

A numerical study of the benthic–pelagic coupling in a shallow shelf sea (Gulf of Trieste)



Giulia Mussap, Marco Zavatarelli*

Dipartimento di Fisica e Astronomia (DIFA), Alma Mater Studiorum, Università di Bologna, Italy

HIGHLIGHTS

- Benthic–pelagic coupling successfully simulated with BFM–POM 1D.
- Sensitivity experiments revealed best reference parameters.
- Mechanistic experiment highlighted the role of filter feeders in a shallow shelf sea.
- Results recognize BFM–POM 1D potential as a support to ecosystem management.

ARTICLE INFO

Article history:

Received 1 July 2016

Received in revised form

20 October 2016

Accepted 9 November 2016

Available online 16 November 2016

Keywords:

Biogeochemistry

Modelling

Benthic–pelagic coupling

Benthos

Adriatic Sea

Gulf of Trieste

ABSTRACT

A coupled physical–biogeochemical 1D model (BFM–POM 1D) with an intermediate complexity benthic formulation was used to carry out sensitivity tests on the coupling parameters (sedimentation and diffusion at the sediment–water interface). Moreover, a mechanistic experiment was designed to investigate the role of filter feeders in regulating the biogeochemical state of the system in a coastal sea. Best reference parameters of sedimentation and diffusion were chosen from the sensitivity experiments carried out based on available observations. The mechanistic experiment revealed the importance of filter feeders' role in trapping pelagic organic matter and regulating benthic–pelagic nutrient fluxes, as well as controlling pelagic primary production. The model demonstrated to be able to qualitatively reproduce the biogeochemical characteristics of the system and adapt to different trophic configurations. The results shown are encouraging and foresee its possible use as a tool to study causal relationships and help in finding solutions for management issues.

© 2016 The Authors. Published by Elsevier B.V.

This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Coastal waters are among the most productive ecosystems in the world (Marcus and Boero, 1998). Their exposure to anthropogenic pressures has led to important system changes and has triggered increasing interest and concern within the scientific community. Hence, a lot of effort is spent in studying and understanding regulating processes and system feedbacks to various conditions and pressures.

The processes connecting the pelagic and benthic realms define the so-called “benthic–pelagic coupling” (hereafter BPC). This term comprises the two-way exchange of matter (particulate and dissolved) physically and biologically mediated, between the bottom sediment and the overlying water column (Marcus and Boero, 1998; Raffaelli et al., 2003; Soetaert et al., 2000). Coastal

environmental dynamics of shallow seas are greatly influenced by benthic biogeochemical processes (Burdige, 2011), as the intensity of the BPC mainly depends on water depth (Suess, 1980).

The processes defining the BPC dynamics related to organic matter and nutrients are schematized in Fig. 1. The physically mediated sediment–water exchanges contributing to structure the BPC entirely depend on the sinking and resuspension fluxes of particulate organic matter (POM) and on the diffusive oxygen, carbon dioxide and inorganic nutrients at the sediment–water interface. On the other hand, the biological process consists of the grazing of the “filter feeders” functional group on the sinking organic particles. Such group includes the non-moving benthic organisms feeding directly on the pelagic system by filtering the suspended particles (e.g. bivalve molluscs). The particle feeding complements the transfer of organic matter from the water column to the sediment operated by the sedimentary flux, thereby adding to the BPC processes a highly active component (Gili and Coma, 1998). Such process is sometimes defined as biodeposition (Haven and Morales-Alamo, 1966) and consists of the sequestration of

* Corresponding author.

E-mail address: marco.zavatarelli@unibo.it (M. Zavatarelli).

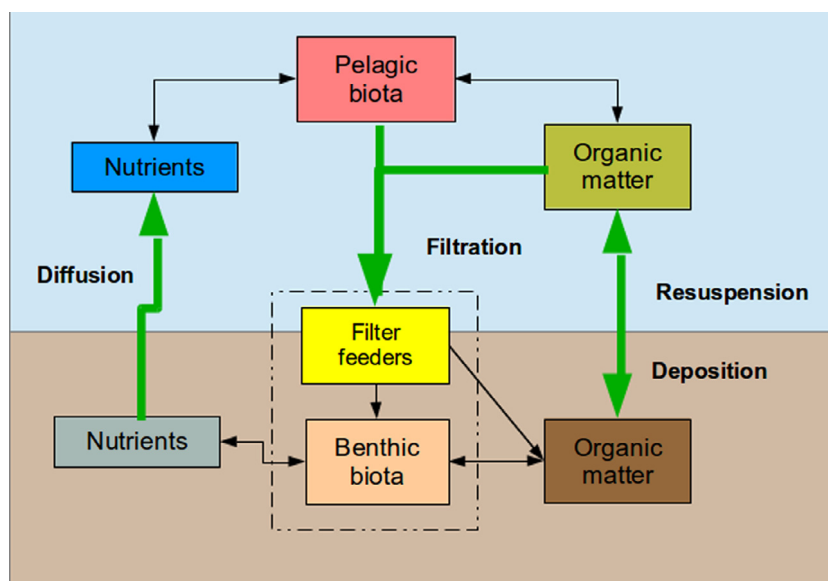


Fig. 1. A scheme representing the organic and inorganic matter related benthic–pelagic coupling. Green double-headed arrows represent the benthic–pelagic processes of diffusion, filtration, deposition and resuspension. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

organic matter from the pelagic system and its deposition into the benthic domain in the form of faeces and pseudo-faeces. Biodeposition has therefore a twofold and opposite impact on the pelagic dynamics: it removes living phytoplankton (Herman et al., 1999) and it contributes to the oxygen and nutrient pool via the bacterial organic matter recycling processes (Dame, 1993; Norkko et al., 2001), modulated by the diffusion at the benthic–pelagic interface. Such impact causes biodeposition to be considered as a possible process controlling eutrophication (Grall and Chauvaud, 2002; Officer et al., 1982) under given environmental conditions. Bacterial activity on the deposited organic matter causes the interstitial waters to be enriched in inorganic nutrients and carbon dioxide, and depleted in oxygen. The difference in concentration between interstitial waters and the overlying water column leads to an effective diffusive exchange back into the water column (Herndl et al., 1989) modulated by biological processes such as bioturbation, bioirrigation and particle reworking (Aller, 1988, 1994; Bertuzzi et al., 1997).

The strong interactions between pelagic primary production, benthic communities and detritus are thus crucial in defining the trophic conditions in coastal regions. Being relatively fixed in place and long lived, the benthos integrates environmental influences at a particular site over a relatively long timespan (Herman et al., 1999). This is important because the presence, spatial distribution and trophic structure of the fauna significantly influences the physical and chemical characteristics of the sediments and sediment–water exchange (Heip, 1995).

It is therefore essential to study the role of the benthos in coastal areas, especially those affected by problems such as eutrophication and bottom oxygen depletion (hypoxia/anoxia).

Numerical modelling allows to test specific hypotheses and to investigate the integrated effects of various factors under given assumptions (Henderson et al., 2001). Moreover, it can inform on the behaviour of the ecosystem as a whole (De Mora et al., 2016). With an appropriate validation against field data, this method may have a key role in developing a strategy for environmental management and sustainability. However, modelling the benthic system has always been a challenge within the scientific community due to the scarcity of information available (Capet et al., 2016). The reason for this is related to the difficulty of sampling the benthos, which is problematic and time consuming (Cardoso et al., 2010; Ebenhöf et al., 1995).

Most biogeochemical models for water column processes either neglect the sediments or apply a rather crude approximation for the benthic response (Soetaert et al., 2000). In fact, models of pelagic and benthic biogeochemistry are typically not coupled or connected (Capet et al., 2016; Mussap et al., 2016).

As a continuation of a previous work with the pelagic model BFM–POM 1D implemented in the Gulf of Trieste (northern Adriatic Sea, Mussap et al., 2016), the implementation has been extended to include the benthic realm and the BPC, by coupling the pelagic model with a benthic model of intermediate complexity.

The aim of this paper is to establish and test the structure of the benthic compartment and its interactions with the water column. We aim to provide an understanding of the extent to which the benthic “biogeochemical machinery” determines the sediment–water fluxes. We start by investigating the sensitivity of the system with respect to deposition and diffusive fluxes, and subsequently we carry out a mechanistic experiment involving the removal of the filter feeders functional group in order to understand their role in the BPC.

