Université du Québec
à Rimouski

MODÉLISATION DES PROCESSUS PHYSIQUES ET BIOLOGIQUES INFLUENÇANT LA SÉDIMENTATION DES PARTICULES BIOGÉNIQUES DANS LE GOLFE SAN JORGE (PATAGONIE, ARGENTINE)

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À ma famille, en particulier à ceux que j’ai perdu, éloignée de chez moi

“Hay hombres que de su cencia
tienen la cabeza llena;
hay sabios de todas menas
mas digo, sin ser muy ducho
es mejor que aprender mucho
el aprender cosas buenas”

José Hernández (¨El Gaucho Martín Fierro”, 1872)

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RÉSUMÉ

Les processus marins, comme la pompe biologique, définissent et influencent le flux de matière organique particulaire (MOP) vers les sédiments marins. Bien que le Golfe San Jorge (GSJ) soit l'une des zones les plus productives au monde, peu d'études ont été faites pour connaître et évaluer le transport vertical de MOP. Dans le but de mieux comprendre les modes de production et d'export de matière organique dans la colonne d'eau du GSJ (Patagonie, Argentine), ce mémoire vise à répondre à deux grandes questions : quelle est l'influence des organismes migrateurs, comme le zooplancton, dans la dynamique de ces flux, et comment les processus de formation et de transformation de la matière organique particulaire détritique vont, quant à eux, affecter le flux vertical de carbone. La principale hypothèse est que le flux de carbone est influencé par la dynamique détritique, qui modifie les interactions écosystémiques, et que celle-ci est fortement influencée par le transport actif du zooplancton, principal agent de production des détritus. L'utilisation de modèles numériques est de plus en plus courante pour étudier la dynamique des écosystèmes marins et pour la gestion environnementale. La première partie de ce mémoire présente l'influence d'une nouvelle paramétrisation de la migration verticale diurne du zooplancton (DVM) dans un modèle 1D couplé à un modèle de type NPZD. Les résultats de cette première partie montrent que le phytoplancton et les détritus augmentent en présence du mouvement migratoire, alors que le zooplancton diminue. La seconde partie présente une conceptualisation des principaux processus affectant différents types de détritus, ainsi que des formulations permettant d'intégrer ces processus dans un modèle biogéochimique eulérien, dans le but de mieux simuler le flux du carbone organique et son rôle dans la pompe biologique dans le GSJ.

Mots clés : modèle NPZD, migration du zooplancton, phytodétritus, pelotes fécales, flux de carbone

ABSTRACT

Marine processes, such as the biological pump, modulate and influence the particulate organic matter (POM) flux towards the seabed. Although the San Jorge Gulf (SJG) is one of the most productive areas of the world, only few studies focused on vertical transport and carbon fluxes. In order to clearly understand organic matter production and its export in the water column of the SJG (Patagonia, Argentina), this thesis addressed two main questions: what is the influence of migrating organisms, such as zooplankton, and the influence of aggregation and transformation processes of particulate organic matter in the vertical carbon flux. The general hypothesis proposed here is that carbon flux will be affected by detrital dynamics, modifying ecosystems interactions and that this is strongly influenced by zooplankton active transport, as the main contributor of detritus. The use of numerical simulation gained a great interest in scientific research community for studying marine ecosystems dynamics and as a management tools. The first chapter presents the effect of a new parameterization of zooplankton diel vertical migration (DVM) in a 1D, coupled to a biogeochemical model. Both phytoplankton and detritus results show an increase in their concentrations, while zooplankton concentration decreases with the addition of the migration behavior. The second chapter presents a conceptual model of principal processes affecting different detritus types and the formulations, which will after allow coupling it with an Eulerian biogeochemical model to better simulate organic carbon flux and its role in the biological pump in the SJG.

Keywords: NPZD model, zooplankton migration, phytodetritus, faecal pellets, vertical carbon flux

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INTRODUCTION GÉNÉRALE

POMPE BIOLOGIQUE

La biosphère marine est une composante importante du cycle du carbone global, responsable de près de la moitié de l'absorption annuelle du dioxyde de carbone (CO_2) atmosphérique (Le Quéré et *al.*, 2008). La pompe biologique est l'ensemble des processus par lequel le CO_2 atmosphérique est incorporé par les organismes marins, exporté vers le fond et finalement séquestré dans les sédiments marins (Turner, 2002). Cela commence avec la formation de matière organique dans la zone euphotique, où le phytoplancton incorpore une partie du CO_2 dissout dans la colonne d'eau. Par la suite, l'export du carbone en profondeur est contrôlé en partie par des organismes d'ordre supérieur via le broutage et le relâchement de pelotes fécales (Richardson et Jackson, 2007), par la sédimentation de la matière organique particulaire (cellules vivantes et mortes du phytoplancton, etc.), ainsi que par le mélange de la fraction organique dissoute. La métabolisation de la matière organique se produise principalement dans les couches profondes de la colonne d'eau, où ce sont les bactéries qui sont essentiellement responsables de leur reminéralisation en composés inorganiques.

