid point having approximately the same location as the station sampled by the above quoted authors, yielded daily values ranging between 267 (December) and 1331 (April) mg C m⁻² d⁻¹. A recent project measured the net primary production rate in the middle and southern Adriatic during March (Malaguti, personal communication). The value found in the middle Adriatic Sea is about 100 mg C m⁻² d⁻¹, while the observed value in the southern Adriatic ranged between 250 (March 1998) and 300 (March 1997) mg C m⁻² d⁻¹. The model

yielded annual average values of 85 (middle Adriatic) and 51 mg C m⁻² d⁻¹ (southern Adriatic). In March the daily net primary production rate ranged between 111 and 150 mg C m⁻² d⁻¹ in the middle Adriatic Sea and between 116 and 145 mg C m⁻² d⁻¹ in the southern Adriatic Sea.

On the basis of the comparison between simulations and observations, we argue that the differences in phytoplankton biomass between model and observations are not to be ascribed to simulated low primary production rates.

Much more important in determining the model deficiency seems to be the nutrient initial conditions and the magnitude of the external nutrient input. Simulations carried out by increasing and decreasing the nutrient initial conditions by 50% (not shown) produced, obviously, an increase or a decrease of the phytoplankton biomass. However, the factor that apparently has the greater effect on the evolution of the phytoplankton in the northern Adriatic Sea is the external nutrient input. In Fig. 7 is shown the phytoplankton seasonal cycle in the "deep northern", middle and southern Adriatic obtained by running the model without any Po river borne nutrient input. By comparison of the cycle with the corresponding one of Fig. 5, it can be seen that the phytoplankton concentration in the northern Adriatic Sea (during the period of sustained biomass) is reduced by about 50%. This indicates that the specification of the river discharged nutrients plays the major role in the underestimation of the phytoplankton biomass.

Despite a possible underestimation of riverborne nutrients, the different temporal evolution of the phytoplankton biomass in the three sectors of the model domain, along with the differences in the concentration values, indicates that during most of the high surface biomass period, a well-defined north-to-south biomass gradient is reproduced and maintained by the model. This topic will be discussed further in Section 4.3.

4.2. The vertical distribution of phytoplankton and nutrients

We show here seasonal and annual vertical profiles of hydrological and biogeochemical properties to be compared with observations. Seasons are defined as follows: winter is from January to March, spring from April to June, summer from July to September and autumn from October to December.

The mean seasonal temperature profiles averaged over the "deep" northern, central and southern Adriatic regions of the idealized model domain (Fig. 8 a, b, c, respectively) are shown to illustrate the annual thermal cycle of the average water column.

The comparison of the model seasonally averaged temperature profiles with the climatological profiles obtained by Zavatarelli et al. (1998) from the hydrological data of the ABCD.II data set indicates a good agreement between model behavior and observations, as the seasonal alternation between stratification and mixing shown in the data is satisfactorily mirrored in the simulated model temperature profiles. However, differences arise in the extreme values predicted by the model, in particular in the "deep" northern Adriatic, where the summer surface temperatures are about 2°C



Fig. 7. Simulation without river nutrient input. The modeled phytoplankton annual cycle. Surface averaged concentrations for the northern, middle and southern areas indicated in Fig. 4a: (a) chlorophyll-*a* (mg chl-a m⁻³); (b) diatoms (mg C m⁻³); (c) flagellates (mg C m⁻³).



Fig. 8. Mean simulated seasonal profiles of temperature averaged over the northern, middle and southern Adriatic areas shown in Fig. 4a. Winter corresponds to January–March, spring to April–June, summer to July–September and Autumn to October–December.

lower and the spring temperatures are about 2° C higher. During autumn the whole water column appears to be cooler than the corresponding profile obtained from the data. The lower autumn temperatures are probably due to the missing effect of the subsurface Mediterranean Levantine Intermediate Water, entering the Adriatic from the Otranto Strait, which corresponds to a net heat import into the basin (Artegiani et al., 1997a).