2. Materials and methods

2.1. The model

The coupled numerical model used in its pelagic component is the Biogeochemical Flux Model (BFM, Vichi et al., 2007). In the model, the trophic and chemical interactions are represented through the concepts of chemical functional families (CFFs) and living functional groups (LFGs Vichi et al., 2007). With respect to the previous implementation form (Mussap et al., 2016), an additional phytoplankton LFG was added (the “large” phytoplankton, i.e. dinoflagellates). Such functional group is characterized by a low growth rate and low grazing pressure, and is known to develop in the Gulf of Trieste (Mozetic et al., 1998). The pelagic BFM is coupled “on-line” to the one-dimensional version of the Princeton Ocean Model (POM 1D, Blumberg and Mellor, 1987). A full description of the coupling between the two models can be found in Mussap et al. (2016). As in Mussap et al. (2016), the implementation of the hydrodynamical model is diagnostic, with prescribed climatological, time dependent (monthly varying) temperature and salinity vertical profiles (obtained from *in situ* data).

The surface wind stress is the only surface forcing function needed for the physical component of the modelling system (given the diagnostic implementation). On the other hand, the BFM primary production is forced by the surface incident shortwave radiation penetrating the water column. Vertical extinction is calculated on the basis of phytoplankton (self-shading) and detritus concentration (both prognostically computed), and seasonal inorganic suspended matter (ISM) profiles which are fed to the model. Surface boundary conditions for nutrients are defined by relaxing surface concentrations to monthly varying climatologies of phosphate, nitrates, ammonium and silicate (Mussap et al., 2016). Climatological initial conditions for biogeochemical pelagic components are vertically-homogeneous and consistent with observed winter concentrations. The climatological annual cycles and forcing functions are the same as in Mussap et al. (2016). The one-dimensional coupled model does not account for any lateral flux of BFM state variables. The underlying assumption is that the implementation area is in steady state from the biogeochemical state variables lateral flux point of view. This assumption (and possible limitation) is justified by the fact that the model is implemented in the centre of an area that observational programs for the Gulf of Trieste defined as rather uniform (see Section 2.3).

In Mussap et al. (2016) the benthic domain was not represented and a simple benthic nutrient cycling procedure was adopted as a “bottom” closure of the pelagic domain. The implementation described here adopts an intermediate complexity benthic model directly coupled to the pelagic component. The model is based on the extensive model effort of Ebenhöh et al. (1995) and Ruardij and Raaphorst (1995), and includes a LFG based description of the benthic fauna and the organic matter recycling processes. Fig. 2 schematizes the structure of the benthic model, where large double-headed arrows indicate BPC processes.

The sediment vertical structure resolves two dynamical layers (oxic and anoxic, Fig. 3) where different processes take place. Organic matter has an implicit vertical distribution and sediment oxygen dynamics are resolved, including the dynamical shifting of the oxic layer.

The benthic LFGs taken into account (Fig. 2) are: epifaunal predators ($Y_i^{(1)}$), deposit feeders ($Y_i^{(2)}$), filter feeders ($Y_i^{(3)}$), meiobenthos ($Y_i^{(4)}$), infaunal predators ($Y_i^{(5)}$) and aerobic and anaerobic bacteria ($H_i^{(1)}$ and $H_i^{(2)}$). Similarly, the CFFs are: phosphate in the oxic and anoxic layer ($K^{(1)}$ and $K1^{(1)}$), nitrate ($K^{(3)}$), ammonium in the oxic and anoxic layer ($K^{(4)}$ and $K1^{(4)}$), silicate ($K^{(5)}$) and reduction equivalents ($K^{(6)}$). Dissolved oxygen and dissolved inorganic carbon in the sediments are also taken into account ($G^{(2)}$ and $G^{(3)}$ respectively).

Benthic organic matter is partitioned into particulate (POM, $Q_i^{(6)}$) and dissolved (DOM, $Q_i^{(1)}$), and its dynamics are regulated by biological activity (uptake and release by benthic organisms and bacteria) in addition to the sedimentation process. The dynamics of DOM in the sediment are mainly controlled by production/consumption terms and by vertical diffusion.

The average location of bacteria is controlled by either the oxic horizon or the detritus penetration depth. They are allowed to directly uptake/release inorganic nutrients from the sediments. Since bacteria are supposed to have almost constant internal ratios, the inputs are eventually compensated by excretion fluxes if the nutrient uptake is higher than the optimal one.

The main processes affecting the oxygen concentration are the biological oxidation of the organic matter, the nitrification reaction of ammonium and the reoxidation of the reduction equivalents. In this intermediate complexity benthic configuration, nutrients are released to the water column at constant specific rates, according to the pore-water concentration. Nitrogen remineralization is partitioned into ammonium and nitrate flux with a constant value. Bioturbation and bioirrigation are parameterized as enhanced diffusion (Ebenhöh et al., 1995).

2.2. The benthic–pelagic coupling

The pelagic and benthic systems are reciprocally interacting at the sediment–water interface (located at depth $z = -H$ in the pelagic system coordinates, Fig. 3). The main forcing for the benthic system is the particulate matter sedimentary flux from the water column pool.

Benthic–pelagic coupling processes are: POM sedimentary flux and diffusive inorganic Carbon (C), Nitrogen (N), Phosphorus (P), Silicon (Si), Oxygen and reduction equivalents fluxes. Resuspension processes are not included in the current BPC implementation, nor is the benthic primary production. The implementation of such processes is planned as a further continuation of the work. It is assumed that the surface burial velocity is a constant value, which is multiplied by the concentration of the sinking variables (POM and phytoplankton) to give the output rates from the water column to the sediments:

$$\left. \frac{dQ_i^{(6)}}{dt} \right|_{R_i^{(6)}}^{sed} = w_{bur} R_i^{(6)} |_{z=-H} \quad (1)$$

$$\left. \frac{dQ_i^{(6)}}{dt} \right|_{P_i^{(1,4)}}^{sed} = w_{bur} \xi_i \sum_{j=1}^4 (1 - \Psi_{p^{(j)}}) P_i^{(j)} |_{z=-H} \quad (2)$$

where $i = C, N, P, Si$ and

$$\left. \frac{dQ_i^{(1)}}{dt} \right|_{P_i}^{sed} = w_{bur} \xi_i \sum_j P_i^{(j)} |_{z=-H} \quad (3)$$

in which it is also considered that phytoplankton is fractionated into particulate and dissolved components, mainly for mechanical reasons. The pelagic state variables $R_i^{(6)}$ and $P_i^{(j)}$ are the particulate detritus and the phytoplankton functional groups (diatoms and large phytoplankton). The parameter $\Psi_{p^{(j)}}$ indicates the fraction of the biomass that is considered to be labile and is readily available in dissolved phase (different for each phytoplankton group). Nutrients are considered to be more available than carbon in this phase, therefore the non-dimensional constant ξ_i regulates the C, N, P partitioning into dissolved and particulate detritus ($\xi_i = 1$ for C, $\xi_i > 1$ for N and P).

The diffusive flux is calculated by computing the difference of nutrient concentration in the sediments ($K_i^{(j)}$) and in the bottom layer of the water column ($N_i^{(j)} |_{z=-H}$, converted in mmol m^{-2}), and multiplying the result by a constant rate γ :

$$\left. \frac{dK_i^{(j)}}{dt} \right|^{diff} = -\gamma [K_i^{(j)} - N_i^{(j)} dz]_{z=-H}. \quad (4)$$

The w_{bur} and γ values adopted for the numerical simulations are given in Table 1 of Section 2.4 below.