La pompe biologique couplée à la pompe de solubilité, qui implique des processus physiques et chimiques comme le transport vertical, la dissolution, la turbulence et la dégradation oxydative, a séquestré environ 30 % de la production anthropique de CO_2 depuis le début de l'ère industrielle (Sarmiento, 1993). Par conséquent, ces processus agissent comme une rétroaction négative dans un contexte de réchauffement climatique (Boyd et Doney, 2003). Une analyse des processus qui contribuent à cet effet a révélé que, sans la pompe biologique, l'influence négative du changement climatique dans les océans serait encore plus drastique (Sarmiento et *al.*,1998). Les résultats de différents exercices de modélisation indiquent une augmentation du CO_2 atmosphérique d'un facteur trois (de 280 µatm à 720 µatm) en absence de ces deux pompes. De plus, la dissolution du CO_2 dans les eaux de surface de l'océan produit une diminution du pH et par conséquent l'acidification du milieu marin (Sarmiento, 1993).

La quantité de carbone atteignant les fonds marins est affectée par plusieurs facteurs, en commençant par la quantité de carbone particulaire produite (production primaire et secondaire). Le carbone particulaire de densité plus grande que celle du milieu marin peut ensuite sédimenter vers le fond à des taux variant en fonction de la densité, de la forme et de la taille des particules. La formation d'agrégats par coagulation peut donc affecter la vitesse de sédimentation des particules qui est elle-même affectée par les courants verticaux et la turbulence du milieu. L'agrégation modifie les propriétés des particules et les interactions avec le milieu environnant (Jackson et Burd, 1998). La combinaison des particules petites de sédimentation lente, à des agrégats qui sédimentent plus rapidement, favorise l'enlèvement des particules de la surface marine. Par exemple, les agrégats tel que la neige marine (> 0.5 mm) sédimentent plus rapidement que les cellules solitaires du phytoplancton (20-370 m d^{-1} et 0-30 m d^{-1}, agrégats et phytoplancton, respectivement ; Turner, 2002 ; Smayda, 1971). Ce processus d'agrégation a aussi un effet direct sur la concentration de particules dans la colonne d'eau (Stemann et *al.*, 2004). Cependant, deux processus clés ont été identifiés pour l'export du carbone organique particulaire dans la colonne d'eau et méritent une attention particulière : le transport effectué par le zooplancton, particulièrement par des organismes qui migrent verticalement et la chute gravitationnelle des agrégats biogéniques avec l'ajout des particules de biominéraux (Honjo et *al.*, 2008 ; Lampitt et *al.*, 1993). Le premier processus fait référence particulièrement au relâchement de pelotes fécales en profondeur par le zooplancton et le deuxième à des agrégats tel que la neige marine qui est constituée par de grandes quantités de particules d'une grande diversité de sources (ex. carcasses abandonnées, agrégats de pelotes fécales et flocons de diatomées) qui ensemble atteignent des tailles supérieures à 500 µm (Alldredge et Silver 1988). Les processus mentionnés précédemment, permettent au carbone organique d'arriver à une profondeur significative rapidement par rapport au reste de la matière particulaire de vitesse lente (ex. fragments phyto et zooplancton mort), qui va être en partie métabolisé dans les eaux de surface avant d'arriver en profondeur en raison d'une densité similaire à l'eau environnante (Honjo et *al*., 2008).