We begin to illustrate the seasonal vertical variations of the ecological and biogeochemical properties simulated by the model by showing (Fig. 9) a Hövmoller diagram of the simulated chlorophyll-*a* concentrations at point 1 of Fig. 4a (representative of the "deep" northern Adriatic). The chlorophyll-*a* peak biomass period extends near the surface from January to March, but, almost simultaneously, higher chlorophyll-*a* concentrations begin to develop below the surface, progressively deepening throughout the entire spring and summer season. This gives rise to a distinct subsurface chlorophyll-*a* maximum that from June to August is located at about 25–30 m depth (a depth roughly corresponding to the development of the seasonal thermocline). During the same time period surface concentrations reach minimal values and recover during autumn as shown in Fig. 5.

The composition of the phytoplankton population (Fig. 9b, c) indicates the strong dominance of diatoms with respect to the flagellates, which show only a weak concentration increase during the bloom periods in winter and late autumn.

The "deep" northern Adriatic seasonal vertical profiles of chlorophyll-a are shown in Fig. 10a, while the climatological profiles of Zavatarelli et al. (1998) relative to the "deep" northern Adriatic are reproduced in Fig. 10b. In Fig. 10c we show also plots of the "shallow" northern Adriatic profiles, because they show a surface biomass increase during winter in agreement with the CZCS data of Fig. 1. The winter biomass increase is very evident in the observations of the "shallow" northern Adriatic, and the model is capable of capturing this feature, since the Po river nutrient input is considered as it would be present in shallow waters. The larger bottom depth of our idealized setup, however, produces biomass values closer to the typical values of the "deep" northern Adriatic. Overall, comparing Fig. 10a with Fig. 10b or 10c, it is evident that the model fails to reproduce the vertical distribution of the phytoplankton biomass, since it forms a subsurface chlorophyll-a maximum (progressively deepening from winter to summer). Such a feature does not appear clearly in the climatological profiles of the "deep" northern Adriatic, which show in spring and autumn only a smaller and shallower increase of concentration with depth. In winter and summer the model concentration maximum is deeper than the concentration increase shown by the climatological data. The reason for the failure to simulate the vertical distribution of chlorophyll-a can be ascribed to the gross estimate of light attenuation in the model. Light extinction is calculated as a function of biogenic particulate matter concentration (detritus, phytoplankton, microzooplankton, etc.) and suspended sediment (silt). In the absence of sufficient silt data for the Adriatic, the silt concentration in the model is set to a value constant in space and time. This leads to an overestimation of light penetration in the northern Adriatic region, where the concentrations of inorganic suspended material are known to be higher than the value specified in the model. A confirmation of the important role of the inorganic



Fig. 9. Monthly mean simulated profiles for the Point 1 in Fig. 4a (northern area) as a function of month of the climatological year: (a) chlorophyll-*a* (mg chl-*a* m⁻³); (b) diatoms (mg C m⁻³); (c) flagellates (mg C m⁻³).



Fig. 10. Northern Adriatic seasonal average mean vertical profiles of chlorophyll-*a*. (a) Simulated vertical profiles; (b) observed vertical profiles for the deep northern Adriatic; (c) observed vertical profiles for the shallow northern Adriatic. (b) and (c) redrawn with modifications from Zavatarelli et al. (1998). Seasons as in Fig. 8.

suspended matter in influencing the vertical distribution of the phytoplankton comes from the model study carried out by Vichi et al. (1998a–c) with the one-dimensional version of the POM-ERSEM system implemented at a coastal site in the northern Adriatic Sea. They show that the subsurface chlorophyll maximum is inhibited by a more realistic tenporal distribution of the inorganic suspended matter. However, scarcity of data does not allow us to perform an accurate sensitivity study as was done for the one-dimensional experiments.



