



How phosphorus limitation can control climate-active gas sources and sinks



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ABSTRACT

Since the 1950's, anthropogenic activities have increased nutrient river loads to European coastal areas. Subsequent implementation of nutrient reduction policies have led to considerably reduction of phosphorus (P) loads from the mid-1980's, while nitrogen (N) loads were maintained, inducing a P limitation of phytoplankton growth in many eutrophied coastal areas such as the Southern Bight of the North Sea (SBNS). When dissolved inorganic phosphorus (DIP) is limiting, most phytoplankton organisms are able to indirectly acquire P from dissolved organic P (DOP). We investigate the impact of DOP use on phytoplankton production and atmospheric fluxes of CO₂ and dimethylsulfide (DMS) in the SBNS from 1951 to 2007 using an extended version of the R-MIRO-BIOGAS model. This model includes a description of the ability of phytoplankton organisms to use DOP as a source of P. Results show that primary production can increase up to 30% due to DOP uptake under limiting DIP conditions. Consequently, simulated DMS emissions also increase proportionally while CO₂ emissions to the atmosphere decrease, relative to the reference simulation without DOP uptake.

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1. Introduction

Most of the coastal marine ecosystems bordering industrialized countries are strongly affected by changes in anthropogenic nutrient loads. Since the 1950's, dissolved inorganic phosphorus (DIP) and dissolved inorganic nitrogen (DIN) concentrations in inland waters and coastal areas have substantially increased in response to population increase, industrialization, and intensive farming practices. As a result, these coastal marine ecosystems undergo eutrophication (Cloern, 2001). However, due to management policies aiming at reducing eutrophication (implementation of wastewater treatment and banishment of P-based detergents), phosphorus (P) loads decreased after the mid-80's in several coastal ecosystems, while nitrogen (N) loads remained generally high because of continued use of artificial fertilizers in agriculture (Cadée and Hegeman, 2002; Loebler et al., 2009; Philippart et al., 2007). Consequently, phytoplankton growth in these coastal areas is now limited by P availability (e.g. Harrison et al., 1990; Philippart et al., 2007; Rabalais et al., 2002; Trommer et al., 2013; Ly et al., 2014).

Changes in ambient nutrient concentrations modify the magnitude of primary production but can also affect the phytoplankton community composition (e.g., increased occurrence of harmful algal blooms) (Paerl, 1988; Philippart et al., 2000; Heisler et al., 2008), grazing and transfer to higher trophic levels (Malzahn et al., 2007; Finkel et al., 2010), and biogeochemical cycles (Borges and Gypens, 2010). These changes in

ecosystem structure impact the emission/absorption by aquatic ecosystems of greenhouse gases (GHG), such as CO₂, and other climate-active gases, such as dimethylsulfide (DMS) (Gypens et al., 2009; Gypens and Borges, 2014). Correctly predicting changes in ecosystem structure in response to environmental change is then of prime importance in order to estimate and predict the role of aquatic ecosystems on global biogeochemical cycles and on the emission/absorption of GHG and climate-active gases by marine ecosystems.

Accurately predicting these changes requires that models correctly describe the link between phytoplankton growth and uptake of nutrients. Although high nutrient loads generally result in high algal biomass, phytoplankton nutrient requirements are specific (Quigg et al., 2003; Lagus et al., 2004), depending on acclimation to light intensity (Klausmeier et al., 2008; Sunda and Huntsman, 1997) or on the ability to store nutrients (as polyphosphate, nitrogen and ferritin reserves) (Geider and La Roche, 2002; Klausmeier et al., 2008). Moreover, most phytoplankton organisms are also able to acquire nutrients from organic sources when inorganic forms (their preferred source) are limiting. To acquire nutrients from organic sources, phytoplankton organisms can directly ingest prey or particulate organic matter by phagotrophy (mixotrophy) or absorb dissolved organic matter by osmotrophy. When DIP is limiting, most phytoplankton organisms are also able to indirectly acquire P from dissolved organic P (DOP; e.g., sugar phosphates, phospholipids, nucleotide phosphates) by synthesizing ecto-enzymes that hydrolyze DOP to release DIP (Kuenzler and Perras, 1965; Cembella et al., 1984; Flynn et al., 1986; Hoppe, 2003; Glibert and Legrand, 2006; Liu et al., 2012). Alkaline phosphatase (AP) is one of

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Table 1
Parameter values.