2.3. Gulf of Trieste: background information

The northern Adriatic has been recognized for many years as a region of high marine production (Fonda Umani, 1996). However, the area is affected by strong anthropogenic pressure which might trigger or worsen eutrophication and hypoxia/anoxia events. The Gulf of Trieste, situated on the northern-east coast of the Adriatic Sea, is characterized by a shallow depth (~ 20 m), a large interannual and seasonal variability and a cyclonic circulation. The circulation is mainly driven by freshwater inputs by the Isonzo river (Vichi et al., 2003). Generally speaking the Gulf, as with most of the Mediterranean, is P-limited (Fonda Umani et al., 2007; Mussap et al., 2016; Puddu et al., 2003). Following Mussap et al. (2016), the implementation site chosen

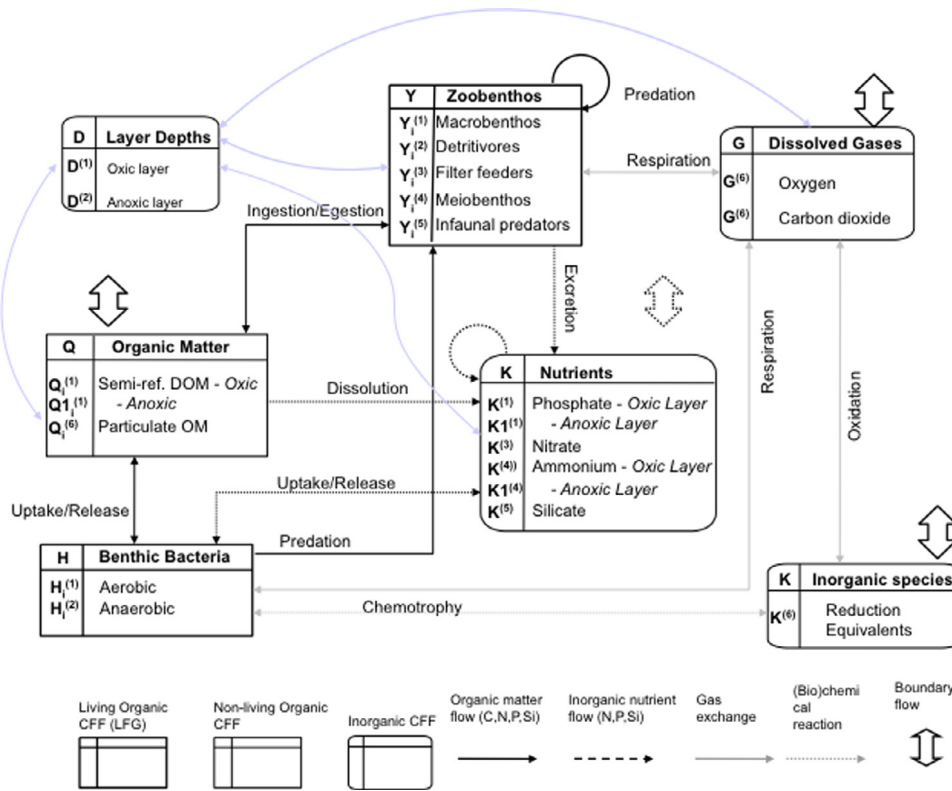


Fig. 2. Scheme of the state variables and benthic interactions of the BFM. Living (organic) Chemical Functional Families (CFFs) are indicated with bold-line square boxes, non-living organic CFFs with thin-line square boxes and inorganic CFFs with rounded boxes. The fat double-headed arrows indicate fluxes of the benthic–pelagic coupling.

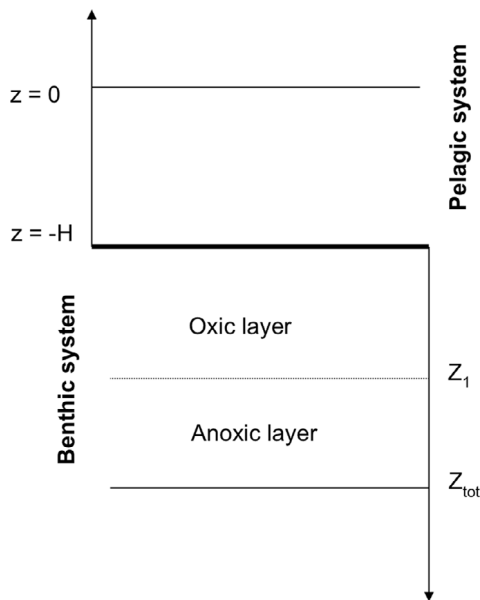


Fig. 3. Scheme of the benthic levels.

was based on the macroareas defined by the regional environmental agency (ARPA-FVG). The implementation area is code-numbered MA21 and is located in the centre of the Gulf (Fig. 4, http://dati.arpa.fvg.it/fileadmin/Temi/Acqua/CW_TW/MA21.pdf). The available *in situ* data relative to the whole area were analysed and used to set initial conditions, surface boundary conditions and to validate pelagic model performance (see Mussap et al., 2016).

In the Gulf of Trieste, soft bottoms are not homogeneous in composition and can vary from sand with patches of beach rocks to muds (Brambati et al., 1983). However, sediments are mostly

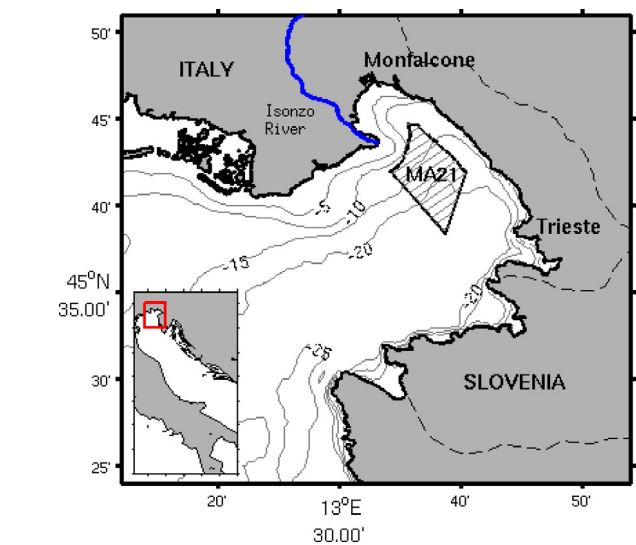


Fig. 4. Map and bathymetry (in meters) of the Gulf of Trieste with location of the implementation area MA21. After Mussap et al. (2016).

composed of silty sands (Ogorelec et al., 1991; Zuschin et al., 1999) with a mean porosity of ~0.7.

Mean annual sediment–water fluxes measured by (Bertuzzi et al., 1997) with *in situ* benthic chambers can be found in Table 2.

Information concerning the northern Adriatic Sea benthos is sparse and still relies to some extent on the dated assessment carried out by Vatova (1949). In 1969 Orel and Mennea focused on the fauna of the Gulf of Trieste and found it was characterized by a well-developed infauna and epibenthic macrofauna, mostly composed by deposit and filter feeders (~60% deposit feeders, ~30% of epibenthos and ~10% filter feeders). Since then, various authors (Fedra et al., 1976; Solis-Weiss et al., 2004, 2007) have

Table 1
Sensitivity experiments relative γ and w_{bur} .

Experiment	γ (d ⁻¹)	w_{bur} (m d ⁻¹)
A1	10 ⁻⁴	0.1
A2	10 ⁻⁴	0.5
A3	10 ⁻⁴	1.0
A4	10 ⁻⁴	1.5
A5	10 ⁻²	0.1
A6	10 ⁻²	0.5
A7	10 ⁻²	1.0
A8	10 ⁻²	1.5
A9	1	0.1
A10	1	0.5
A11	1	1.0
A12	1	1.5

tried to describe the benthic community biomass composition, all with different results. This could be tied to the fact that since the 1980s the Gulf has been subject to repeated stress such as hypoxia/anoxia and marine snow events, as well as to an increasing anthropogenic pressure. These events have inevitably impacted the benthic community and altered its abundance, distribution and composition. Effects of such events are long-lasting and ecosystem recovery requires a significantly long period of time (Giani et al., 2012; Kollmann and Stachowitsch, 2001). Moreover, benthic fauna is influenced by bottom-water oxygen availability, which is one of the main factors controlling sediment–water exchange fluxes and organic carbon degradation in the sediment (Nestlerode and Diaz, 1998). These stresses, together with the different season, area and sampling method can explain the diverse compositions observed. As a consequence, it is difficult to define the area with a standard composition distribution. Nonetheless, it can be said that overall, polychaetes and molluscs compose ~90% of the Gulf's benthic community, represented deposit and filter feeders respectively. The distribution found by Solis-Weiss et al. (2004), which was derived from an extended dataset (1966–2001) and analysed via an innovative technique (GIS), will be used for the purpose of validating model results (Fig. 7(A)).