Fig. 11. Mean simulated and observed annual profiles averaged in the northern Adriatic area shown in Fig. 4a. (a) Phosphate (mmol m^{-3}); (b) Silicate (mmol m^{-3}); (c) Nitrate (mmol m^{-3}); Ammonium (mmol m^{-3}). Seasons as in Fig. 8.

The annually averaged vertical distribution of nutrients indicates, for phosphate (Fig. 11a) and silicate (Fig. 11c), a relatively good agreement with the observed annual average, despite a slight tendency toward overestimation. In contrast, the nitrate profile (Fig. 11b) indicates a strong overestimation with respect to observations. We can argue that the reason for this different behaviour depends on the model setup and on the biogeochemical characteristics of the Adriatic Sea. In fact, the absence of a southern open boundary and the presence of the Po nutrient source determines the buildup of the nutrient concentration, which appears stronger in the nitrate profile than in the phosphate and silicate profiles. This is because the northern Adriatic Sea is characterized, in general, by phosphorus limitation and by the strong development of diatom populations (Zavatarelli et al., 1998). Therefore, the strong phosphorus and silicate uptake by phytoplankton and the sinking of particulate matter contribute to the export of the phosphorus and the silicon toward the deeper part of the water column, leaving unutilized nitrate in the upper part of the water column.

In the middle Adriatic the vertical distribution of phytoplankton shows a pattern similar to the one observed in the "deep" northern Adriatic (Fig. 12a), but concentration values (due to the reduced influence of the river-borne nutrient inputs) are lower for both diatoms (Fig. 12b) and flagellates (Fig. 12c), which have very low concentrations.



Fig. 12. Monthly mean simulated profiles for Point 2 in Fig. 4a (Middle Adriatic area) as a function of month of the climatological year: (a) chlorophyll-*a* (mg chl-*a* m⁻³); (b) diatoms (mg C m⁻³); (c) flagellates (mg C m⁻³).



Fig. 13. Middle Adriatic area averaged mean seasonal profiles of chlorophyll-*a*. (a) Simulated vertical profiles. (b) Observed vertical profiles redrawn with modifications from Zavatarelli et al. (1998). No observations are available for winter. Seasons as in Fig. 8.

The horizontally averaged profiles of chlorophyll-*a* distribution (Fig. 13a) show a seasonal cycle characterized by the development from winter to summer of a subsurface chlorophyll-*a* maximum at about 50 m depth. The climatological vertical profiles of Fig. 13b have, for spring and summer, a remarkable similarity to simulations, showing a well-defined concentration maximum.

The annual vertical profiles of nutrients in the middle Adriatic are shown in Fig. 14. Also in this region the nitrate values (Fig. 14b) predicted by the model are higher than the observations. The silicate model profile, in contrast indicates that above 100 m depth the model predicted concentrations are lower than the observations, probably because the model is missing other silicate sources (lateral input by rivers and by the Otranto Strait), and silica regeneration processes occur only in the benthic domain.

4.3. The horizontal distribution of phytoplankton and nutrients and the role of advection

We now show the horizontal distributions of phytoplankton in the basin in order to highlight the influence of the advective/diffusive processes on the biogeochemical components of the ecosystem. Recall that the initial condition for the



Fig. 14. Mean simulated and observed annual profiles averaged in the northern Adriatic area shown in Fig. 4a. (a) Phosphate (mmol m^{-3}); (b) Silicate (mmol m^{-3}); (c) Nitrate (mmol m^{-3}); (d) Ammonium (mmol m^{-3}). Seasons as in Fig. 8.

biogeochemical state variables is homogeneous in space; therefore, any horizontal and vertical gradient is created by the interactions of the food web dynamics with the physical environment.