Parameter	Value	Units	Explanation	Source
CP_F	65	mol C mol P ⁻¹	C:P ratio for F metabolites	Lancelot et al. (2005)
k_p^A	0.3	mmol P m ⁻³	Half-saturation constant for DIP uptake by diatoms	Ghyoot et al. (2017)
k_p^{NF}	0.25	mmol P m ⁻³	Half-saturation constant for DIP uptake by nanoflagellates	Ghyoot et al. (2015)
k_p^P	0.3	mmol P m ⁻³	Half-saturation constant for DIP uptake by <i>Phaeocystis</i> colonies	Ghyoot et al. (2015)
k_{uptP}^{reg}	0.01	–	Half-saturation constant for upt_P regulation by S_P	Ghyoot et al. (2015)
upt_P^{maxDA}	0.31	h ⁻¹	Max P uptake rate by diatoms	Ghyoot et al. (2017)
upt_P^{maxNF}	0.22	h ⁻¹	Max P uptake rate by nanoflagellates	Ghyoot et al. (2015)
upt_P^{maxOP}	0.44	h ⁻¹	Max P uptake rate by <i>Phaeocystis</i> colonies	Ghyoot et al. (2015)
$X_{S_P}^{maxDA}$	0.15	–	Maximum $S_P/(F/CP_F)$ ratio for diatoms	Ghyoot et al. (2017)
$X_{S_P}^{maxNF}$	0.2	–	Maximum $S_P/(F/CP_F)$ ratio for nanoflagellates	Ghyoot et al. (2017)
$X_{S_P}^{maxOP}$	0.2	–	Maximum $S_P/(F/CP_F)$ ratio for <i>Phaeocystis</i> colonies	Ghyoot et al. (2017)

the well-known enzymes responsible for the hydrolysis of DOP. The ability to acquire P from different sources can be particularly important in oligotrophic ecosystems (Arenovski et al., 1995; Mather et al., 2008), but also in eutrophic waters (Rousseau et al., 2004; Burkholder et al., 2008) frequently subjected to nutrient imbalance and where bloom-forming harmful algal species, known to be particularly competitive under unbalanced nutrient conditions, can occur (Glibert and Legrand, 2006).

Taking into account the capacity of phytoplankton to grow on organic nutrient sources can modify the intensity of primary production and, therefore, has to be included in model development and prediction. Here, we investigate the impact of the use of organic P on phytoplankton production and its consequences for biogeochemical cycles, in particular, CO₂ and DMS exchanges with the atmosphere in the Southern Bight of the North Sea (SBNS). Since the late 1980's, the area is P limited and constitutes therefore an ideal case study (Billen et al., 2001, 2005; Soetaert et al., 2006). The SBNS is characterized by a high primary production resulting from a succession of diatom and *Phaeocystis* blooms (Lancelot et al., 2007). This latter species has not been reported to be mixotrophic but, in contrast, it has been shown to induce AP synthesis to use DOP as P source when DIP is low (Veldhuis et al., 1987; van Boekel and Veldhuis, 1990). It can be hypothesized that utilization of DOP allows to sustain massive spring blooms of *Phaeocystis* in the nitrate-enriched waters of the SBNS. *Phaeocystis*, as other haptophytes in general, is an important producer of dimethylsulfoniopropionate (DMSP) (Keller et al., 1989), the precursor of DMS. The impact of organic P use on (i) ecosystem primary production and (ii) CO₂ and DMS fluxes is studied using an extended version of the R-MIRO-BIOGAS model (previously validated in the SBNS; Gypens et al., 2004, 2014) that includes a description of the ability of phytoplankton organisms to use DOP as a source of P (Ghyoot et al., 2015).

2. Material and methods

The MIRO-BIOGAS model describes the dynamics of phytoplankton (diatoms, nanoflagellates and *Phaeocystis*), zooplankton (microzooplankton and copepods) and bacteria involved in the degradation of organic matter and the regeneration of inorganic nutrients in the water column and the sediment (Lancelot et al., 2005). The model also includes the description of the carbonate system (Gypens et al., 2004) and the DMS(P) cycle (Gypens et al., 2014). The description of the carbonate system is based on the evolution of dissolved inorganic carbon (DIC) and total alkalinity (TA). It allows the calculation of partial pressure of CO₂ (pCO₂), pH and air-sea CO₂ fluxes (Gypens et al., 2004). The DMS(P) cycle describes the DMSP and DMS dynamics; those consist of biological transformations by phytoplankton and bacteria as well as physico-chemical processes (i.e., photodegradation and DMS air-sea exchange) (Gypens et al., 2014).

The ability of phytoplankton organisms to use the DOP as a source of P when DIP is limiting was added to the MIRO model according to the simplified formulation suggested in Ghyoot et al. (2015). The biomass

of autotrophic organisms is divided into three pools: F (functional and structural metabolites (e.g., deoxyribonucleic acid, ribonucleic acid proteins) containing C, N, P and Si for diatoms), S_C (monomeric carbon provided by photosynthesis or catabolism of C reserves), and R_C (carbon reserves). A fourth pool, analogous to S_C, describes the internal soluble DIP used for F synthesis (S_P). This description decouples photosynthesis from growth. On this basis, the phytoplankton growth is controlled by the availability of carbon, light, and inorganic nutrients. The nutrient limitation follows the minimum law in which P limitation depends on X_{S_P} (the ratio between S_P and the P contained in F (computed based on the C:P ratio of F, CP_F), i.e., X_{S_P} = S_P/(F/CP_F)) and N limitation depends on external DIN. In this simplified formulation, AP activity (APA) releasing DIP from DOP is implicitly considered by allowing the direct uptake of DOP when DIP becomes limiting. The total P (DIP + DOP) uptake (upt_P; mmol P m⁻³ h⁻¹) is a function of the external DIP + DOP concentrations and the internal S_P status expressed by the ratio X_{S_P}/X_{S_P}^{max} (Eq. (1)):