MIGRATION VERTICALE DU ZOOPLANCTON (TRANSPORT ACTIF)

La migration verticale est un phénomène biologique marin bien connu. Il est considéré comme un des plus importants déplacements cohérents d'organismes aquatiques, notamment en termes de biomasse (Ringelberg, 2009). Pour le cas de la migration verticale diurne (MVD), elle a été observée chez la majorité des espèces zooplanctoniques d'eau douce et océanique (Ringelberg, 2009). Divers comportements ont été décrits pour le zooplancton en milieu marin, lesquels ont été reliés avec différents facteurs environnementaux (ex. température, lumière, nourriture) et différentes conditions propres des organismes (ex. physiologie, ontogénie) (Batchelder et *al*., 2002 ; Pearre, 2003). La MVD réfère à la descente active des organismes sur plusieurs dizaines voire centaines de mètres en profondeur pendant le jour et à sa remontée vers la surface durant la nuit. Ce type de mouvements verticaux du zooplancton est associé à plusieurs stratégies. D'abord, il permet d'exploiter différentes niches écologiques présentes à diverses profondeurs réduisant ainsi la compétition interspécifique pour le refuge et la nourriture (Ringelberg, 2009). En même temps, le mouvement permet la recherche de nourriture et la réduction du niveau d'exposition aux rayonnements solaires (Ringelberg, 2009). Il peut aussi être associé à une stratégie permettant d'éviter les prédateurs (Pearre, 2003). La diminution exponentielle de la lumière à mesure qu'elle pénètre dans la colonne d'eau implique que la prédation visuelle est plus intense proche de la surface pendant le jour (Dodson, 1990). Dans un même ordre d'idée, le zooplancton va diminuer sa prédation sur le phytoplancton qui se trouve dans les eaux de surface, mais le broutage pourrait être compensé durant la nuit (Dodson, 1990).

Il existe plusieurs évidences qui démontrent l'importance de la MVD dans le transfert de la matière organique dissoute et particulaire vers les eaux profondes de l'océan et donc son étroite relation avec le cycle du carbone (Ducklow et *al*., 2001). Le transport du carbone organique particulaire par le zooplancton comprend les processus de défécation, de prédation, de mortalité et la sédimentation des carcasses (Honjo et *al*. 2008). D'autre part, des processus physiologiques tel que l'excrétion contribuent à l'export du carbone organique dissous en profondeur (Ducklow et *al*., 2001 ; Steinberg et *al*., 2002).

Divers travaux ont déterminé l'importance de la migration diurne zooplanctonique sur le cycle du carbone dans l'océan (Honjo et *al*., 2008 ; Ducklow et *al*., 2001 ; Steinberg et *al*., 2000 ; Lampitt et *al*., 1993) et surtout comment elle peut affecter les résultats si celle-ci n'est pas prise en compte dans les analyses écosystémiques (Ariza et *al*., 2015 ; Bianchi et *al*., 2013). Le transport actif et la respiration produits par la communauté migratoire zooplanctonique peut représenter 10-30 % du flux gravitationnel moyenne total dans certaines régions, et par exemple dans le Pacifique Nord peut être encore plus significatif (Steinberg et *al*., 2008 ; Steinberg et *al*., 2000). Les valeurs indiquent un apport considérable du zooplancton au flux du carbone comparé à celui du micronecton, même si leurs contributions et leurs effets agissent à différentes profondeurs (Ariza et *al*., 2015). En conséquence, le bilan du flux de carbone sans l'incorporation de cette communauté peut être sous-estimé.

SÉDIMENTATION DES DÉTRITUS ET DES AGRÉGATS

Seulement une fraction (~ 15 %) du carbone organique produit dans la zone épipélagique est transférée vers la zone bathypélagique (Stemmann et *al*., 2004). La couche épipélagique est la zone comprise entre la surface et la pycnocline, incluant aussi la zone euphotique (Honjo et *al*., 2008). Avant cette étape du transfert, une grande partie du carbone est transformée dans les eaux mesopélagiques, c'est-à-dire au-dessous de la pycnocline et dessus la zone limite habitée par le zooplancton (Honjo et *al*., 2008). Les zones côtières marines ne reçoivent qu'une petite partie de la matière organique produite dans les couches de surface, dont presque 9 % sera enterrée dans les sédiments (Smith et Hollibaugh, 1993) après avoir été transportée par la chute des particules (Alldredge et Jackson, 1995). Les particules de grande taille telles que les pelotes fécales (ex. ~ 90 µm pour les copépodes) et les agrégats marins (> 1 mm pour le macro-gels) contribuent de manière importante à l'export du carbone organique vers les sédiments en raison de leur grande vitesse de chute (de l'ordre d'une centaine de mètres par jour, ex. pelotes fécales 100-250 m d^{-1} ; Turner, 2002 ; Gooday et *al*.,1990).

La sédimentation réfère dans ce mémoire au mouvement vertical dirigé vers le fond de particules en suspension dans l'eau. La vitesse de sédimentation réfère à la vitesse de ce mouvement en l'absence de turbulence ou de mouvements verticaux du fluide qui induirait, par exemple, une resuspension des particules.