We show first (Fig. 15) the sea surface elevation fields as simulated by the model. The February map (Fig. 15a) shows a well-developed western coastal jet, stronger in the northern part of the basin, as found by the analysis of the observational data (Artegiani et al., 1997b). A strong cyclonic circulation dominates the middle Adriatic, while a weak flow develops in the southern portion of the basin. The cyclonic circulation persists in all months but shifts its center from the middle to the northern areas from winter to late summer and autumn. This is in general agreement with the hydrographic observations (Artegiani et al., 1997b) describing the structure of the Adriatic Sea baroclinic circulation. The intensity of the boundary jet along the western side decreases during summer (Fig. 15b), while it is large in winter and autumn. The jet does not extend further south than approximately 2/3 of the total length of the western coastline, probably due to the closed southern boundary. We believe that the dominant circulation features of the Adriatic Sea are reasonably well reproduced despite the coarse resolution, the idealization of the basin and the climatological forcing.



Fig. 15. Monthly mean simulated sea surface elevation for (a) February, (b) September, (c) December. The geostrophic circulation is indicated with arrows indicating the direction of the flow. The intensity of the flow is proportional to the gradients of the surface elevation.

Associated with this horizontal advective field, there is a non-uniform distribution of surface chlorophyll-*a* in the domain. In Fig. 16, we show the average chlorophyll-*a* distribution. We notice that north-south gradients develop together with east-west asymmetries characterized by larger biomass on the north-western sides of the model domain.

In order to highlight the role of the horizontal advective and diffusive processes we show in Fig. 17 maps of the February averaged rate of change in phytoplankton concentration induced by the horizontal advection (Fig. 17a), the horizontal diffusion (Fig. 17b) and by the biological processes (Fig. 17c). The biological processes determine the concentration difference between the northern and southern sector of the model domain. In the region of the western coastal jet, the negative advective rate of change indicates an export of the phytoplankton biomass towards southern regions of the model domain, thereby contributing to the generation of the east–west asymmetries. The horizontal diffusion rate of change is smaller than the advective rate and acts in the opposite direction.

Finally, the simulated surface chlorophyll-*a* concentrations are compared with surface pigment distributions as calculated from the CZCS satellite data, from which



Fig. 16. Monthly mean simulated surface distribution of chlorophyll-a (mg chl-a m⁻³) for (a) February, (b) September, (c) December of the model climatological year.

the monthly area averages of Fig. 1 were computed. In Fig. 18 we show the climatological (1979–1985) average for the three months of February, September and December, as shown also for the model results (Fig. 16). The qualitative similarity between the horizontal distributions indicates that the model reproduces the high phytoplankton biomass in the northern region affected by river runoff and the southward extension of high chlorophyll-*a* concentrations along the western side of the model domain due to horizontal advection. In the case of winter, a relative quantitative agreement can be found in the biomass concentrations. The model results for the summer season (September) show a good qualitative agreement with the CZCS picture giving indication of the low phytoplankton biomass concentrations in the open sea areas. It is important to note that both the CZCS and simulated fields show the highest values of chlorophyll-*a* in the northern part of the basin in December and lowest values in September in the southern region.



Fig. 17. February distribution of the simulated advective rate of change (a), horizontal diffusion rate of change (b), biological rate of change (c) acting on the surface phytoplankton carbon content. Units are mg C m⁻³ d⁻¹.

Average Pigments from CZCS, 1979-85



a: February b: September c: December Fig. 18. Monthly mean surface distribution of the simulated chlorophyll-a (mg chl-a m⁻³) for (a) February, (b) September, (c) December from CZCS.

5. Conclusions

This first modeling exercise has demonstrated the feasibility of coupling a general circulation model to a complex ecosystem model. Despite the idealized model set-up, the results have given strong indications that a clear seasonal cycle in the biogeochemical properties can be reproduced and that this is almost entirely dependent on the riverborne nutrient inputs from the Po and the seasonal and spatial variations of the physical environment.