$$upt_P = upt_P^{max} \cdot \frac{(DIP + DOP)}{(DIP + DOP) + k_p} \cdot \frac{(1 - X_{S_P}/X_{S_P}^{max})^4}{(1 - X_{S_P}/X_{S_P}^{max})^4 + k_{uptP}^{reg}} \cdot \frac{F}{CP_F} \quad (1)$$

where upt_P^{max} = Maximal transport rate of P at optimal temperature (h⁻¹)

k_p = Half-saturation constant of P uptake (mmol P m⁻³)

X_{S_P} = Ratio between S_P and P included in F, i.e., S_P/(F/CP_F) (mmol P mmol P⁻¹)

$X_{S_P}^{max}$ = Maximal ratio between S_P and P included in F (mmol P mmol P⁻¹)

k_{uptP}^{reg} = Half-saturation constant of upt_P regulation by S_P (mmol P mmolP⁻¹)

CP_F = Carbon to phosphorus ratio of F (mmol C mmol P⁻¹)

Parameter values and references are given in Table 1.

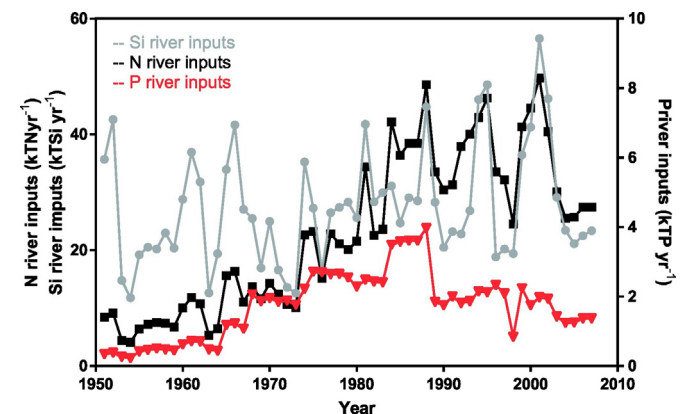


Fig. 1. Evolution of annual river loads of silica (Si), nitrogen (N) and phosphorus (P) in the Belgian coastal zone from 1951 to 2007 simulated by R-MIRO-BIOGAS.

The proportions of DIP and DOP that are taken up are functions of (i) their respective concentrations and (ii) a preference function for DIP over DOP (f_{DIP} ; Eq. (2)) based on the external DIP. DOP uptake decreases to zero when the external DIP is high. On the opposite, when DIP is low, most of the P input is provided by DOP.

$$f_{DIP} = 1 - \frac{DIP}{DIP + k_{fDIP}} \quad (2)$$

The half-saturation constant for DOP uptake inhibition by DIP (k_{fDIP} ; Eq. (2)) has been estimated at $0.2 \text{ mmol P m}^{-3}$ (Ghyoot et al., 2015). This simplified formulation was derived from a mechanistic model

explicitly describing the ability of phytoplankton to use DOP when DIP is limiting, by synthesizing AP that releases DIP from DOP and describing the main processes related to the P metabolism, including DIP transport, intracellular accumulation and assimilation (Ghyoot et al., 2015).

To take account for the ability of bacteria to also use DOP (by the use of AP) as P source when DIP is limiting (e.g. Hoppe, 2003; Labry et al., 2005; Ivancić et al., 2010), the description of bacterial growth and associated nutrient uptake were modified from the original description of Lancelot et al. (2005). A P limitation of bacterial growth was added as a Michaelis-Menten function. The half-saturation constant for P limitation was estimated at $0.01 \text{ mmol P m}^{-3}$ (Codeço and Grover,