Le carbone organique présent dans le fond marin est consommé, respiré ou finalement minéralisé dans le sédiment (Ducklow et *al*., 2001). L'abondance, la distribution et la biomasse des organismes benthiques constituent des bons indicateurs de la quantité et de la qualité de matière organique biodisponible qui arrive en profondeur (Gooday et *al*., 1990). Cet apport de matière organique peut être saisonnier et la réponse d'assimilation par des organismes est rapide dans les environnements peu profonds (Lampitt et *al*., 1993). La dynamique saisonnière est surtout évidente dans les zones côtières (tempérées et froides), alors que dans la région tropicale et dans l'océan ouvert est moins marqué (Gooday et *al*., 1990).

Quelques études ont démontré l'importance de l'agrégation dans le transport vertical de matière organique (Stemann et *al*., 2004 ; Alldredge and Jackson, 1995 ; Alldredge et *al*., 1990). La coagulation des petites particules en agrégats de plus grande taille permet la sédimentation rapide de la matière organique non vivante, qui d'une autre façon passerait plus de temps dans la colonne d'eau (Honjo et *al*., 2008). Ces agrégats agissent en même temps comme source de nourriture supplémentaire pour la communauté planctonique : par exemple le zooplancton peut brouter des petites particules qui d'une autre façon ne seraient pas disponibles pour leur nutrition (Alldredge et Jackson, 1995 ; Lampitt et al., 1993). La composition de la neige marine et des agrégats macroscopiques est très hétérogène (Turner, 2002). La classification des agrégats marins peut être effectuée en fonction de leur taille (nano, micro et macrogels) ou même sur la composition des particules prédominantes (Turner, 2002 ; Alldredge, 2000). À l'heure actuelle, il n'y pas de consensus général quant à la composition et au rôle des agrégats dans l'écosystème marin (Boyd et Trull, 2007). Cependant, les agrégats normalement comprennent une série de différentes sources de matière organique vivante (ex. picophytoplancton et bactéries) et no vivant (ex. pelotes fécales et exopolymères ; Alldredge et *al*., 1993).

SITE D'ETUDE ET PROBLEMATIQUE

Les plateaux continentaux sont des zones caractérisées par une forte production biologique et ont donc une grande importance dans le bilan global du carbone. Plus précisément, la région côtière de la Patagonie argentine, localisée en milieu tempéré, appartient à l'un des grands écosystèmes marins du monde (LME, *Large Marine Ecosystems*, Bisbal,1995). Elle présente une productivité primaire élevée de l'ordre de 300 g C m^{-2} an^{-1} (Behrenfeld et Falkowsi, 1997). Sur ce même plateau, le golfe San Jorge (GSJ) est un bassin semi-ouvert, situé entre le cap Dos Bahías au nord et le cap Tres Puntas au sud (44-47°S), couvrant une surface de 39 340 km^2. Le rôle du GSJ en tant que source ou puit de CO_2 atmosphérique n'a été que peu étudié. Des résultats d'études numériques suggèrent que ce rôle varie de manière saisonnière (Arruda et *al*., 2015 ; Bianchi et *al*., 2005).

L'écosystème du GSJ supporte une grande biodiversité, ainsi qu'une intense pêcherie (Yorio et *al*., 2015). Cette région est l'aire d'alimentation et de reproduction de plusieurs espèces commerciales de poissons et de calmars (Garcia et *al*., 2008). Les pêcheries peuvent conduire à la détérioration de l'écosystème en raison des prises accidentelles, de l'altération du fond marin et de l'ajout de déchets dans la colonne d'eau (Góngora et *al*., 2012). Il faut noter que dans le cas du GSJ ces ajouts peuvent atteindre jusqu'à 0.1 g m^{-2} an^{-1}, durant une saison de pêche (septembre-mai), et cela en considérant seulement la pêche du merlu (González-Zeballos et Yorio, 2006). Les déchets de la pêche sont riches en matière organique, ce qui peut représenter une importante source de carbone supplémentaire capable d'accélérer le métabolisme de l'écosystème, et qui pourrait en particulier constituer une source de nourriture pour des espèces généralistes comme le crustacé *Munida sp*, favorisant ainsi sa prolifération (Vinuesa et Varisco, 2007).