Moreover, the model reproduces some of the particular characteristics of the Adriatic Sea phytoplankton seasonal cycle, such as the early surface production period (autumn to winter, rather than winter to spring, particularly in the northern Adriatic). In addition, horizontal surface trophic gradients are generated that are in qualitative agreement with the known characteristics of the surface biomass distribution of the Adriatic Sea. In the vertical, the model produces a temporal evolution of primary production processes related to the stratification/destratification cycle of the water column, more likely to be correct for the middle to southern Adriatic than in the northern Adriatic. This is probably due to the missing effects of light attenuation depending on the inorganic suspended matter vertical profile, which we cannot easily parameterize in the model.

We argue that the basic nutrient and primary production cycles in the Adriatic basin are driven firstly by the Po riverine nutrient inputs, pycnocline dynamics and horizontal advection changes.

Despite the correct simulation of some features, the model still has many weak points. The physical model, for instance, has shown a bias of a few degrees in the temperature cycle simulation that is probably due to the closed southern boundary. The nitrate concentrations appear higher than the climatological values, and this is a consequence of the biogeochemical dynamics and the absence of a southern open boundary (corresponding to the Otranto channel) which eliminates the nutrient exchanges occurring between the Adriatic and the Ionian Sea. In terms of biogeochemical dynamics the model seems to produce phosphorus limitation, and the development of diatom populations determines also strong silicate uptake.

In the ecosystem model, finally, we believe that there is an important missing effect connected with the penetration of light in the water column. This is due to the lack of data necessary to specify the suspended sediment concentration affecting the extinction of light. In fact, the silt concentration in the model is probably underestimated. These aspects probably determine the discrepancies between data and model behavior described in Section 4.2 and in the future will deserve a close scrutiny in order to improve the model simulations.

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Appendix A

The POM model integrates the Navier–Stokes equations in the rotating earth frame under the Boussinesq, incompressible and hydrostatic approximations. Furthermore, we consider full thermodynamic processes in the water column, including temperature and salinity effects.

The equations are then written as

$$\frac{D}{Dt}\mathbf{U}_{h} + f X \mathbf{U}_{h} = -\frac{1}{\rho_{0}} \nabla_{h} p + F_{\mathbf{U}_{h}}, \qquad (A.1)$$

$$\frac{\partial p}{\partial z} = -\rho g, \tag{A.2}$$

$$\nabla \cdot \mathbf{U} = \mathbf{0},\tag{A.3}$$

$$\rho = \rho(\theta, S, p), \tag{A.4}$$

$$\frac{D\theta}{Dt} = F_{\theta} - \frac{\partial I}{\partial z},\tag{A.5}$$

$$\frac{DS}{Dt} = F_S,\tag{A.6}$$

where $\mathbf{U} = (u, v, w)$; $\mathbf{U}_{h} = (u, v)$; $\mathbf{f} = 2\Omega \sin \vartheta k$; where ϑ is the latitude, \mathbf{k} is the unit vector in the *z* direction and the symbol "X" in (A.1) indicates a vector product, ρ_{0} is the constant density $\mathbf{V} = (\partial/\partial x, \partial/\partial y, \partial/\partial z)$, $\mathbf{V}_{h} = (\partial/\partial x, \partial/\partial y)$, $D/Dt = \partial/\partial t + \mathbf{U} \cdot \mathbf{V}$, ρ is the density field, *p* is the pressure, *g* is the gravity, θ and *S* are the potential temperature and salinity fields, and *I* is the solar radiation penetrating the water column, supposed to be of the form

$$I = Q_s(\rho_0 C_p)^{-1} T_r e^{-\lambda z}$$

Here C_p is the water specific heat, T_r is the transmission coefficient for heat (taken to be 0.71); Q_s is the incoming solar radiation (in W m⁻²) at the surface, and λ is the short wave extinction coefficient considered from Jerlov (1976) to correspond to clear

waters ($\lambda = 0.042 \text{ m}^{-1}$). The F terms in (A.1), (A.5) and (A.6) represent the turbulent flux divergences, and they are written as

$$F_{u} = \frac{\partial \tau_{xx}}{\partial x} + \frac{\partial \tau_{yx}}{\partial y} + \frac{\partial \tau_{xz}}{\partial z},\tag{A.7}$$