2.4. Numerical experiments

A set of twelve numerical experiments was designed to test the sensitivity of the model to deposit and diffusive processes. The suite of values for the parameters w_{bur} (Eqs. (1) and (2)) and γ (Eq. (4)) are listed in Table 1. Parameter w_{bur} defines the speed at which organic matter enters the sediment from the lower water column layer. This differs from the sinking velocity, which defines the velocity of organic matter sedimentation through the water column. The sinking velocity for organic detritus was chosen to be 1.5 m d⁻¹, while the sinking velocity for the “diatoms” and “dinoflagellates” functional groups varies from 0 to 5 m d⁻¹, depending on the nutrient stress state. This value lies at the lower end of the known range of the sinking velocity for organic matter, which varies from 0.1 to 10² m d⁻¹ depending on the mass and size characteristic of the sinking particles. The choice was essentially dictated by a previous experience in modelling the coastal water column.

Parameter γ represents the speed at which inorganic nutrients are released back into the water column after having gone through benthic interactions. In our previous work (Mussap et al., 2016), the value of constant benthic remineralization was chosen so as to fit water column observations. However, once the full benthic system was activated, these values had to be reparameterized for the BPC. In order to do so, a matrix of twelve experiments was designed and results were analysed to find the best combination.

Through the comparison with the available observations, a reference simulation (A10) for BPC parameters was defined.

The A10 configuration was used to carry out a mechanistic experiment concerning the role of filter feeders in defining the BPC fluxes. In fact, filter feeders are known to have a key role in shallow coastal environments in regulating fluxes, nutrients and oxygen concentrations. Experiment NO_FF investigated the system's sensitivity to their presence by eliminating the FF functional group from the system.

In all simulations, the model was integrated for 5 years, which was found to be the period of time necessary for the pelagic system to converge with the benthic system (Vichi et al., 2003; Mussap et al., 2016).

3. Results

Sensitivity experiments

The results of the 12 sensitivity experiments are described by the contour plots in Fig. 5, showing the variation in selected model state variables (annual average computed from the last integration year) and fluxes due to the combined change in w_{bur} and γ . The state variables shown are: particulate organic phosphorus concentration in the sediment (POP; mmol m⁻²), filter feeders biomass (FF; mg C m⁻² d⁻¹) and the inorganic phosphate concentration in the interstitial waters (mmol P m⁻², Fig. 5(B), (C) and (F) respectively); while the fluxes are: vertically integrated net pelagic primary production (NPP; mg C m⁻²d⁻¹), POP FF filtration flux (mmol P m⁻² d⁻¹) and the difference between the sediment–water P flux and the sedimentary P flux (Δ Pflux, mmol P m⁻² d⁻¹, Fig. 5(A), (D) and (E) respectively). It is stressed that in all the 12 sensitivity experiments the surface nutrient flux differences were in the order of 10⁻⁹ mmol P m⁻² d⁻¹. Therefore the differences in the variables examined in Fig. 5 can be completely ascribed to the changes in the w_{bur} and γ parameters.

The results show that both NPP and POP (Fig. 5(A) and (B) respectively) increase as the two w_{bur} and γ rise. However, at a constant w_{bur} value, each of these variables decreases for γ values below 10⁻². In fact, it is interesting to note that for $1 \geq \gamma \geq 10^{-2}$, their variation appears insensitive to the change in γ and their value seems entirely dictated by the change in w_{bur} . Conversely, for $\gamma < 10^{-2}$ a progressively smaller γ determines a reduced NPP, which results in a diminished injection of POP in the sediment, thereby reducing organic matter availability for the benthic fauna. This can be seen in the FF abundance (Fig. 5(C)), which decreases with decreasing γ . FF abundance also decreases with the increase in burial velocity (w_{bur}), as progressively less food is available in the water column. This can be reflected in the P filtration flux (Fig. 5(D)), which likewise decreases with increasing w_{bur} . High w_{bur} values also lead to smaller Δ Pflux (Fig. 5(E)), which accounts for the difference between sediment P losses (diffusion) and P gains (particulate P sinking), as the inward flux is enhanced. Highest Δ Pflux values occur at $w_{bur} = 0.5$ and $1 \geq \gamma \geq 10^{-2}$. However, above and below this range Δ Pflux decreases, suggesting a threshold area. At low Δ Pflux ($w_{bur} > 0.5$) inorganic P accumulates in the sediments (Fig. 5(F)). Highest concentrations occur at maximum w_{bur} values and minimum γ values. For $\gamma > 0.1$ inorganic P concentrations in the sediments are mainly controlled by γ (although not visually detectable).

It must be noted that in all sensitivity experiments oxic conditions were maintained in both the pelagic and benthic domains.

Definition of the reference BPC parameters

On the basis of the sensitivity experiments, reference BPC parameters were chosen by comparing the simulation results with the available observations relative to water column vertical profiles, benthic biomass and benthic fluxes. The BPC parameters

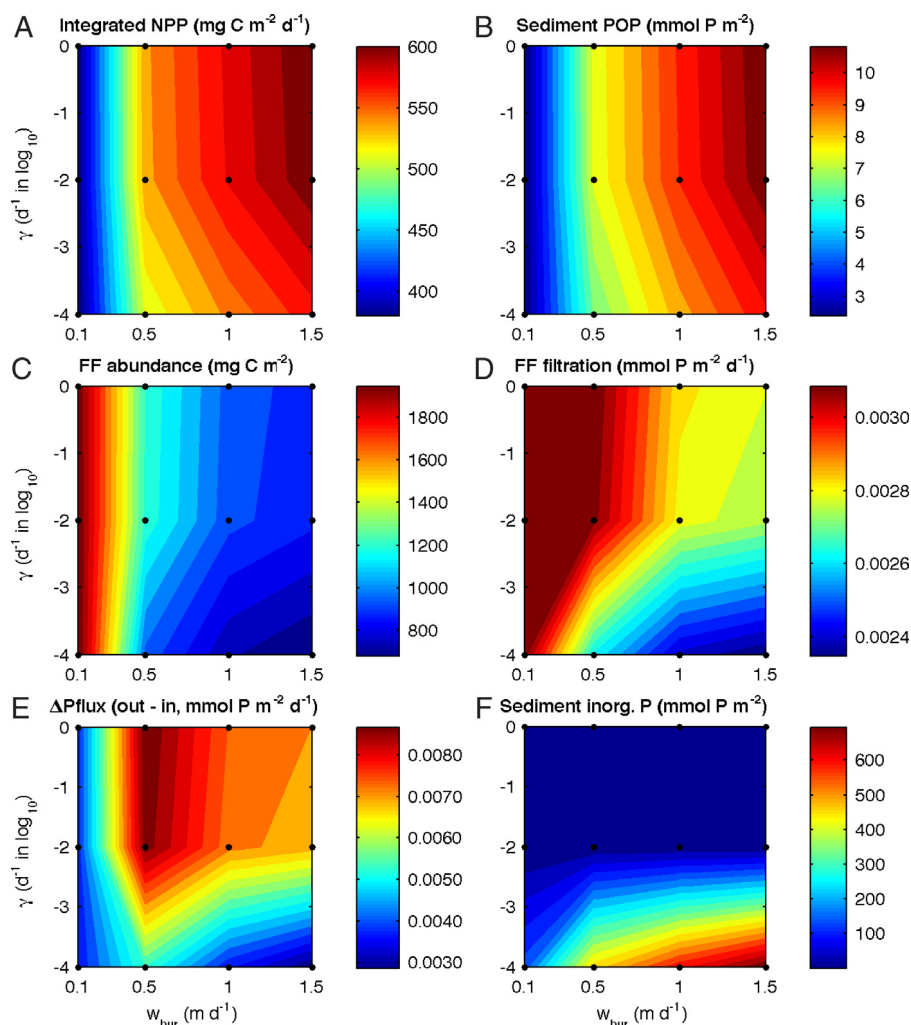


Fig. 5. Sensitivity experiments contour plots of (A) vertically integrated net pelagic primary production, (B) particulate organic phosphorus concentration in the sediment, (C) filter feeders biomass, (D) particulate organic phosphorus filter feeders filtration flux, (E) the difference between the P diffusive flux and the sedimentary P flux, and (F) inorganic phosphate concentration in the interstitial water variation of the annually averaged value is shown in relation to w_{bur} (x-axis) and γ (y-axis, log scale). Black points represent the 12 sensitivity experiments.

that yielded results closer to the observations are those adopted for experiment A10 of Table 1 ($\gamma = 1 \text{ [d}^{-1}\text{]}$ and $w_{bur} = 0.5 \text{ [m d}^{-1}\text{]}$). The selected parameters were those that provided the minimum number of profiles characterized by a marked deviation from the observed variability and a composition of the benthic fauna qualitatively closer to the observation data. The vertical profiles obtained with such parameter choice are shown in Fig. 6 and are compared to the corresponding observed average and standard deviation value.

