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Seasonal modulation of microbially mediated carbon fluxes in the northern Adriatic Sea — a model study

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ABSTRACT

A model study of the seasonal changes in the food web structure of the northern Adriatic Sea is presented. A 1–D ecosystem coupled model (POM/ERSEM) forced with climatological functions has been applied at two different station locations in the northern Adriatic Sea, one under the direct influence of the Po river inflow and one representing a more open sea situation. The ability of the model to reproduce the main physical and biogeochemical patterns allows us to study the underlying carbon fluxes, which determine these features. Analysis of the seasonal carbon-transfer pathways among the main trophic levels shows a possible seasonal modulation at both stations, but a different food web development. It seems that the prevailing path could be related to the seasonal variability of the water column (nutrient input and/or vertical stratification). Moreover, results from this numerical experiment suggest that the northern Adriatic shallow coastal area has a predominantly multivorous food web and has significant microbial recycling, even if this latter pattern is not so evident as in open sea areas.

Key words: carbon cycle, ecosystem model, food web structure, microbial loop, northern Adriatic

INTRODUCTION

The ecosystem dynamics of the Adriatic Sea is poorly known despite a significant scientific effort. This probably depends on the very different trophic characteristics of the major Adriatic Sea sub-basins, ranging from mesotrophic to oligotrophic conditions. The northern Adriatic, in particular, shows strong spatial and temporal variability of trophic conditions. Coastal areas are particularly affected by significant and sometimes persistent events of eutrophication related to the relevant river discharges. The most important freshwater source is the Po river, which attains a mean flow rate of about 1500 $m^3 s^{-1}$. The flow rate shows two characteristic climatological peaks in spring and in autumn, related to the abundance of the rainfall and snow melting in the Alps (Raicich, 1994). The freshwater seasonal signal interacts with the seasonal variability of the wind and heat flux forcing, giving rise to a complex circulation pattern depicted in Fig. 1 (Artegiani *et al.*, 1997a, 1997b).

The climatological biogeochemical seasonal characteristics have been described by Zavatarelli *et al.* (1998b). The Po river influence is relevant in all the main biogeochemical cycles, determining nutrient availability and changing the light absorption characteristics of waters. From the biological point of view, the north-western area shows seasonal phytoplankton blooms in which the dominant species (diatoms and/or flagellates) have been very variable over the years (Boni and Solazzi, 1989).

The main aim of the present work is to understand how the seasonal signals derived from the Po river inflow and from the vertical structure of the water column influence the material exchanges within the trophic web. The Adriatic Sea is a coastal ecosystem with important river run-off influences and here we want to look, in particular, at the complex pathways of carbon flux in the development of the seasonal food web. To examine these kinds of interactions, we have applied a 1–D ecosystem model in two areas of the northern Adriatic Sea, corresponding to the S1 and S3 stations (Fig. 1) of the PRISMA-I Italian project (Programma di Ricerca e Sperimentazione sul Mare

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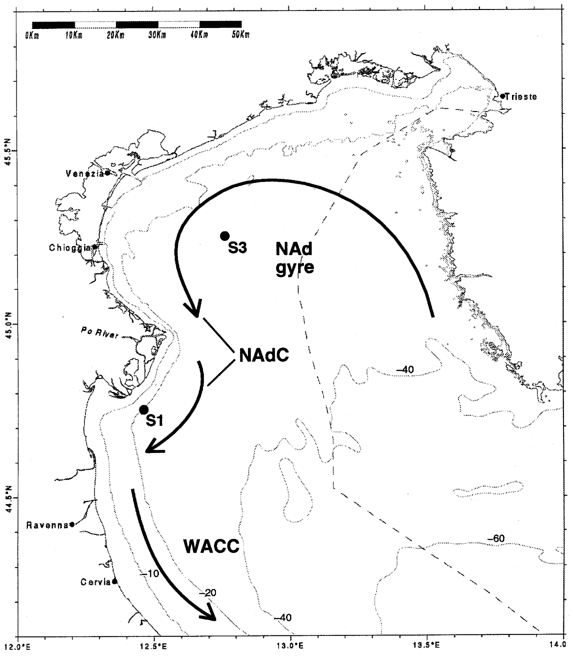
Figure 1. Bathymetry of the northern Adriatic Sea, with the general circulation patterns and station locations. Curved arrows indicate the surface flow field directions from climatological studies. NAdC, Northern Adriatic Current; WACC, Western Adriatic Coastal Current. The S1 station is directly influenced by the Po river input and it is at the limit of the NAd Current influence. The S3 station is representative of the northern Adriatic Gyre circulation pattern.