$$F_v = \frac{\partial \tau_{xy}}{\partial x} + \frac{\partial \tau_{yy}}{\partial y} + \frac{\partial \tau_{zy}}{\partial z},\tag{A.8}$$

$$F_{\theta} = \frac{\partial \tau_{\theta x}}{\partial x} + \frac{\partial \tau_{\theta y}}{\partial y} + \frac{\partial \tau_{\theta z}}{\partial z},\tag{A.9}$$

$$F_{S} = \frac{\partial \tau_{Sx}}{\partial x} + \frac{\partial \tau_{Sy}}{\partial y} + \frac{\partial \tau_{Sz}}{\partial z}, \tag{A.10}$$

where τ_{ij} is the symmetric tensor representing the Reynolds stresses. As usual for the ocean, the horizontal turbulent stresses are treated differently from the vertical ones. The horizontal turbulent stresses are parameterized with the Smagorinsky scheme (Smagorinsky, 1993) and the vertical ones with the Mellor–Yamada scheme (Mellor and Yamada, 1983), which solves two equations, one for the turbulent kinetic energy and the second for mixing length, and provides the vertical diffusion coefficients for the momentum and the scalar properties $K_{\rm M}$ and $K_{\rm H}$, to which a constant background diffusivity $K_{\rm MOL} = 10^{-5} \, {\rm m}^2 \, {\rm s}^{-1}$ is added.

The boundary conditions to solve the Eqs. (A.1)-(A.10) are as follows:

(a) at the surface, $z = \eta$, we impose

$$w = 0, \tag{A.11}$$

$$K_{\rm H} \frac{\partial \theta}{\partial z} = \left[(1 - T_r)Q_S - Q_{\rm B} - Q_{\rm H} - Q_{\rm E} - \frac{\partial Q}{\partial \theta} (\theta - \theta^*) \right] (\rho_0 C_p)^{-1}, \tag{A.12}$$

$$\boldsymbol{S} = \boldsymbol{S}^*(\boldsymbol{x}, \boldsymbol{y}, \boldsymbol{t}) \tag{A.13}$$

$$K_{\rm M} \, \frac{\partial \mathbf{u}_{\rm h}}{\partial z} = \mathbf{\tau}_{\rm w}.\tag{A.14}$$

In (A.12), $Q_{\rm S}$ is the short wave radiation flux, $Q_{\rm H}$, $Q_{\rm E}$, $Q_{\rm B}$ are the sensible, latent and long-wave radiation fluxes emitted at the surface (in W m⁻²), θ is the model predicted sea surface temperature, θ^* is a climatological seasonally varying sea surface temperature, and $\partial Q/\partial \theta$ is taken to be 40 W m⁻² °C⁻¹ (Oberhüber, 1988); then $(\partial Q/\partial \theta)(\theta - \theta^*)$ is a heat flux correction term introduced to avoid excessive cooling/heating of the sea surface. In (A.13) S^* is climatological seasonally varying sea surface salinity. In Eq. (A.14) $\tau_{\rm W}$ is the wind stress (b) at the bottom, z = -H (bottom depth)

$$w = -\mathbf{u}_{\mathbf{h}} \cdot \nabla H, \tag{A.15}$$

$$K_{\rm M} \frac{\partial \boldsymbol{u}_{\rm h}}{\partial z} = \boldsymbol{\tau}_{\rm B},\tag{A.16}$$

$$K_{\rm H} \frac{\partial \theta}{\partial z} = K_{\rm H} \frac{\partial S}{\partial z} = 0. \tag{A.17}$$

In Eq. (A.16) $\tau_{\rm B}$ is the bottom stress, which is supposed to be quadratic and with a drag coefficient depending on a logarithmic boundary layer law, e.g.,

$$C_{\rm D} = \left[\frac{1}{k} \ln \frac{H + z_{\rm b}}{z_0}\right]^{-2},\tag{A.18}$$

where k is the Von Karman constant, z_b is the height of the nearest point to the bottom and z_0 is the bottom roughness length (0.01 m).