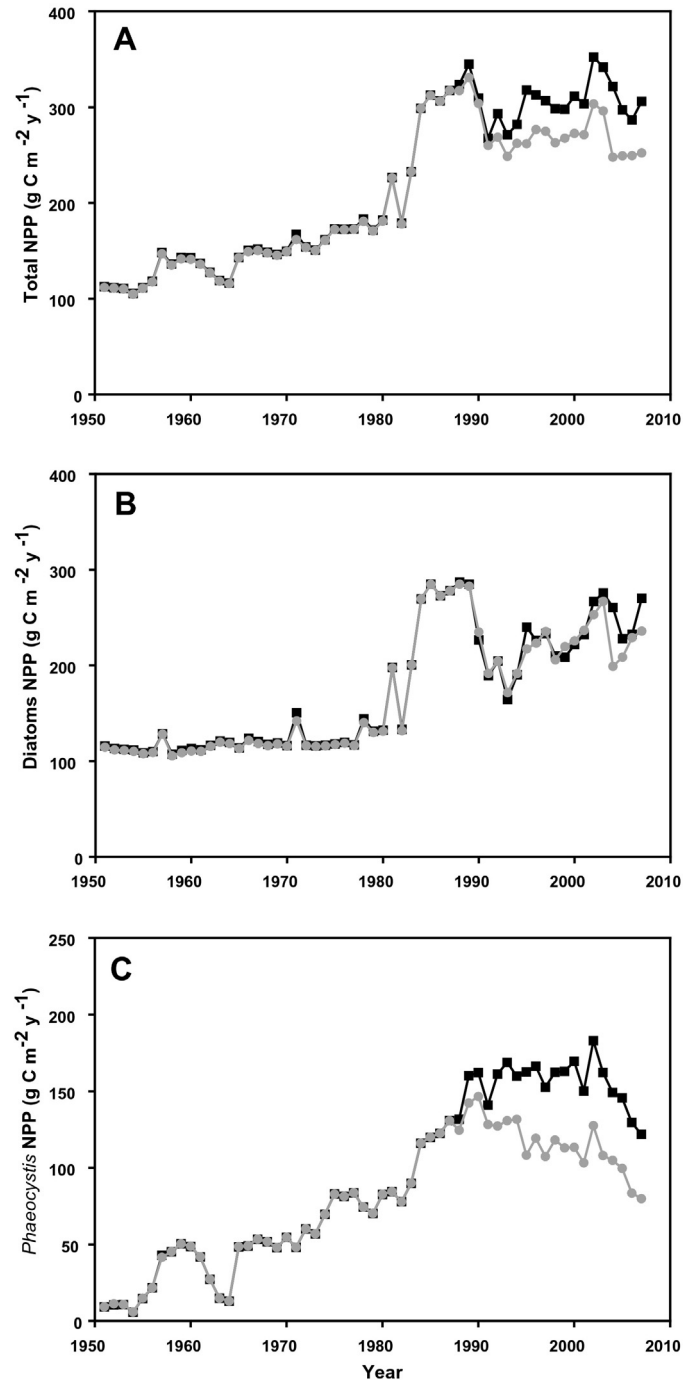


Fig. 2. Evolution of (A) total net primary production, (B) diatom net primary production and (C) *Phaeocystis* net primary production in the Belgian coastal zone from 1951 to 2007 simulated by R-MIRO-BIOGAS with (black line) and without (grey line) taking into account the ability to use DOP as a P source for phytoplankton growth.

2001). The relative proportions of DIP and DOP taken up to sustain bacterial growth are estimated similarly to phytoplankton (f_{DIP} ; Eq. (2)). The half-saturation constant for DOP uptake inhibition by DIP (K_{DIP} ; Eq. (2)) has been estimated at $0.01 \text{ mmol P m}^{-3}$ to take account the higher affinity of bacteria for DIP.

To estimate the impact of nutrient loads modification on the coastal zone, the marine biogeochemical model was coupled to the RIVERSTRAHLER model. The RIVERSTRAHLER model (Garnier et al., 2002) describes carbon and nutrient transformations along the river system as a function of meteorological conditions and a GIS (geographic information system) description of human activity on the watershed (Billen et al., 2001, 2005; Passy et al., 2013). The coastal model is implemented in a multi-box OD frame (Lancelot et al., 2005) from the Western Channel to the Belgian Coastal Zone (BCZ) using the 10-days RIVERSTRAHLER input as river forcing, forced by daily wind speed, sea surface temperature (SST), monthly atmospheric $p\text{CO}_2$, daily global solar radiation (climatology for 1989–1999) and river DIC and TA inputs (Seine and Scheldt rivers) computed as a function of freshwater discharge (Gypens et al., 2009). Two simulations were performed for the 1950–2007 period after a 10 year spin-up and analysis of output results focusses on the BCZ. In the reference simulation we consider that DIP is the only P source available for phytoplankton, while bacteria can use both DIP and DOP. In the second simulation, we consider DIP and DOP as P source for both bacteria and phytoplankton.

3. Results

3.1. Diatom and *Phaeocystis* production

N and P annual river loads increased from 1950 to the mid 1980's (Fig. 1). Afterwards, P loads decreased and N loads remained high, leading to a change in N:P ratio and P limitation of primary production. In response to the changes in nutrient river loads, total net primary production (NPP) increased in the BCZ (Fig. 2A). From 1951 to 2007, total NPP increased from 111 to $252 \text{ g C m}^{-2} \text{ y}^{-1}$. NPP change was accompanied by a change in the relative importance of phytoplanktonic communities (with diatoms to *Phaeocystis* ratio decreasing from 10 to 1.5 during the simulated period; Fig. 2B, C). Each year, the seasonal succession was characterized by a succession of spring diatoms, *Phaeocystis* and summer diatoms (Lancelot et al., 2005). After the decline of the *Phaeocystis* bloom, the area was characterized by intense bacterial activity. The relative importance of these blooms varied from year to year (Gypens et al., 2007, 2009; Lancelot et al., 2007). From 1950 to 1970, annual production of diatoms was largely higher than that of *Phaeocystis* with average values, respectively, around 115 and $33 \text{ g C m}^{-2} \text{ y}^{-1}$. *Phaeocystis* production represented on averaged 20% on annual NPP production. From 1970 onwards, the combination of increased nutrient loads and of the increase of the N:P ratio, favored *Phaeocystis* production, bringing it to a level similar to that of diatoms (Fig. 2B, C). This was particularly exacerbated in the 1990's when the sustained N loads