Adriatico). The two stations have been chosen because they exhibit similar seasonal vertical hydrodynamical variability, but they have different relationship with the Po river inflow. Figure 1 shows the position of the two stations: the S1 station is directly influenced by the allocthonous input from the Po river and is stratified for much of the year due to the freshwater input; the S3 station is inserted in the Northern Adriatic Current circulation system some distance from freshwater nutrient input and is well mixed during the winter.

The ERSEM ecosystem model (Baretta *et al.*, 1995; Baretta-Bekker *et al.*, 1997) coupled with the POM hydrodynamical model (Blumberg and Mellor, 1987) is briefly described below. A comparison of the carbon fluxes calculated at the two stations with a climatological implementation of the model is then presented and discussed.

MODEL DESCRIPTION

The coupling of the European Regional Seas Ecosystem Model (ERSEM, Baretta *et al.*, 1995; Baretta-Bekker *et al.*, 1997) with the Princeton Ocean Model (POM; Blumberg and Mellor, 1987) has been tested in different areas of the Adriatic Sea by several authors (Allen and Blackford, in press.; Allen *et al.*, 1998; Zavatarelli *et al.*, 1998a) and for the S1 station by Vichi *et al.* (1998a;b). The 1–D version of POM solves the primitive equation of motion calculating the vertical fields of velocity, temperature, salinity and the turbulent diffusion coefficients using the Mellor–Yamada 2.5 turbulence closure scheme (Mellor and Yamada, 1982).

The ERSEM version used in this work is version 11, also called ERSEM II (Baretta-Bekker *et al.*, 1997) and is a biomass-based ecosystem model. The basis of the model is to resolve the material exchanges in the trophic web by providing several pathways between the different ecosystem components considered as functional groups. Thus, even if some of the parameters characterizing the cellular physiology are fixed, the food web can dynamically adjust to different situations by channelling the material fluxes to different functional groups. ERSEM can be subdivided in two main parts, one resolving the dynamics of the pelagic system (different groups of phytoplankton, bacteria, microzooplankton and mesozooplankton, as well as nutrient and oxygen dynamics), and one describing the benthic food web and the early diagenetic processes. A list of all the model state variables is given in Baretta *et al.* (1995), the more important ones for this work being summarized in Table 1. A detailed description of the single-functional-group parametrizations can be found in Baretta-Bekker *et al.* (1995) for the microbial loop, Broekhuizen *et al.* (1995) for the mesozooplankton, Ebenhöh *et al.* (1995) for the benthos and Ruardij and Van Raaphorst (1995) for the nutrient dynamics in the sediments. The most recent improvements in the model can be found in Baretta-Bekker *et al.* (1997); these concern the nutrient dynamics in the phytoplankton functional group and the bacterial ability to take mineral nutrients directly from the water as a function of their internal carbon-to-nutrient ratios.

Model set-up and forcing functions

The water column depth is 20 m for the S1 station and 29 m for the S3 station. The number of vertical model levels at each station is 20, implemented with a depth-varying vertical distribution. The depth of the first layer is 0.15 m, the depth is then increasing logarithmically until the mid-depth of the water column where it becomes uniformly 1.3 m. The 20th level is

Table 1. Pelagic ERSEM state variables and components implemented in the simulation and aggregated groups for the carbon fluxes simulation. The material flow through the ERSEM trophic chain is expressed in terms of carbon, nitrogen, phosphorus and silica.