The model works with a time step of 108 s for the external mode and a time step of 4370 s for the full baroclinic equations. The coupling between ERSEM and POM is done at the level of the internal mode time step, where for the 27 ERSEM variables a "physical" rate of change is calculated, e.g.:

$$\left. \frac{\partial C}{\partial t} \right|_{\text{phys}} = \frac{\partial C}{\partial t} + \mathbf{U} \cdot \nabla C - F_{\text{c}}. \tag{A.19}$$

Here C is the concentration and F_c is the divergence of turbulent eddy fluxes, mixing and dispersing the tracers, of the same form used for salinity (see (A.10)).

The 27 pelagic state variables of the model are:

- 1. for the nutrients: phosphate, nitrate, ammonium, and silicate.
- 2. for the gases: oxygen, carbon dioxide.
- 3. the carbon, phosphorus, nitrogen and silicon components of: detritus and diatoms. The carbon, phosphorus and nitrogen components of: flagellates, microzooplankton, heterotrophic nanoflagellates and bacterioplankton.
- 4. the carbon component of mesozooplankton.

Land based nutrient fluxes (river input) are applied at the sea surface only through the definition of the following surface ($z = \eta$) boundary condition:

$$K_{\rm H} \frac{\partial N}{\partial z} = R N_{ij} \frac{\delta(x - x_i)\delta(y - y_j)}{\Delta x_i \,\Delta y_j},\tag{A.20}$$

where N is the surface nutrient (phosphate, nitrate, ammonia and silicate), R and N_{ij} are the annually averaged Po river discharge and river water nutrient concentration respectively, δ is the Dirac function which is = 1 only if $x = x_i$ and $y = y_j$. The subscripts *i*, *j* indicate here the grid point representing the river estuary and $\Delta x_i \Delta y_j$ indicates the surface area pertinent to the estuary grid point.

The vertical light penetration in ERSEM is computed by an exponential decay equation that utilizes extinction coefficients (λ_{tot}) calculated as follows:

$$\lambda_{\rm tot}(x, y, z, t) = \lambda + \beta_{\rm p} P(x, y, z, t) + \beta_{\rm b} B(x, y, z, t) + \beta_{\rm d} D(x, y, z, t) + \beta_m M$$
(A.21)

where λ is the Jerlov (1976) extinction coefficient for clear water, P, B, and D are the phytoplankton, bacteria and organic detritus (carbon content) concentrations respectively, and M is the inorganic suspended matter (silt) concentration. The β 's are specific coefficients for the different groups of particulate material considered.

The pelagic state variables are coupled with the benthic state variables through a molecular diffusive flux of nutrients from the pore waters to the water column. In the benthic compartment the model computes nutrient and particulate organic matter concentrations and parameterizes the benthic animal functional groups.

After Eq. (A.19) has been calculated, the following equation is integrated:

$$\frac{\partial C}{\partial t}\Big|_{\text{tot}} = \frac{\partial C}{\partial t}\Big|_{\text{phys}} + \frac{\partial C}{\partial t}\Big|_{\text{bio}},\tag{A.22}$$

where $\partial C/\partial t|_{bio}$ represents the set of biogeochemical interactions constituting ERSEM and described by Baretta et al. (1995).

The solution is found with an Euler forward time integration scheme, which requires time step cutting in case a preset time rate of change of one of the biogeochemical variables is exceeded. During time step cutting physics $\partial C/\partial t|_{phys}$ is held constant.

Time step cutting occurs when the integration of the biogeochemical state variables with the physical time step would produce negative concentrations or, conversely, when the calculated time rate of change would produce a doubling of the biomass within one time step.