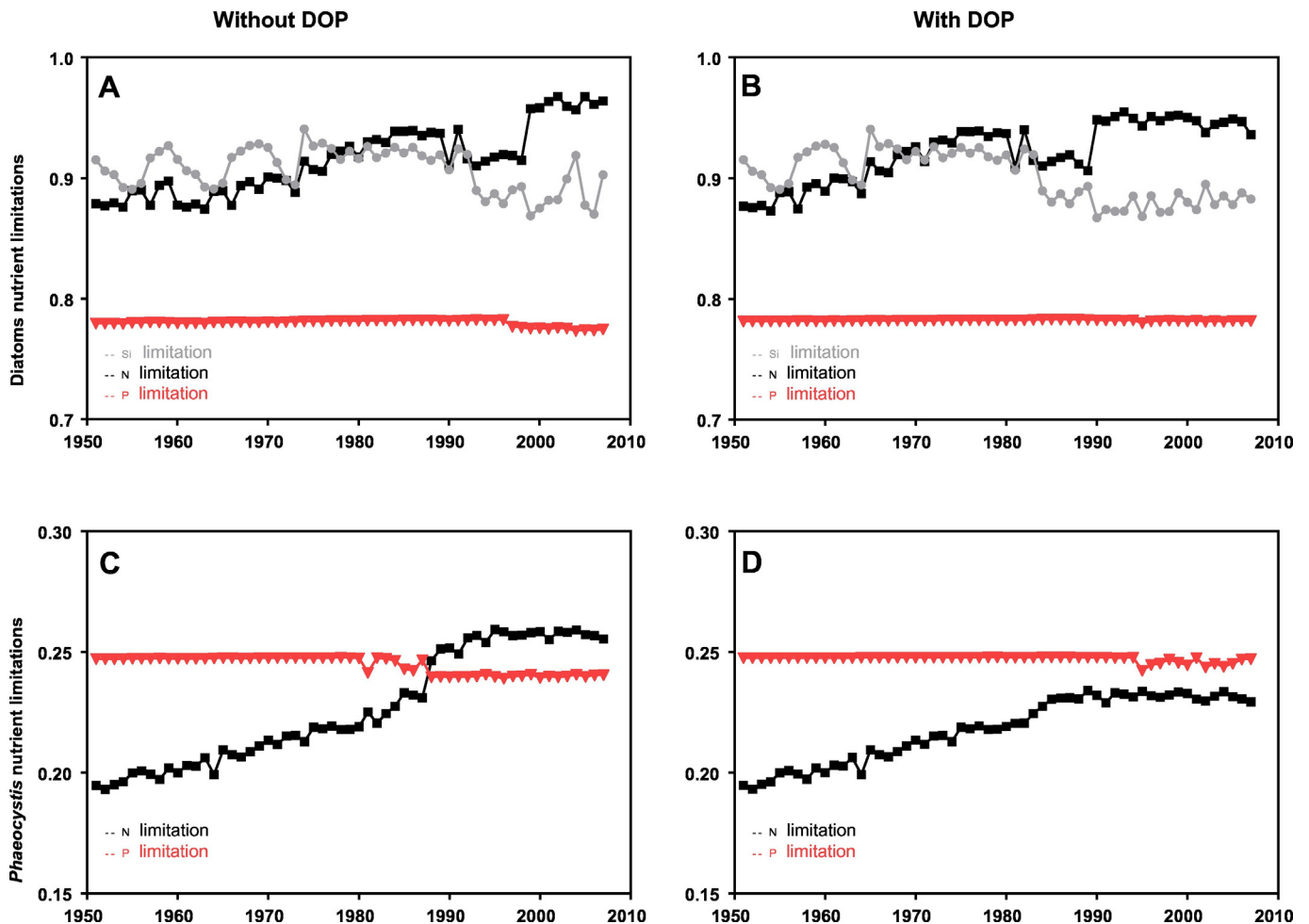


Fig. 3. Evolution of (A, B) diatoms and (C, D) *Phaeocystis* nutrient limitations in the Belgian coastal zone from 1951 to 2007 simulated by R-MIRO-BIOGAS with (B, D) and without (A, C) taking into account the ability to use DOP as a P source for phytoplankton growth.

started to combine with decreasing P river loads (Fig. 2B, C). In 1993, *Phaeocystis* production account for 45% of the total NPP.