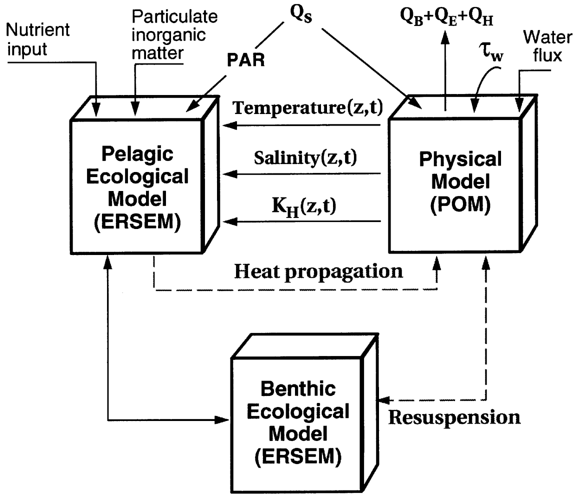
ERSEM functional groups	Aggregated groups for carbon fluxes experiment
P1 = Diatoms *(P1c, P1n, P1p, P1 s)*	AUTOTROPH = [*P1c, P2c, P3c*]
P2 = Flagellates *(P2c, P2n, P2p)*	
P3 = Picophytoplankton *(P3c, P3n, P3p)*	
Z4 = Omnivorous *(Z4c, Z4n, Z4p)*	HETEROTROPH = [*Z4c, Z5c, Z6c*]
Z5 = Microzooplankton *(Z5c, Z5n, Z5p)*	
Z6 = Heterotrophic flagellates *(Z6c, Z6n, Z6p)*	
B1 = Bacteria *(B1c, B1n, B1p)*	BACTERIA = [*B1c*]
N1p = Phosphate	
N3n = Nitrate;	
N4n = Ammonium	
N5s = Silicate	
R1 = Dissolved Organic Matter *(R1c, R1n, R1p)*	DOC = [*R1c*]
R6 = Particulate Organic Matter *(R6c, R6n, R6p)*	POC = [*R6c*]
O2o = Dissolved oxygen	
O3c = Dissolved carbon dioxide	

the bottom, where all the interaction fluxes with the sediments are calculated.

A schematic view of the interactions between different submodels and forcing functions is given in Fig. 2 as a box diagram. Each box represents a set of differential equations and it exchanges information with the other boxes depending on the external forcing functions (see the figure legend for an explanation of symbols). The physical forcing functions at the station locations (wind stress and heat flux) were obtained from the ECMWF (European Centre for Medium-range Weather Forecast) meteorological re-analysis data relative to the period 1982–1993. The water flux was calculated using surface salinity climatological data extracted from the Adriatic BiogeoChemical Dataset (ABCD, Zavatarelli *et al.*, 1998b) and imposed with a relaxation boundary condition for the salt flux. All the forcing functions have been applied as linear interpolations of monthly mean data and then repeated for each year of integration to give a perpetual yearly cycle.

The major forcing for the pelagic ecological model is the input of nutrients from the Po river. Unfortunately, it is not possible to obtain monthly means of nutrient discharge, because the time series of observations are discontinuous and the time gaps in the measurements can severely bias the mean. So as to impose a nutrient flux, we considered the relaxation surface boundary condition used for salinity, and we have computed the seasonal mean of surface nutrient concentrations from the ABCD data set, considering two areas surrounding the S1 and S3 stations. Seasonal means are calculated considering a 3 month time window centred on February, May, August and

Figure 2. General scheme of the model coupling and forcing functions. The Physical Model calculates the vertical fields of temperature (*T*), salinity (*S*) and turbulent diffusion coefficient (K_H), and the hydrodynamical forcing functions are: water flux; wind stress (τ_w); radiative flux (Q_s); evaporation, latent heat and short wave radiation fluxes (Q_E, Q_H and Q_B). The Pelagic Model is forced by the solar radiation (corrected by a Photosynthetically Available Radiation factor) and nutrient and particulate inorganic suspended matter input. Dashed arrows represent processes that are not yet implemented in the model, such as sea bed resuspension and the response of the physical environment to the biological light adsorption in the water column.