During the numerical experiments it was found that the calculation of $\partial C/\partial t|_{phys}$ can produce (limited) negative concentrations, because the numerical scheme used to compute Eq. (A.22) is not positive definite (e.g. it can generate negative concentration values). A correction of this numerical problem will involve the use of a positive definite numerical scheme. To obviate this problem during the execution of the numerical simulations described in the present paper, negative concentrations were corrected to a small positive value, and the extra amount of mass (carbon, nitrogen, phosphorus and silicon) introduced was tracked during the execution time. In all the simulations the total amount of mass introduced was always well below 1% of the total amount of mass defined by the initial conditions.

For a detailed description of the ERSEM equations the reader should refer to the publications quoted in the introduction or to Vichi et al. (1998c). However, since the present study deals mainly with the phytoplankton production processes we provide here some information about the ERSEM algorithms describing the primary production (see Varela et al., 1995).

The temporal rate of change of phytoplankton carbon content, $\partial P_c/\partial t$, determined by the carbon fixation, $\partial P_c/\partial t|^{\text{pp}}$, and respiration, $\partial P_c/\partial t|^{\text{rsp}}$, processes is given by

$$\frac{\partial P_{\rm c}}{\partial t} = \frac{\partial P_{\rm c}}{\partial t} \bigg|^{\rm pp} - \frac{\partial P_{\rm c}}{\partial t} \bigg|^{\rm rsp}. \tag{A.23}$$

The carbon fixation is defined as follows:

$$\frac{\partial P_{\rm c}}{\partial t} \bigg|^{\rm pp} = r_{P_{\rm c}} P_{\rm c}, \tag{A.24}$$

where r_{P_c} is the specific growth rate, written as

$$r_{P_s} = r_{\max} f^{\mathrm{T}} f^{\mathrm{I}} f^{\mathrm{s}} \tag{A.25}$$

 r_{max} is the maximum potential phytoplankton specific growth rate (set for diatoms and flagellates to 2.5 and 2.0 d⁻¹, respectively), regulated by non-dimensional regulation factors that are function of temperature (f^{T}), light (f^{I}), and (for diatoms only) silicate concentration (f^{s}).

 $f^{\rm T}$ is defined by a characteristic temperature coefficient, Q_{10} , chosen to be 4.0 for both phytoplankton functional groups, and at the reference temperature $T_0 = 10^{\circ}$ C. f^1 is computed according to Steele (1962), and f^s is computed with a Michaelis-Menten relation utilising a half saturation value for silicate of 0.3 mmol Si m⁻³.

The phytoplankton respiration is defined by the following equation:

$$\frac{\partial P_{\rm c}}{\partial t} \bigg|^{\rm rsp} = (a+b)P_{\rm c},\tag{A.26}$$

where b is the rest respiration rate:

$$b = b_{\text{const}} f^{\mathrm{T}} \tag{A.27}$$

and b_{const} is set to 0.25 d⁻¹ for diatoms and to 0.15 d⁻¹ for flagellates. *a* is the activity respiration specific rate defined as the difference between the specific growth rate and the exudation specific rate depending on nutrient stress:

$$a = \gamma \alpha f^{\text{nutr}} r_{P_{\text{c}}} \tag{A.28}$$

 γ is set to 0.1 d⁻¹ for diatoms and to 0.25 for flagellates, and α is set to 0.05 for diatoms and to 0.2 for flagellates. f^{nutr} is either $f^{\text{n.p.s}}$ or $f^{\text{n.p.}}$.

The regulation factors $(f^n \text{ and } f^p)$, depending on the availability of nutrients (phosphorus and nitrogen) other than silicate, are considered only in the computation of the phytoplankton catabolic carbon losses and (as stated in the introduction) are computed following the Droop (1973,1975) assimilation kinetics as formulated by Nyholm (1977a,b).

The joint nutrient limitation effect of nutrients $(f^{n,p})$ is computed as

$$f^{n,p} = (f^n f^p)^{1/2}.$$
 (A.29)

$$f^{n,p,s} = \min(f^{n,p}, f^s).$$
 (A.30)

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