Une forte réduction de la concentration d'oxygène dissout par-dessous la pycnocline et qu'augment avec la profondeur, a été observée jusqu'aux couches profondes du golfe. De plus, les échantillons récoltés à partir des pièges à sédiment présentent des hautes concentrations en particules agrégées et une densité élevée de pelotes fécales de zooplancton ainsi que des fragments indifférenciés de matière organique ont été observés (Rapport final Coriolis II ; Massé-Beaulne, 2016). Ces résultats suggèrent un fort export de carbone ainsi qu'une intense activité hétérotopique entre 90-100 m, gamme de profondeur maximale mesurée au centre du GSJ (Palma et *al*., 2004). Ici, il est important de préciser qu'il n'existe pas d'information sur l'origine ou la dynamique des agrégats ainsi que sur le rôle écologique que ce type de particule pourrait jouer dans la zone centrale du golfe où elle a été étudiée principalement.

La vitesse de sédimentation et la vitesse de reminéralisation des particules en suspension sont deux facteurs déterminant du flux vertical de carbone et par conséquent de l'efficacité et de l'intensité de la pompe biologique dans l'océan (Turner, 2002 ; Boyd et

Stevens, 2002). Le couplage entre les processus physiques et biologiques peut expliquer les interactions entre les particules et la manière dont elles peuvent être incorporées ou non de nouveau au système planctonique (Fennel et Neumann, 2001). D'une une perspective théorique, le taux de sédimentation peut être décrite par la loi de Stokes, en considérant la chute des particules sphériques en absence de mouvement vertical de l'eau et de motilité biologique (Boyd et Stevens, 2002). Cependant, la vitesse à laquelle une particule sédimentera, par exemple une cellule de phytoplancton, changera en fonction de ses caractéristiques. Par exemple, la densité peut dépendre de l'état physiologique, qui peut faire varier la flottabilité : la division cellulaire réduit le volume (Bienfang et *al*., 1982), la présence de nutriments comme le silicate favorise la formation des agrégats polysaccharides extracellulaires (par exemple PET par les diatomées ; Bienfang et Harrison, 1984 ; Bienfang et *al*., 1983) et le rôle de la vacuole dans certaines espèces de diatomées avant la sénescence favorisent la flottabilité (Eppley et *al*., 1967 ; exemple Fig. 1*a*). La sédimentation dépendra aussi de la forme et de la taille (de la Rocha et Passow, 2007 ; Turner, 2002 ; exemple Fig. 1*b*). De plus, les mouvements verticaux associées à la turbulence augmentent la probabilité de rencontre et d'agrégation des particules, probabilité qui dépendent aussi de la taille et de la concentration des particules dans le milieu (Stolzenbach et Elimelech, 1994 ; Kiørboe, 1997).

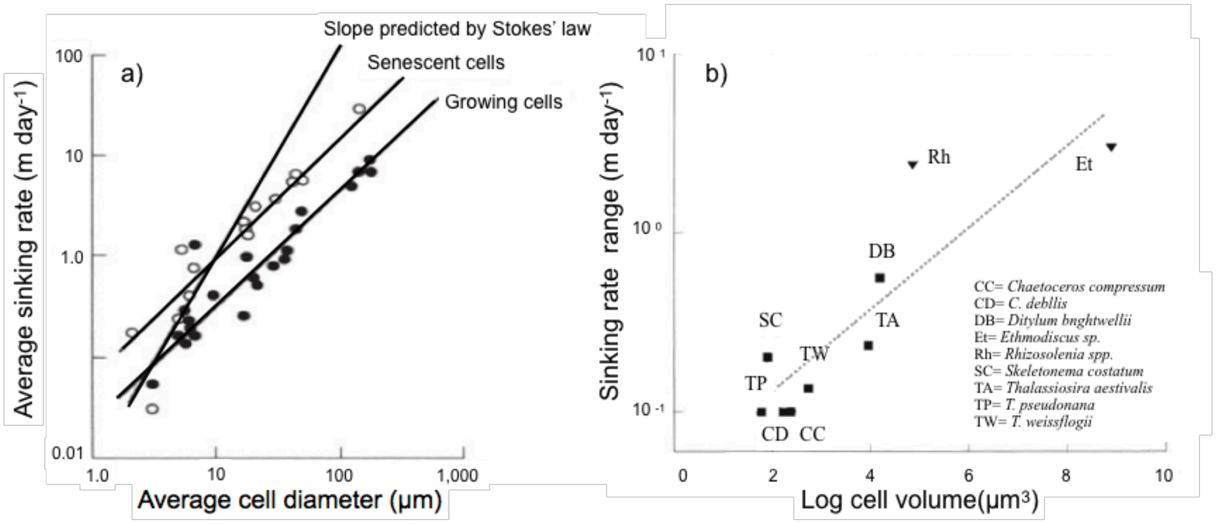

Figure 1. a) Vitesse moyenne de sédimentation du phytoplancton en fonction de l'état physiologique et de la taille des cellules (tiré de Mann et Lazier, 2013) et b) Rang de la vitesse de sédimentation pour neuf espèces de diatomées en fonction du logarithme de leur taille (tiré de Waite et *al*., 1997).