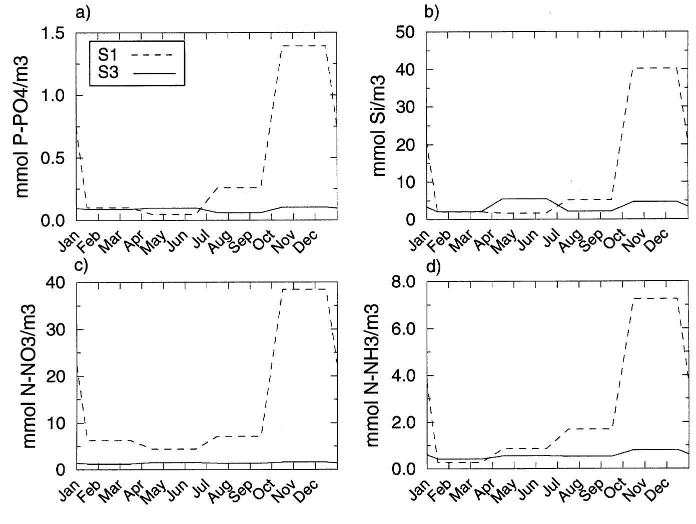


Figure 3. Seasonal surface boundary conditions for nutrients at S1 and S3 (from the ABCD data set). (a) Phosphates; (b) silicates; (c) nitrates; (d) ammonium.

November. The seasonal surface nutrient concentrations depicted in Fig. 3 have been used as surface relaxation boundary conditions for the nutrient equations. Figure 3 also shows the different control of the river inflow on the surface nutrients at the two stations. S3 has relatively constant surface concentrations throughout the year; S1 has a higher variability, especially related to the autumn discharge. The absence of a spring nutrient peak at S1 (Fig. 3), related to the climatological maximum in the Po river run-off, probably results from the lack of data. The surface nutrient concentrations, especially for nutrients with low turnover times such as phosphate, is in fact the final value of the interaction between physical processes and biology, and the data gaps may bias the surface values of such biogeochemical components. Because of these considerations, the analysis of the results was carried out for the winter, summer and autumn periods.

The last forcing function considered in the pelagic model (Fig. 2) is the concentration of inorganic suspended matter, which has been shown to be crucial for the correct simulation of the phytoplankton seasonal cycle, especially in river-dominated areas (Vichi *et al.*, 1998b). In the numerical experiments, we used the same forcing functions for the S1 station as in Vichi *et al.* (1998b), and a stationary and uniform estimation value of 2 g m^{-3} for the S3 station. The porosity parameters of the benthic model and other related parameters have been calibrated on this area. The S3 sediments are characterized by a porosity of 0.4, while at S1 the sea bed is classified as silty clays with a porosity of 0.7. Following these values and according to Ruardij and Van Raaphorst (1995), the phosphate absorption coefficients have been set to 100 for the S3 station and 400 for S1.

DESCRIPTION OF NUMERICAL EXPERIMENT

The model was run for 3 years for the two stations and the results from the last year of integration are shown here. The steady state is reached for the physical variables and primary producers, but for the nutrient bottom concentrations we have an increase, owing to the continuous nutrient input and the absence of parametrization of lateral advection.

Vertical distribution of hydrological and biogeochemical properties

In Fig. 4 the comparison between the simulated seasonally averaged vertical profiles and the corresponding observations from the ABCD data set are shown for winter and summer. The model/observed data agreement is significant for both stations, all the main vertical distribution patterns being well matched. The model is able to reproduce the strong mixing which takes place during winter at S3 but fails to maintain the density stratification as strongly as in the observed S1 data. During winter, the agreement between the S3 simulated nutrient concentrations and the observed data is much higher than at S1, probably due to the high remineralization processes occurring at S1 which are not simulated as realistically.

During summer, the disagreement between the simulations and the observations for the S3 station seems to concentrate in the lower part of the water column, giving rise to a strong bottom concentration of phosphate (Fig. 4b). This is probably related to the low activity of the S3 sediments, characterized by carbonatic sediments with low sedimentation rates and high phosphate retention. The model uses