Simulated chlorophyll seasonal profiles (Fig. 6(A)) are in accordance with the observed seasonal trends, showing an increase with depth during spring and summer, and more uniform profiles in winter and autumn. Surface values are overestimated in winter and underestimated in spring and summer, while the autumn simulated profile always falls within one standard deviation. Spring and summer concentrations in the bottom meter sharply decrease, most probably due to the grazing activity of filter feeders.

As in Mussap et al. (2016), oxygen concentrations (Fig. 6(B)) are generally underestimated in respect to the mean observed vertical profile. This is mostly evident in spring, when concentrations are on the limit of the standard deviation. Nonetheless, the profile shapes are well represented.

Simulated nitrates seasonal profiles (Fig. 6(C)) nicely follow the however scarce observational profiles. The same is true for

phosphate (Fig. 6(D)), although the simulated summer and autumn profiles show an increase in concentration with depth that is not reflected in the observations. Contrastingly, ammonium (Fig. 6(E)) is overestimated in winter and spring, while it falls closer to observations in summer and autumn. However, it must be noted that very few observations were available for this variable.

Fig. 7 shows the comparison relative to benthic biomass composition between Solis-Weiss et al. (2004) and model results (A and B respectively). For this comparison, the group defined as “polychaetes” in Solis-Weiss et al. (2004) are represented by deposit feeders, while “molluscs” and “crustaceans” are compared with model filter feeders and epibenthos respectively. “Others” were considered to be a mixture of meiobenthos and infaunal predators. The pie charts highlight how the model slightly overestimates deposit feeders and epibenthos, while it underestimates filter feeders.

Finally, Table 2 summarizes the benthic fluxes measured by Bertuzzi et al. (1997) with *in situ* benthic chambers and those simulated in experiment A10. The model slightly overestimates the phosphate flux and greatly underestimates the silicate and oxygen fluxes. However, nitrate and ammonium fluxes are in the range of observations. The slightly high phosphate flux can be echoed in bottom water column concentrations, which, as already seen in Fig. 6(D), are slightly overestimated. The same and opposite is true for oxygen.

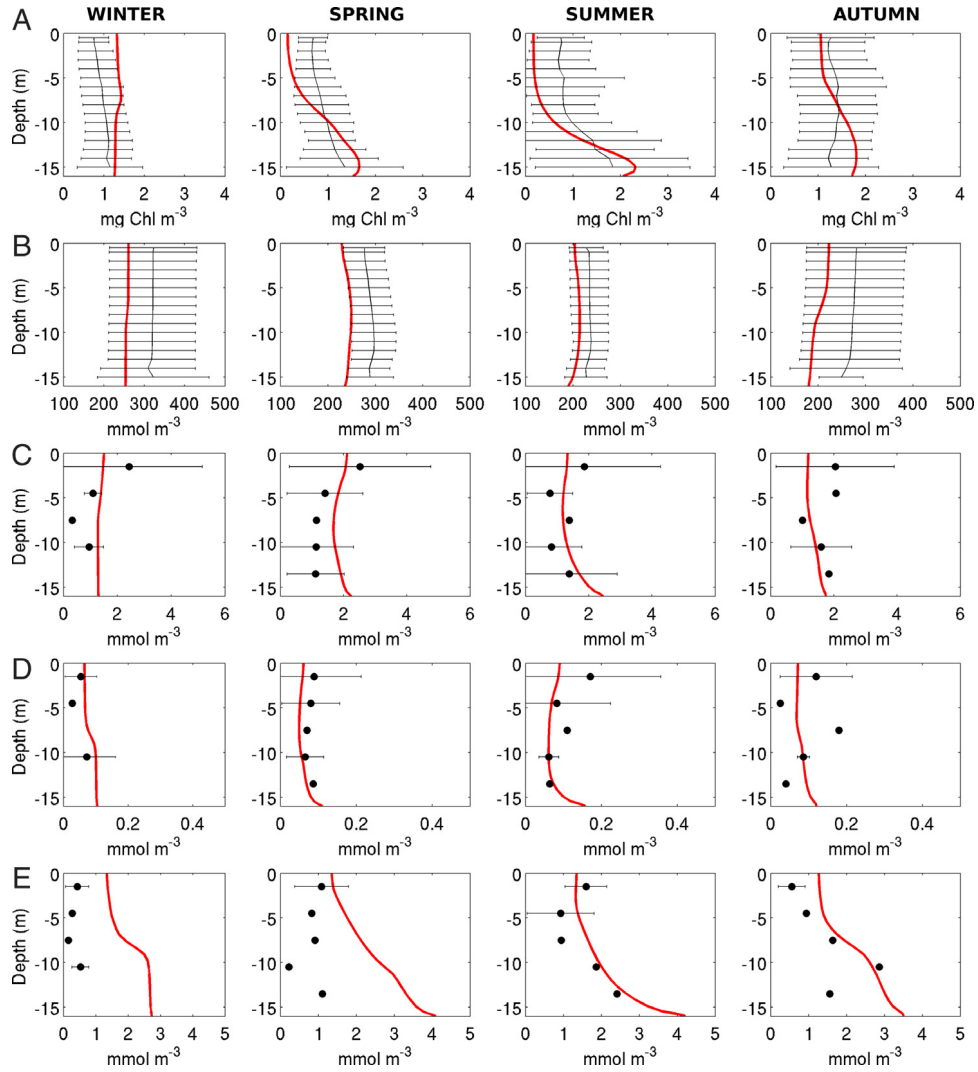


Fig. 6. Model (red) and data (black) comparison for (A) chlorophyll, (B) oxygen, (C) nitrates, (D) phosphate and (E) ammonium as climatological seasonal profiles for site MA21. The continuous red line is the simulated mean seasonal profile, while observations are plotted as seasonal means with the range of variability (where data allows it). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

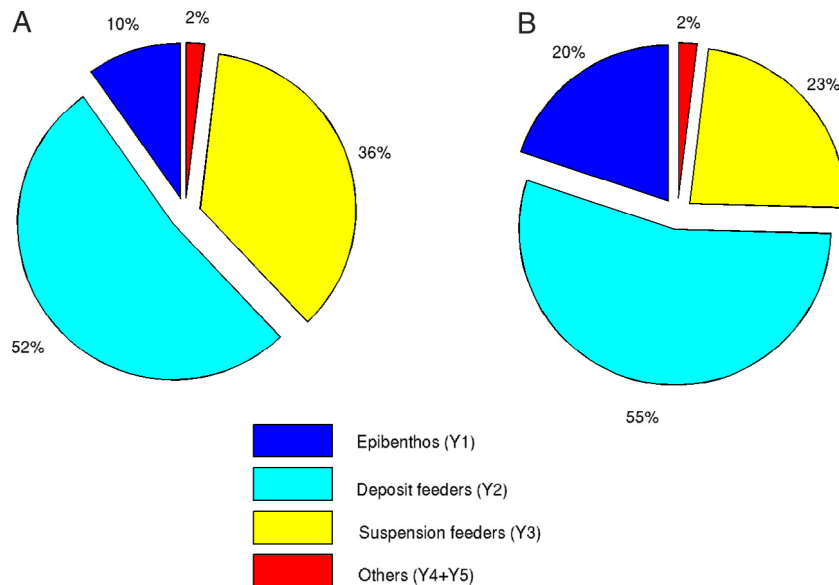


Fig. 7. Observed (A) and modelled (B) benthic fauna distribution pie charts in percentage. Observations after Solis-Weiss et al. (2004).

Table 2Mean (\pm standard deviation) annual benthic fluxes of N, P, Si and O₂ (mmol m⁻² d⁻¹).