The ability of phytoplankton to use DOP as additional source of P when DIP is limiting modified the magnitude of phytoplankton production. For diatoms, the increase in P availability was not sufficient to strongly modify the annual biomass that only slightly increased at the end of the simulated period (Fig. 2B). From 1988 onwards, *Phaeocystis* production increased up to 50% due to DOP use (Fig. 2C). DOP use mainly impacted model results at the end of the simulated period when P river loads decreased (Fig. 1), inducing a P limitation of phytoplankton growth (Fig. 3A, C). From 1951 to the end of the 80's, N is the limiting nutrient of *Phaeocystis* growth (Fig. 3C). During this period, P limitation is quite constant but NPP increase (Fig. 2C). At the end of the 80's, *Phaeocystis* growth limitation shifted from a N limitation to a P limitation (Fig. 3C) as a result of P river loads decreased (Fig. 1). Considering both DOP and DIP as P sources resulted in decreased P limitation (Fig.

3D) and favored *Phaeocystis* production from 1980 onwards (Fig. 2C). The increase in biomass will modify all the nutrient limitations and therefore that of N also that will be much more important and could become the nutrient limiting *Phaeocystis* growth (Fig. 3D). For diatoms, the increase in P availability is not sufficient to strongly modify the annual biomass (Fig. 2B) and the limitations do not change very much. However, the use of DOP alleviated the P limitation of diatom growth (Fig. 3B), particularly in summer (not shown) when biomass can increase as a result of DOP used.

3.2. Climate-active gas fluxes

The exchange with the atmosphere of CO₂ and particularly of DMS responded to the modification of the primary production from 1951 to 2007. The increase (decrease) of river nutrient loads increased (decreased) primary production, atmospheric CO₂ sink (Fig. 4A) and DMS