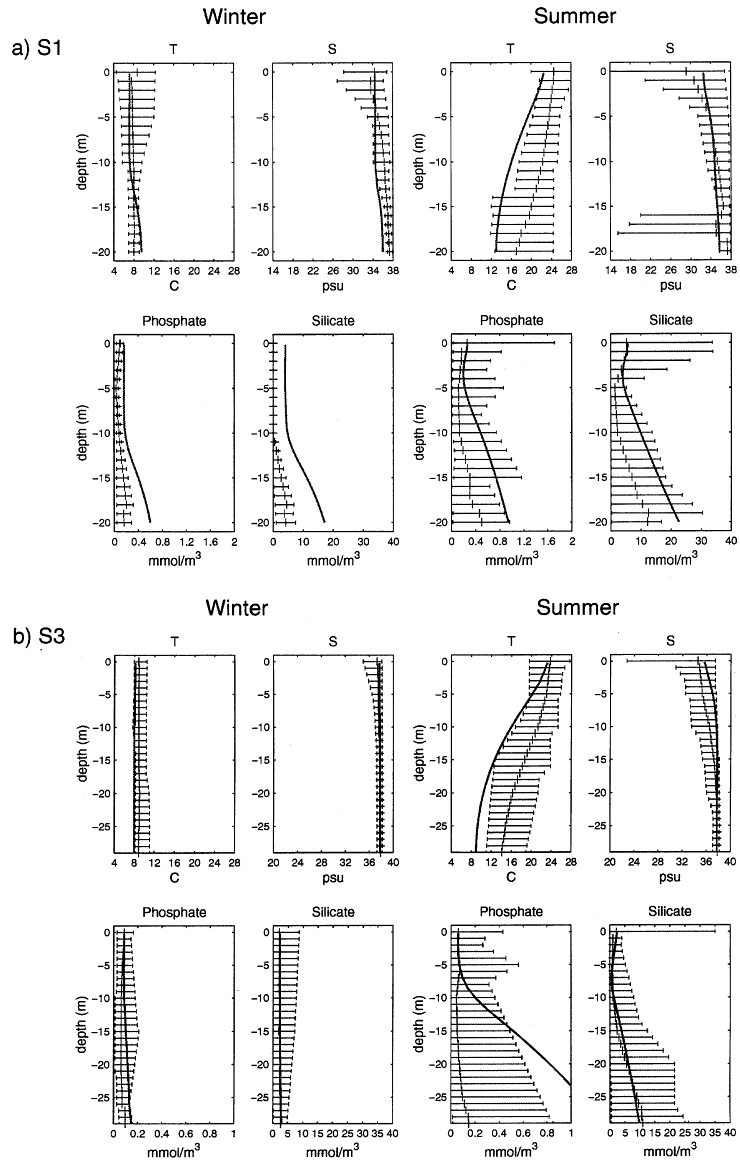


Figure 4. Model and observed data comparison at S1 (a) and S3 (b) for temperature, salinity and nutrients in winter and summer. The continuous line is the simulated seasonal mean. The climatological observed means are shown with the range of variability.

empirical equations by Ruardij and Van Raaphorst (1995) to compute the phosphate absorption coefficients from porosity, but in future this may need to be better tuned to S3 sediments.