Reference	NO ₃ ⁻	NH ₄ ⁺	PO ₄ ³⁻	Si(OH) ₄	O ₂
Bertuzzi et al. (1997)	0.17 \pm 0.73	0.8 \pm 0.7	0.029 \pm 0.05	2.59 \pm 2.3	-20.4 \pm 8.9
BFM-POM 1D	0.27 \pm 0.16	0.63 \pm 0.38	0.048 \pm 0.03	0.47 \pm 0.41	-5.14 \pm 3.5

Experiment NO_FF

Once a reference experiment was defined relative to the parameterization of the deposit/diffusion parameters (experiment A10), a mechanistic experiment was carried out to evaluate the role of filter feeders in defining benthic–pelagic dynamics. This was achieved by running experiment A10 with the FF functional group excluded. Such experiment will be named NO_FF hereafter.

In order to effectively compare NO_FF results with the A10 experiment, the percentage differences between the two was calculated for several state variables and are reported in Fig. 8. The variables shown are integrated NPP, deposit feeders biomass, bottom P flux (sediment to water column), bottom POC, organic matter in the sediments and benthic aerobic bacteria.

The removal of FF from the system causes NPP to increase throughout the year in respect to the A10 experiment, except for January and December when they coincide (Fig. 8(A)). The deposit feeders biomass is close to that of experiment A10 for the first five months of the year, and then increases of up to 30% until December (Fig. 8(B)). The bottom phosphate flux (Fig. 8(C)) has a very similar behaviour, showing important differences only after May. Bottom POC has slightly higher concentrations in the first months of the year, but a sharp increase occurs between April and May (Fig. 8(D)). Concentration differences reach up to over 110% between July and August and then decrease until December, when they become small.

A different trend can be seen for organic matter and benthic aerobic bacteria in the sediments (Fig. 8(E) and (F) respectively). The removal of FF determines a decrease of both state variables for most year. This behaviour can be related to the annual FF biomass concentration seen in experiment A10 (Fig. 9).

In fact, FF abundance in experiment A10 shows an oscillating trend during the first three months of the year, followed by a strong peak in April. High fluctuating concentrations are maintained until July and rapidly drop from September to November. When compared to the OM in the sediments and benthic aerobic bacteria, it is possible to notice that the period in which differences are nearly null coincides with lowest FF concentrations (March). Similarly, when FF peak, negative differences are stronger (between April and May). Less OM enters the sediments when FF are isolated from the system, and consequently less bacteria are present too. The increase in OM in the sediments around October (and consequently of aerobic bacteria) is given by the increase in NPP, deposit feeders biomass and bottom POC.

4. Discussion and conclusions

In this paper we have shown results from numerical simulations carried out in the Gulf of Trieste with a complex 1D coupled biogeochemical model. The focus was on the interactions between the benthic and pelagic realms and their regulating factors. The sensitivity experiments allowed to test the correct functioning of model dynamics and empirically define the BPC reference parameters. The mechanistic experiment involving the removal of filter feeders from the system acknowledged their role in a shallow shelf sea.

Results of the sensitivity test revealed two main features: (1) at high γ values ($\gamma \geq 10^{-2}$) the BPC dynamics are mostly governed by the w_{bur} value and (2) below this value the diffusive flux plays a

constraining role. Small γ values mean a slower return of inorganic nutrients to the water column, which results in an accumulation in the sediments. As seen in Fig. 5, highest concentrations of inorganic phosphate in the sediments coincide with lowest FF abundance (and consequently lowest P filtration flux) and lowest $\Delta Pflux$.

When considering the $\gamma \geq 10^{-2}$ domain, as organic matter enters the sediment faster, NPP, POP and inorganic phosphate in the sediments increase. On the other hand, FF abundance, the filtration flux of P and $\Delta Pflux$ decrease. In fact, the faster velocity of organic matter entering the sediment limits the filter feeders growth, while it causes higher organic and inorganic P concentrations in the sediment. It also causes a decrease in $\Delta Pflux$ as the inward flux is enhanced. At the same time, the relatively high values of γ send the inorganic phosphate back to the water column, stimulating primary production. Therefore, the faster the organic matter enters the sediment, the higher the nutrients concentrations both in the sediment and the water column. This results in a highly productive system.

Contrastingly, for $\gamma \leq 10^{-2}$, the diffusive flux plays a bigger role than w_{bur} . In fact, the decreasing diffusion determines lower NPP, POP, FF abundance, P filtration flux and $\Delta Pflux$. On the contrary, it causes inorganic phosphate to accumulate in the sediment. The decreasing $\Delta Pflux$ indicates a stronger incoming flux, which gets closer to the value of the outward flux. This highlights how, in order to avoid the accumulation of inorganic nutrients in the sediment and maintain the system balanced, the flux exiting the sediment has to be greater than the one entering it.

The domain of γ and w_{bur} values in which results were best compared to the available observations coincides with the $\Delta Pflux$ threshold where maximum values are reached. In other words, when the difference between the outgoing flux and the incoming flux is greatest. This happens at $w_{bur} = 0.5$ m d⁻¹ and $1 \geq \gamma \geq 10^{-2}$. In fact, experiment A10 was chosen to define the reference BPC parameters, however it must be noted that experiment A6 yielded very similar and equally valid results. Moreover, while carrying out sensitivity experiments it was found that values of diffusion higher than 1 d⁻¹ produced unrealistic results.

The reference (A10) experiment reproduced the mean seasonal pelagic biogeochemical characteristics observed in the Gulf of Trieste. Results were qualitatively valid, showing misfits only for surface chlorophyll concentrations (winter, spring and summer), oxygen spring concentrations and ammonium winter and spring concentrations. The model demonstrated to be capable of reproducing the major benthic biota composition, although overestimating epibenthos and deposit feeders, and underestimating filter feeders. This disagreement with observed data could be linked to excess concentrations of organic matter in the lower water column. In fact, high organic matter densities and content in the sediment generally favour deposit feeding organisms (Marinelli and Williams, 2003; Pearson and Rosenberg, 1978). This is supported by benthic fauna distribution results of the sensitivity experiments (not shown), where composition is strongly linked to the burial velocity of organic matter (w_{bur}). In fact, FF abundance is inversely proportional to w_{bur} : with increasing burial velocity, progressively less FF and more deposit feeders are present in the system. Indeed, sedimentation is partially linked to variations in macrofaunal community (Norkko et al., 2001).

The model only partially reproduces observed benthic fluxes, performing quite poorly in the silicate and oxygen fluxes.

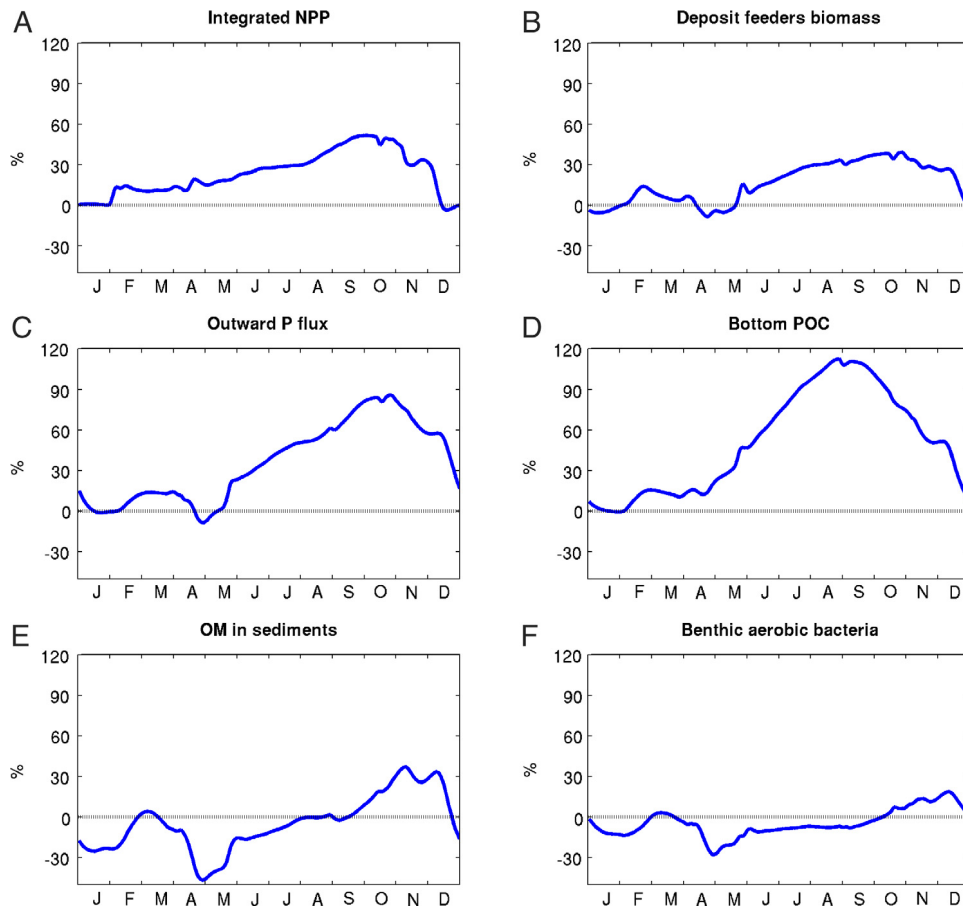


Fig. 8. Percentage difference between the A10 experiment and experiment NO_FF for (A) integrated NPP, (B) deposit feeders abundance, (C) bottom P flux, (D) bottom POC, (E) organic matter in the sediments and (F) benthic aerobic bacteria.