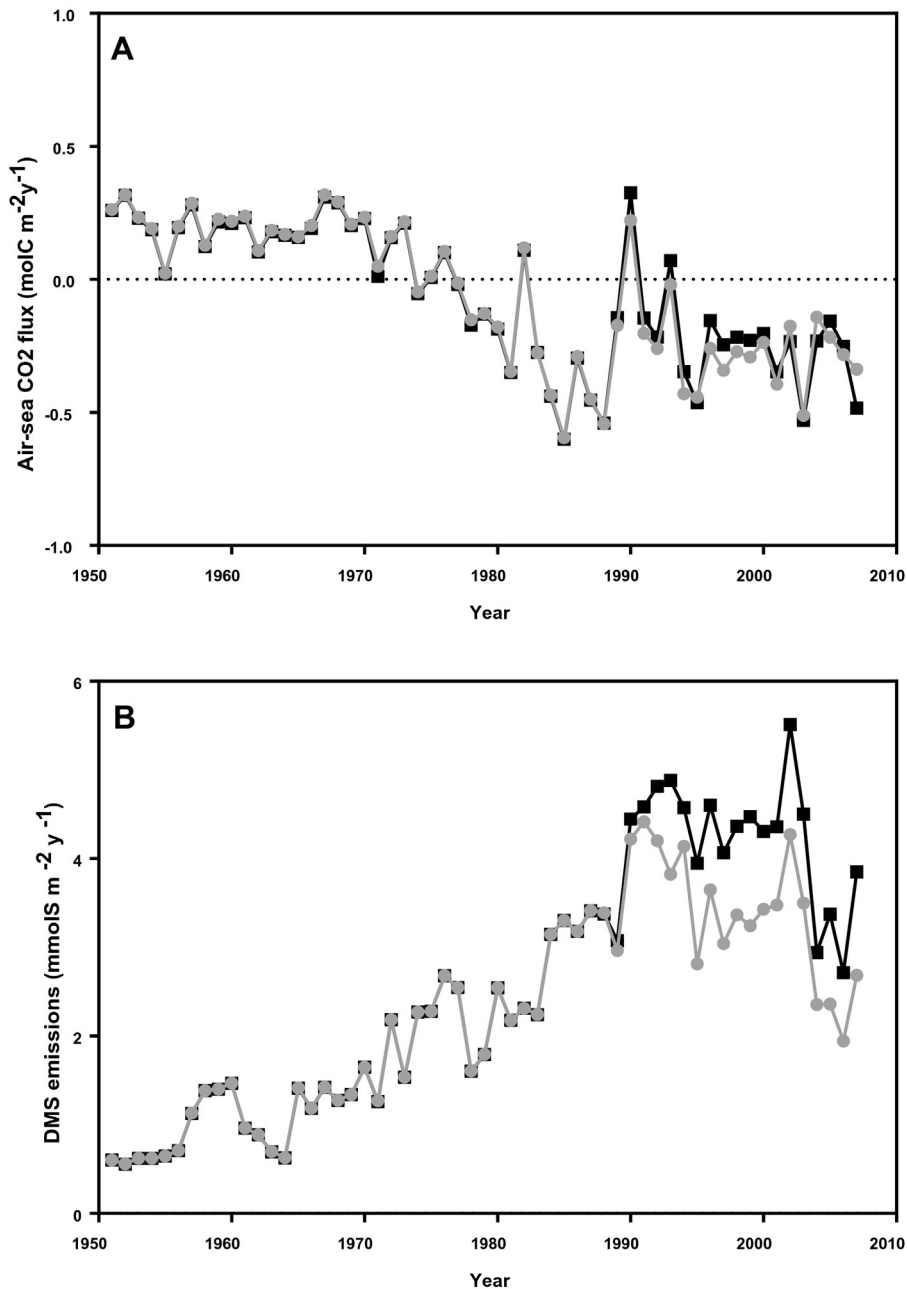


Fig. 4. Evolution of (A) air-sea CO₂ flux and (B) DMS emissions in the Belgian coastal zone from 1951 to 2007 simulated by R-MIRO-BIOGAS with (black line) and without (grey line) taking into account the ability to use DOP as a P source for phytoplankton growth.

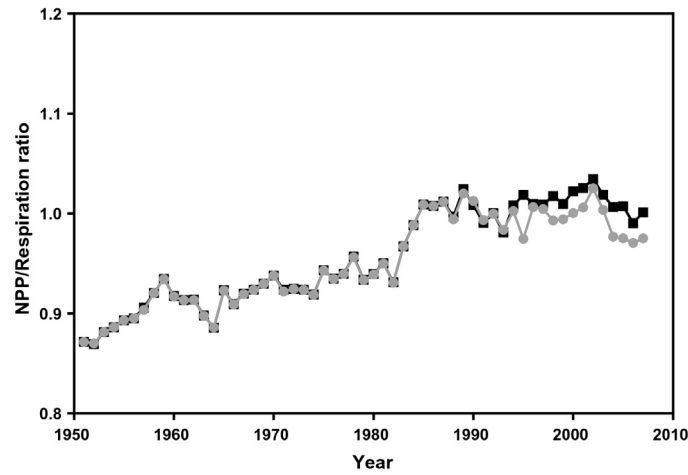


Fig. 5. Evolution of total NPP to respiration ratio in the Belgian coastal zone from 1951 to 2007 simulated by R-MIRO-BIOGAS with (black line) and without (grey line) taking into account the ability to use DOP as a P source for phytoplankton growth.

emissions (Fig. 4B). From 1951 to 2007, the atmospheric CO₂ flux varied from a source of CO₂ of 0.7 mol C m⁻² y⁻¹ to a sink of CO₂ of about 0.9 mol C m⁻² y⁻¹. During the same period, DMS emissions increased from 1.6 to 7.3 mmol S m⁻² y⁻¹. The model representation taking into account the capacity of phytoplankton to use DOP modified climate-active gas exchanges with the atmosphere. Simulated DMS emissions (Fig. 4B) increased every year since 1988 when considering the use of DOP by phytoplankton. In parallel, CO₂ fluxes were also modified but less than DMS fluxes and the direction of the change varied from one year to another (Fig. 4A). But in general the sink of CO₂ atmospheric increased at the end of the simulated period (Fig. 4A) in response to use of DOP and increase of primary production. Changes in primary production impacted DMS and CO₂ fluxes differently. The DMS emissions mainly resulted from, and were proportional to, the modification of *Phaeocystis* production. The CO₂ fluxes resulted from the balance of autotrophic and heterotrophic processes. Autotrophic processes were favored compared to heterotrophic processes when phytoplankton growth on organic P was included in the model (Fig. 5).

4. Discussion

The concentration of dissolved nutrients or their ratios are not always reliable to predict primary production or phytoplankton nutrient

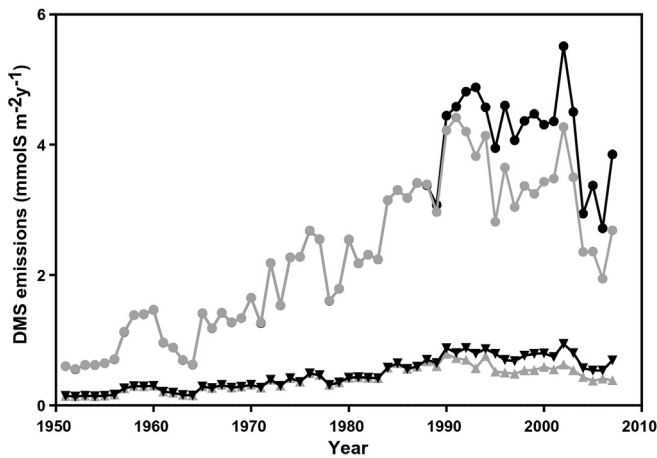


Fig. 6. Evolution of DMS emissions in the Belgian coastal zone from 1951 to 2007 simulated by R-MIRO-BIOGAS with (black line) and without (grey line) taking into account the ability to use DOP as a P source for phytoplankton growth considering that the whole (circle) or just a part (triangle) of bacterial community is able to degrade DMSP.

limitation (e.g. Trommer et al., 2013; Letscher and Moore, 2015). Taking account the use of organic P by phytoplankton and by bacteria can change heterotrophic/autotrophic process balance and influence carbon cycling, particularly in P limited environments (Løvdal et al., 2007). Among the processes influencing nutrient availability or use, APA can be important in eutrophied coastal areas (Veldhuis et al., 1987) and can impact the ecosystem structure and its functioning. Our results confirm that the use of organic compounds as nutrient source need to be taken into account in the representation of primary production in mathematical models to avoid underestimation of primary production if only dependent on the availability of inorganic nutrients (Llebot et al., 2010).