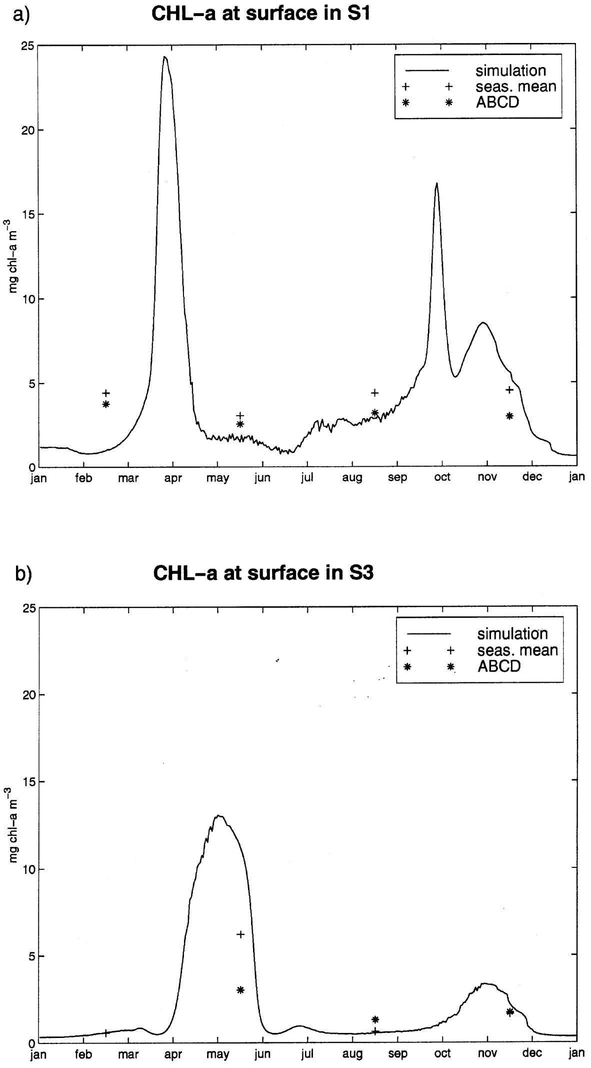
Phytoplankton seasonal cycle

Because data regarding the vertical phytoplankton distribution (biomass or chlorophyll *a* concentration) are not available, the previous comparison of simulations with observations was not possible. Data are available only at the surface and Fig. 5 shows the comparison for S1 and S3. The model qualitatively produces a seasonal bloom pattern known to exist in the northern Adriatic Sea (Gilmartin and Revelante, 1983). The phytoplankton blooms are similar for the model and observations, with maxima in spring and autumn. The simulated seasonal mean is overestimated for both stations, especially at S3 during the spring (Fig. 5b), but the agreement in biomass fluctuations at the seasonal level is significant. The time shift between S1 and S3 spring peaks is related to the different station locations and thus to the different morphology and forcing functions. These differences can be seen also in the dominant species of the bloom (not shown), diatoms at S1 and flagellates at S3.

Carbon fluxes

It is well established that the standing stock biomasses are not always a measure of the activity of a marine

Figure 5. Simulated surface chlorophyll concentration at S1 (a) and S3 (b). The seasonal mean computed from the numerical experiment (+) is compared with the corresponding value from observations (*).



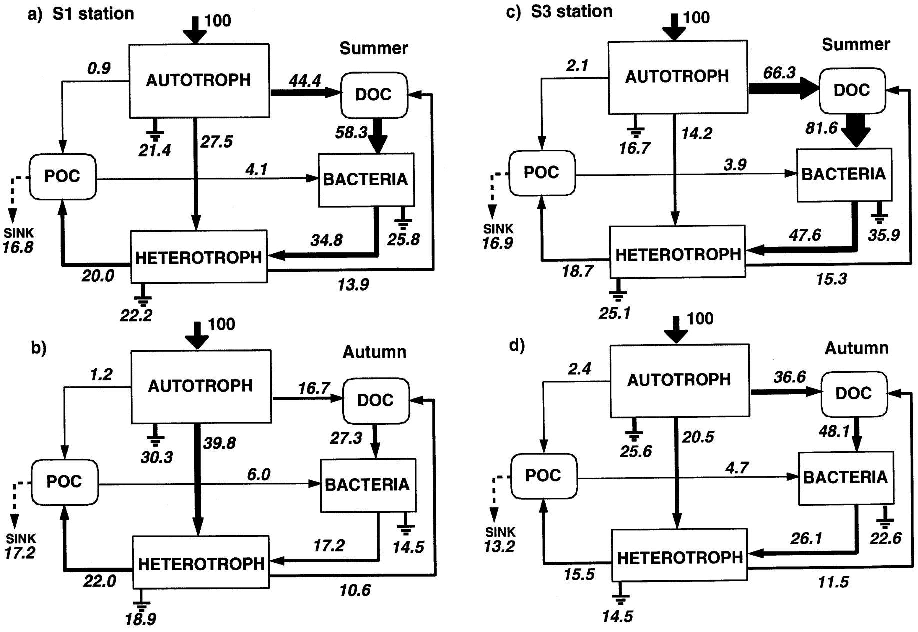
trophic web. Biomasses are only the macroscopic effect of an almost continuous exchange of matter acting on a wide range of time scales. Numerical simulations allow these exchanges to be explored, provided there is a degree of similarity between simulation and observations. Above, we have shown the capability of the present model to reproduce the main seasonal patterns of nutrients. The simulated chlorophyll concentrations were also roughly in agreement with known distributions. Thus the analysis of the carbon fluxes between functional groups may be taken to be a reasonable representation of the processes producing the observed nutrient and biomass distributions.