Concerning the silicate flux, it is well known that dissolution of biogenic silica in the sediment is significantly impacted by the faunal density and composition (Marinelli and Williams, 2003). The difference in the modelled benthic fauna with respect to the known observed structure of the Gulf of Trieste benthic communities might be responsible for the unsatisfactory silicate flux at the interface. Obviously this is an issue that requires more investigation. Also, it might be that the model overestimates the benthic organisms abundance, however this could not be checked against observations. On the other hand, the simulated low oxygen flux could be linked to an exaggerated oxygen demand and bacterial activity in the sediments. Overall, benthic model results point to an overestimation of OM in the water column bottom layer, which leads to imprecise simulation of benthic fauna distribution and benthic–pelagic fluxes.

The mechanistic experiment, consisting in the removal of the FF functional group from the system, yielded interesting results highlighting the role of FF in a shallow shelf sea. The removal of FF leads to a general increase in NPP throughout the year and in deposition being the only process defining the entrance of POC in the sediments. This supports the theory that FF play an important role in the sequestration of suspended particles from the water column, regulating primary production in coastal systems (Gili and Coma, 1998) and acting as a natural eutrophication control. Moreover, the presence of FF affects production in the water column by enhancing rates of pelagic recycling (Doering, 1989). Results highlight the importance of the role of FF in the sequestration of OM in the sediments in a shallow shelf sea, and the strong interconnection between the benthic and pelagic realms. Moreover, they underline how the dynamics of the whole system change based on the presence/absence of FF.

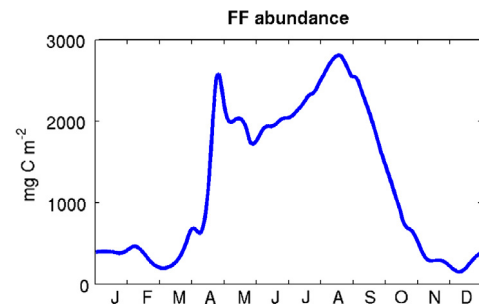


Fig. 9. Filter feeder abundance for experiment A10.

Overall, the experiments carried out in this work demonstrate a good capacity of the model to qualitatively simulate current benthic–pelagic conditions and to adapt to different trophic configurations (i.e. without FF). Seasonal trends were generally captured and ecosystem functions were appropriately represented. Our model is in line with Soetaert et al. (2000) conclusions that the best modelling choice in terms of BPC complexity is to be one where the evolution of particulate matter is part of the solution and the bottom fluxes of dissolved constituents are parameterized based on mass budget considerations.

As already mentioned, modelling the BPC is still a marine biogeochemical modelling still affected by many (and large) uncertainties (Capet et al., 2016). The scarce and non-homogeneous observational datasets represent an important obstacle that must be overcome in view of using BPC modelling as a useful tool for management-related questions. Having available cost-effective decision tools is urgent in order to understand the state of the en-

vironment (Hyder et al., 2015). BFM–POM 1D has the potential to inform us on the trophic interactions and dynamics between the benthic and pelagic realms, explaining and understanding causal relationships (De Mora et al., 2016).

Improvements and future work

The Gulf of Trieste has been subject to many natural and anthropogenic pressures during the last four decades, which have caused modifications of the environmental conditions (Giani et al., 2012). The scarce observational dataset is therefore an important limit in the validation of model performance. Also, representing benthic organisms with functional groups is not an easy task as some species may change their feeding habits depending on life cycle stages and environmental conditions (Marinelli and Williams, 2003). Moreover, benthic primary producers and physical sediment resuspension processes are not included in the current formulation, representing a limit which we intend to fulfil in future works.

Acknowledgements

Giulia Mussap was financially supported by the Erasmus Mundus foundation [specific grant agreement number 2011-1614/001-001 EMJD] and by the project TESSA (Tecnologie per la Cognizione dell'Ambiente a Mare), funded by the Italian Ministry of Education and of Economic Development.

The authors would like to thank OGS as Italian National Oceanographic Data Center/IOC for supplying data originated by Cinzia De Vittor, Dino Viezzoli, Miroslav Gacic and Fabio Brunetti. We would also like to thank ARPA-FVG, the regional environmental agency of Friuli-Venezia Giulia for providing us with data, in particular Massimo Celio.