Both interspecific competition and competition among trophic compartments are important to estimate the importance of GHG and other climate-active gas emissions. Regarding the S cycle and DMS emissions, DMS(P) production and emission are species specific. Therefore, phytoplankton dominance and competition between phototroph organisms will determine the importance of the atmospheric flux together with the importance of viral lysis of phytoplankton cells, the activity of grazers, and the activity and composition of the heterotrophic community. In particular, bacterial DMS production depends on their biomass, composition and relative demands of carbon versus sulfur. As a first approximation, we considered in the model that the whole bacterial community was able to consume and degrade DMSP in DMS or other degradation products as SO₄²⁻ or methanethiol (MeSH) (Gypens et al., 2014). However, this is not correct and previous sensitivity tests showed the importance of this simplification on the magnitude of DMS emissions (Gypens et al., 2014). In absence of sufficient information on seasonal changes in bacterioplankton composition in the studied area and their respective role for DMSP consumption/degradation, it is currently not possible to develop an explicit description of different bacterial groups. However, to test the effect of this hypothesis in our results, an additional simulation was done by modulating bacterial DMS yields based on the variation of bacterial P limitation. Indeed, it has been shown that the availability of nutrients can modulate the composition of heterotrophic bacterial communities (e.g. Thingstad et al., 1998; Pinhassi et al., 2006). In particular, P scarcity was particularly limiting to some *Roseobacter* clades (Pinhassi et al., 2006), which are abundant in the North Sea area (Zubkov et al., 2001, 2002) and important DMS producers (Gonzalez et al., 1999; Moran et al., 2012). Results showed that if the proportion of bacteria able to transform DMSP into DMS decreased, the magnitude of DMS emissions decreased as well, and the maximal DMS emission simulated in 2002 decreased from 5.5 to 0.95 mmol S m⁻² y⁻¹ (Fig. 6). However, whatever the proportion of bacteria able to use and degrade DMSP, considering the ability by phytoplankton to use DOP increased its biomass and related DMSP

production and DMS emissions (Fig. 6). For example, in 2002, DMS emissions increased from 4.3 to 5.5 mmol S m⁻² y⁻¹ and 0.63 to 0.95 mmol S m⁻² y⁻¹ (Fig. 6) when considering respectively a part of or all bacteria population able to use/degrade DMSP. Regarding the carbon cycle and CO₂ fluxes, CO₂ fluxes were related to both autotrophic and heterotrophic processes but (relatively) independent of the bacterio- and phyto-plankton composition. Competition between phototrophic and heterotrophic organisms will therefore determine the importance of the CO₂ atmospheric flux, more than phytoplankton community composition.

In the study area, eutrophication modified primary production and induced a shift from CO₂ source to the atmosphere to CO₂ sink (Gypens et al., 2009; Fig. 4A) and a very strong increase in the DMS emissions to the atmosphere (Gypens et al., 2014; Fig. 4B). Although the SBNS has a relatively small surface area, should such trends be general to eutrophied coastal environments globally, this might have a favorable impact on global warming because CO₂ is the main anthropogenic GHG contributing to the increase of radiative forcing, and DMS could induce cooling of the atmosphere (Charlson et al., 1987). Consequently, it is necessary to correctly model the fluxes of these two gases in coastal environments as well as their response to anthropogenic pressures (specifically eutrophication), in addition to other changes that also affect the open ocean such as acidification and warming of surface waters. For the 2000–2007 period, the mean annual CO₂ sink was 0.28 and 0.30 mol C m⁻² yr⁻¹ for the reference simulation and simulation with assimilation of DOP, respectively. For the same period, the mean annual source of DMS was 3.0 and 3.9 mmol S m⁻² yr⁻¹ for the reference simulation and simulation with assimilation of DOP, respectively. Thus, the inclusion of DOP assimilation by phytoplankton induces a moderate change of CO₂ sink but an important increase of DMS emission (about 40%). This is particularly relevant for the correct quantification of the marine emissions of DMS of continental shelves affected by eutrophication. Although continental shelves only occupy 7% of the total surface of the ocean, continental shelves are also significant sources of DMS emissions (per surface area) with annual average DMS concentration on the European continental shelf (“NE Atlantic Shelves” province) being 50% higher than in the Atlantic Ocean at the same latitude (“N. Atlantic Drift” province) (Lana et al., 2011).

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