While running the model, we kept a continuous record of all the carbon fluxes among the model functional groups, similar to the analysis of Baretta-Bekker *et al.* (1998). The analysis has been restricted to the uppermost part of the water column so as to separate the processes occurring in the surface layers from the bottom, which exhibits more complex dynamics due to the sediment remineralization processes. The approximate depth of the pycnocline during summer has been chosen as the threshold level, this being at 5 m depth for S1 and 7 m for S3. All the fluxes have been integrated vertically, and then seasonally averaged in units of mg C m^{-2} per season. The results have been aggregated to highlight the interactions between the main trophic levels. Autotrophic and heterotrophic compartments have been defined, grouping together some of the model state variables as shown in Table 1. Their carbon exchanges with the bacteria and dissolved/particulate organic carbon pools have been analysed, cross-comparing the two stations and different seasons. All fluxes have been normalized to the seasonal gross primary production. The results for summer and autumn at both stations are shown in Fig. 6.

During summer (Fig. 6a), the major carbon flux at S1 is from DOC to bacteria. This flux is a consequence of the strong release of dissolved carbon by primary producers. Bacteria redirect carbon to the CO_2 pool and to the heterotroph compartment; the latter is comparable to the classical herbivorous pathway from autotrophs to heterotrophs, highlighting an important ecological role of bacteria during this period. During autumn (Fig. 6b) at S1, the model shows a rearrangement of the fluxes in the trophic web. The main exchange is now from primary producers to the consumers' pool and the autotrophic release of DOC is less than half that of the summer.

A possible explanation of the shift can be found by analysing the DOC dynamics together with the dynamics of nutrients, in particular with phosphorus. Figure 7(a) shows the quality (expressed as C:P ratio) of the total dissolved organic matter produced by the functional groups of the trophic web during the simulation. For most of the year, and particularly during the stratified periods (Fig. 4), the quality of the DOM at S1 (Fig. 7a) is above the line that represents the C:P Redfield ratio (106). This curve can be interpreted as a result of the interaction between the main forcing functions and the biology, highlighting the phosphorus limitation of the area. Because bacteria in the model need a higher amount of phosphorus than do phytoplankton, the poor

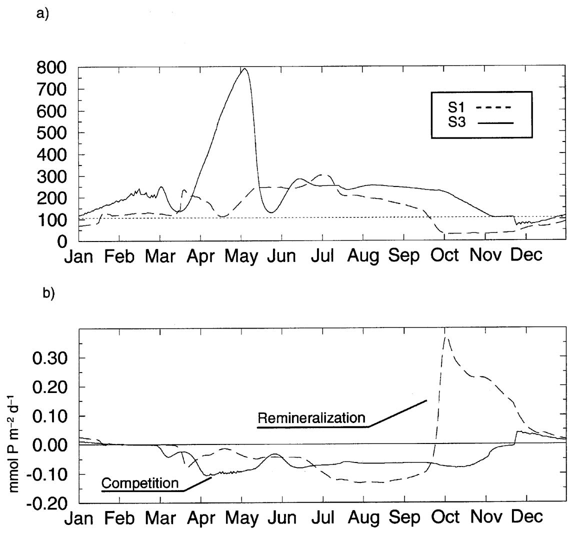
Figure 6. Simulated carbon fluxes at the S1 (a and b) and S3 (c and d) aggregated trophic webs during summer and autumn. The fluxes are normalized to the seasonal primary production and the arrow thickness is proprtional to the flux. The 'ground' symbol represents the respiration flux to the CO_2 pool. Total primary productions (tPP) are, respectively: (a) tPP = 164 gC m^{-2} per season; (b) tPP = 59 gC m^{-2} per season; (c) tPP = 76 gC m^{-2} per season; (d) tPP = 48 gC m^{-2} per season.



nutrient content of the DOM forces bacteria to uptake dissolved phosphate, starting a competition with phytoplankton (Fig. 7b). This behaviour, which is a direct consequence of the bacterial functional equation (Baretta-Bekker *et al.*, 1997), enhances the phosphorus limitation and leads to further production of P-depleted dissolved organic matter. Hence during summer there are no favourable conditions for the herbivorous transfer pathway, and the microbial food web becomes more prevalent. At the end of summer, when the Po river signal gives the higher peak in the surface phosphorus concentration (Fig. 3a, dashed line), the quality of the DOM rapidly increases, and the bacteria change their behaviour to become phosphorus remineralizers (Fig. 7b). Both the river input and the bacterial remineralization enhance the carbon assimilation by phytoplankton and the direct transfer of organic matter to higher trophic levels through the herbivorous chain (Fig. 6b).