References

- Aller, R.C., 1988. Benthic fauna and biogeochemical processes in marine sediments: The role of burrow structures. In: Blackburn, T. (Ed.), *Nitrogen Cycling in Coastal Marine Environments*. John Wiley & Sons, pp. 301–338.
- Aller, R.C., 1994. Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. *Chem. Geol.* 114 (3), 331–345.
- Bertuzzi, A., Faganeli, J., Welker, C., Brambati, A., 1997. Benthic fluxes of dissolved inorganic carbon, nutrients and oxygen in the Gulf of Trieste (northern Adriatic). *Water Air Soil Pollut.* 99 (1–4), 305–314.
- Blumberg, A.F., Mellor, G.L., 1987. *A Description of a Three-Dimensional Coastal Ocean Circulation Model*. American Geophysical Union, p. 208.
- Brambati, A., Ciabattini, M., Fanzutti, G., Marabini, F., Marocco, R., 1983. A new sedimentological textural map of the northern and central Adriatic sea. *Boll. Oceanol. Teor. Appl.* 1, 267–271.
- Burdige, D., 2011. Estuarine and coastal sediments coupled biogeochemical cycling. In: Wolanski, E., McLusky, D. (Eds.), *Treatise on Estuarine and Coastal Science*. Academic Press, Waltham, pp. 279–316.
- Capet, A., Meysman, F.J., Akoumianaki, I., Soetaert, K., Grégoire, M., 2016. Integrating sediment biogeochemistry into 3D oceanic models: A study of benthic–pelagic coupling in the black sea. *Ocean Modell.* 101, 83–100.
- Cardoso, A., Cochrane, S., Doerner, H., Ferreira, J., Galgani, F., Hagebro, C., Hanke, G., Hoepfner, N., Keizer, P., Law, R., et al., 2010. Scientific support to the European commission on the marine strategy framework directive. *Management Group Report*. EUR 24336, p. 57.
- Dame, R.F., 1993. *Bivalve Filter Feeders: In Estuarine and Coastal Ecosystem Processes*, Vol. 33. Springer Science & Business Media.
- De Mora, L., Butenschön, M., Allen, J.I., 2016. The assessment of a global marine ecosystem model on the basis of emergent properties and ecosystem function: a case study with ersem. *Geosci. Model Dev.* 9 (1), 59–76.
- Doering, P.H., 1989. On the contribution of the benthos to pelagic production. *J. Mar. Res.* 47 (2), 371–383.
- Ebenhöh, W., Kohlmeier, C., Radford, P., 1995. The benthic biological submodel in the European regional seas ecosystem model. *Neth. J. Sea Res.* 33 (3–4), 423–452.
- Fedra, K., Ölscher, E., Schertübel, C., Stachowitsch, M., Wurzian, R., 1976. On the ecology of a north Adriatic benthic community: Distribution, standing crop and composition of the macrobenthos. *Mar. Biol.* 38 (2), 129–145.
- Fonda Umani, S., 1996. Pelagic production and biomass in the Adriatic sea. *Sci. Mar.* 60 (2), 65–77.
- Fonda Umani, S., Del Negro, P., Larato, C., De Vittor, C., Cabrini, M., Celio, M., Falconi, C., Tamberlich, F., Azam, F., 2007. Major inter-annual variations in microbial dynamics in the Gulf of Trieste (northern Adriatic sea) and their ecosystem implications. *Aquat. Microb. Ecol.* 46 (2), 163–175.
- Giani, M., Djakovac, T., Degobbi, D., Cozzi, S., Solidoro, C., Umani, S.F., 2012. Recent changes in the marine ecosystems of the northern Adriatic sea. *Estuar. Coast. Shelf Sci.* 115, 1–13.
- Gili, J.-M., Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends Ecol. Evol.* 13 (8), 316–321.
- Grall, J., Chauvaud, L., 2002. Marine eutrophication and benthos: the need for new approaches and concepts. *Global Change Biol.* 8 (9), 813–830.
- Haven, D.S., Morales-Alamo, R., 1966. Aspects of biodeposition by oysters and other invertebrate filter feeders. *Limnol. Oceanogr.* 11 (4), 487–498.
- Heip, C., 1995. Eutrophication and zoobenthos dynamics. *Ophelia* 41 (1), 113–136.
- Henderson, A., Gamito, S., Karakassis, I., Pederson, P., Smaal, A., 2001. Use of hydrodynamic and benthic models for managing environmental impacts of marine aquaculture. *J. Appl. Ichthyol.* 17 (4), 163–172.
- Herman, P., Middelburg, J., Koppel, J., Heip, C., 1999. Ecology of Estuarine Macrobenthos, twenty-ninth ed. In: *Advances in Ecological Research*, University of Groningen, Centre for Ecological and Evolutionary Studies, Rights, pp. 195–240. relation: <http://www.rug.nl/research/cees/>.
- Herdnd, G.J., Faganeli, J., Fanuko, N., Peduzzi, P., Turk, V., 1989. Nutrient dynamics between sediment and overlying water in the bay of piran (northern Adriatic sea-yugoslavia), in: *Proceedings of the Twenty First European Marine Biology Symposium: Gdańsk, 14–19 September 1986*, Poland. Zakad Nar Nauk, p. 297.
- Hyder, K., Rossberg, A.G., Allen, J.I., Austen, M.C., Barciela, R.M., Bannister, H.J., Blackwell, P.G., Blanchard, J.L., Burrows, M.T., Defriez, E., Dorrington, T., Edwards, K.P., Garcia-Carreras, B., Heath, M.R., Hembury, D.J., Heymans, J.J., Holt, J., Houle, J.E., Jennings, S., Mackinson, S., Malcolm, S.J., McPike, R., Mee, L., Mills, D.K., Montgomery, C., Pearson, D., Pinnegar, J.K., Pollicino, M., Popova, E.E., Rae, L., Rogers, S.L., Speirs, D., Spence, M.A., Thorpe, R., Turner, R.K., van der Molen, J., Yool, A., Paterson, D.M., 2015. Making modelling count - increasing the contribution of shelf-seas community and ecosystem models to policy development and management. *Mar. Policy* 61, 291–302.
- Kollmann, H., Stachowitsch, M., 2001. Long-term changes in the benthos of the northern Adriatic sea: A phototranssect approach. *Mar. Ecol.* 22 (1–2), 135–154.
- Marcus, N.H., Boero, F., 1998. Minireview: the importance of benthic–pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnol. Oceanogr.* 43 (5), 763–768.
- Marinelli, R.L., Williams, T.J., 2003. Evidence for density-dependent effects of infauna on sediment biogeochemistry and benthic–pelagic coupling in nearshore systems. *Estuar. Coast. Shelf Sci.* 57 (1–2), 179–192.
- Mozetic, P., Fonda Umani, S., Cataletto, B., Malej, A., 1998. Seasonal and inter-annual plankton variability in the Gulf of Trieste (northern Adriatic). *ICES J. Mar. Sci.* 55 (4), 711–722. *ICES Symposium on Temporal Variability of Plankton and their Physico-Chemical Environment*, KIEL, GERMANY, MAR 19–21, 1997.
- Mussap, G., Zavatarelli, M., Pinardi, N., Celio, M., 2016. A management oriented 1-d ecosystem model: implementation in the Gulf of Trieste (Adriatic sea). *Reg. Stud. Mar. Sci.*
- Nestlerode, J.A., Diaz, R.J., 1998. Effects of periodic environmental hypoxia on predation of a tethered polychaete, *glycera americana*: implications for trophic dynamics. *Mar. Ecol. Prog. Ser.* 172, 185–195.
- Norkko, A., Hewitt, J.E., Thrush, S.F., Funnell, T., 2001. Benthic–pelagic coupling and suspension-feeding bivalves: linking site-specific sediment flux and biodeposition to benthic community structure. *Limnol. Oceanogr.* 46 (8), 2067–2072.
- Officer, C., Smayda, T., Mann, R., 1982. Benthic filter feeding: a natural eutrophication control. *Mar. Ecol. Progr. Ser.* 9 (2), 203–210.
- Ogorelec, B., Mišić, M., Faganeli, J., 1991. Marine geology of the Gulf of Trieste (northern Adriatic): Sedimentological aspects. *Mar. Geol.* 99 (1–2), 79–92.
- Orel, G., Mennea, B., 1969. I popolamenti bentonici di alcuni tipi di fondo mobile del golfo di Trieste. *Pubbl. Staz. Zool. Napoli* 37, 261–276.
- Pearson, T., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.* 16, 229–311.
- Puddu, A., Zoppini, A., Fazi, S., Rosati, M., Amalfitano, S., Magaletti, E., 2003. Bacterial uptake of dom released from p-limited phytoplankton. *FEMS Microbiol. Ecol.* 46 (3), 257–268.
- Raffaelli, D., Bell, E., Weithoff, G., Matsumoto, A., Cruz-Motta, J.J., Kershaw, P., Parker, R., Parry, D., Jones, M., 2003. The ups and downs of benthic ecology: Considerations of scale, heterogeneity and surveillance for benthic–pelagic coupling. *J. Exp. Mar. Biol. Ecol.* 285, 191–203.
- Ruardij, P., Raaphorst, W.V., 1995. Benthic nutrient regeneration in the (ERSEM) ecosystem model of the north sea. *Neth. J. Sea Res.* 33 (3–4), 453–483.
- Soetaert, K., Middelburg, J.J., Herman, P.M., Buis, K., 2000. On the coupling of benthic and pelagic biogeochemical models. *Earth-Sci. Rev.* 51 (1–4), 173–201.
- Solis-Weiss, V.S., Aleffi, I.F., Bettoso, N., Rossin, P., Orel, G., 2007. The benthic macrofauna at hte outfalls of the underwater sewage discharges in the Gulf of Trieste (Northern Adriatic sea, Italy). *Ann. Ser. Hist. Nat.* 17.
- Solis-Weiss, V., Rossin, P., Aleffi, I.F., Bettoso, N., Umani, S.F., 2004. A regional gis for benthic diversity and environmental impact studies in the Gulf of Trieste, Italy. *IOC UNESCO, Publ.*, Vol. 188, pp. 245–255.
- Suess, E., 1980. Particulate organic carbon flux in the oceans–surface. *Nature* 288, 261.
- Vatova, A., 1949. *La fauna bentonica dell'alto e medio Adriatico*. *Nova Thalassia I* (3), 1–110.
- Vichi, M., Oddo, P., Zavatarelli, M., Coluccelli, A., Coppini, G., Celio, M., Fonda Umani, S., Pinardi, N., 2003. Calibration and validation of a one-dimensional complex marine biogeochemical flux model in different areas of the northern Adriatic shelf. *Ann. Geophys.* 21 (1, Part 2), 413–436.

Vichi, M., Pinardi, N., Masina, S., 2007. A generalized model of pelagic biogeochemistry for the global ocean ecosystem. Part I: Theory. *J. Mar. Syst.* 64 (1–4), 89–109. Symposium on Advances in Marine Ecosystem Modelling Research, Plymouth, ENGLAND, JUN 27–29, 2005.

Zuschin, M., Stachowitsch, M., Peresler, P., Kollmann, H., 1999. Structural features and taphonomic pathways of a high-biomass epifauna in the northern Gulf of Trieste, Adriatic sea. *Lethaia* 32 (4), 299–316.