Station S3 shows a similar seasonal shift in carbon-transfer pathways, but with some substantial differences. During summer (Fig. 6c), there is an important microbial mediation of the carbon fluxes, which transfers to the heterotroph compartment almost 50% of the carbon entering the system. In autumn (Fig. 6d) the situation becomes more com-

Figure 7. (a) Quality of the production (rate) of dissolved organic matter expressed as C:P ratio at S1 (dashed line) and S3 (continuous line). The horizontal line represents the C:P Redfield ratio (106), thus when the curves are above the line the DOM is P-depleted. (b) Phosphate flux at the bacterial trophic level; a positive flux indicates bacterial remineralization, while a negative flux indicates direct uptake of dissolved phosphate from the waters and thus competition with phytoplankton.



plex: the major flux is again from the DOC pool to bacteria, but the exchange between the autotrophic and heterotrophic compartments is comparable to the one from bacteria to heterotrophs. Thus the trophic patterns are different at S3 compared with S1, because the herbivorous food web never dominates, but a more open ocean structure with both microbial and herbivorous food webs seems to prevail. The analysis of the quality of the dissolved organic matter at S3 confirms this interpretation. Figure 7(a) shows the persistence throughout the year of phosphorous limitation, with a higher peak in correspondence with the flagellate spring bloom (Fig. 5b). Hence bacteria take up phosphorus directly from the dissolved inorganic pool (Fig. 7b), exacerbating the nutrient limitation of phytoplankton which is unable to complete the assimilation of carbon. Some small changes in the quality of DOM seem to start at the end of the summer, probably when a relatively higher amount of phosphate is available in the system (Fig. 3a).

Considering sensitivity analysis, we imposed a spring nutrient peak equivalent to that in the autumn (Fig. 3) to all inorganic compounds at the surface at S1. We found that the carbon cycling scheme shown in Fig. 6 can change at the S1 station. In particular, the microbial loop path at S1 was diminished in amplitude during summer owing to the higher phosphorous concentration available. The flux of carbon through the bacterial compartment remained consistent, but the proportion between the herbivorous and the bacterial path was 2:1. This means that our simulations were only indicative of possible pathways in the marine trophic web at the S1 and S3 stations and were not conclusive due to inadequacies in data for the nutrient input distribution.

CONCLUSIONS

The 1–D model presented in this paper shows some ability to reproduce the main seasonal patterns, both in the physical and in the biogeochemical environments. The agreement with observations allows us to study the underlying fluxes of matter, which cannot be validated by direct *in situ* observations. The analysis of the aggregated carbon fluxes has highlighted the existence of a seasonal or monthly modulation in the carbon-transfer pattern within the food web. At the S1 station, which is more influenced by the Po river inflow, the numerical experiments have shown a change in the trophic web structure from a summer 'multivorous food web' (Legendre and Rassoulzadegan, 1995) to a more herbivorous-orientated food web in autumn, when a higher availability of phosphate is provided by the river forcing.

At the S3 station, which is controlled by a more phosphorus-limiting situation, the shift is from a summer microbial food web (Azam *et al.*, 1983; Rassoulzadegan, 1993) to a multivorous food web structure during autumn. The summer food chain structure is induced by the phosphorus limitation and leads to the production of P-depleted dissolved organic matter and to the competition for dissolved nutrients between phytoplankton and bacteria. This direct uptake of mineral nutrients enhances the limiting situation and hence the microbial pathway, highlighting the importance of the ecological role of bacteria in coastal waters.

There is a note of caution concerning the sensitivity of the model results to available nutrient input information based on observational data. The model is clearly very sensitive to this factor and our results should be interpreted as evidence that multivorous food webs may exist in some coastal areas.

In the light of these considerations, it seems likely that the prevailing path could be related to the seasonal characteristics of the water column, which are the result of the tight interaction between physical and biogeochemical forcing. In the northern Adriatic Sea, this coupling produces a wide range of transfer pathways, which dynamically reflects the system complexity, but the prevailing ones seem here to be the multivorous food web and the microbial food web, even if this pattern is not so evident as in open ocean areas.

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