Les particules de petites tailles auront un temps de résidence plus grand dans la colonne d'eau par rapport aux plus grandes, ce favorise la probabilité de rencontre, mais en même temps elles deviennent plus vulnérables à la décomposition bactérienne, la désagrégation physique (ex. mélange) et le broutage (Stemann et *al*., 2004). La formation d'agrégats plus grands, macroscopiques, tels que la neige marine, sera aussi influencée par la turbulence ou l'agrégation par sédimentation différentielle. La base pour la formation de ce type d'agrégats est la disponibilité des exopolymères transparents (PET exsudés par le phytoplancton et les bactéries, composés de petites particules (~1-100 µm), transparentes et abondantes avec la particularité d'être collantes, ce que favorise l'adhésion (Alldredge et *al*., 1993).

La modélisation des flux de carbone dans l'océan est un outil permettant d'étudier les processus d'agrégation et de sédimentation de la matière organique. Les modèles les plus répandus, du type NPZD (nitrate, phytoplancton, zooplancton, détritus) ont surtout décrit et quantifié les flux existant entre les différents niveaux trophiques et leurs interactions (deYoung et *al*., 2004). Cependant peu d'emphase a été mise sur les composantes détritiques et les processus d'agrégation et de sédimentation, dus notamment à une compréhension partielle du système (ex. Fisher et Karakas, 2009 ; Boyd et Stevens, 2002 ; Logan et *al*., 1995). Les résultats obtenus par Gruber et *al*. (2006) indiquent que la différentiation au moins en deux tailles de détritus produit diverses interactions avec le milieu physique qui se répercute au niveau écosystémique.

OBJECTIFS ET ORGANISATION DU MEMOIRE

La première partie de ce projet vise à répondre à la question suivante : quelle est la contribution de la migration diurne du zooplancton et comment peut-elle influencer le flux du carbone dans la région centrale du GSJ ? Dans le premier chapitre, la migration verticale diurne a été inclus dans un modèle du type Nitrate-Phytoplancton-Zooplancton-Détritus (NPZD) couplé à un modèle physique, afin d'évaluer son effet sur la production primaire et sur la disponibilité de matière organique particulaire détritique, comprenant le phyto et zooplancton mort, dans la colonne d'eau. Le deuxième chapitre tente de répondre à une question de plus grande envergure, et requiert de l'apport des résultats d'autres projets connexes à celui-ci : quelle est la contribution des particules telles que le phytoplancton, le zooplancton, les pelotes fécales et les agrégats détritiques sur le flux total de carbone dans le GSJ en prenant en compte leurs interactions avec les propriétés physiques dans la colonne d'eau ? Il faut souligner que l'étude détaillée sur la portée et la contribution des agrégats au flux de carbone n'a pas été explorée. Celle-là représente une ligne de travail à développer dans le futur pour avoir une meilleure compréhension du système et son rapport avec la pompe biologique dans le golfe San Jorge.

CADRE DU PROJET

Le sujet de recherche s’insère dans le cadre du projet ¨*Marine ecosystems health of the San Jorge Gulf : present status and resilience capacity* (MARES)¨ qui fait partie d’un projet de plus grande envergure intitulé PROMESSE (Programme Multidisciplinaire de Recherche en Océanographie pour l’étude de l’Écosystème de la Géologie Marine du Golfe San Jorge et de la côte de la province de Chubut, Patagonie, Argentine). Ce travail s’appuie sur une collaboration entre l’UQAR/ISMER et plusieurs organisations de recherche en Argentine, notamment le Ministère de la science et de la technologie, le Conseil national de la recherche scientifique et de la province de Chubut. Des travaux de terrain ont été effectués lors d’une mission sur le navire *R/V Coriolis II* dans le GSJ en février 2014. Seulement une partie des résultats obtenus dans la mission seront utilisés comme base pour la réalisation de ce mémoire.

CHAPITRE 1

EFFETS DE LA MIGRATION VERTICALE DU ZOOPLANCTON SUR LE FLUX DU CARBONE : LE GOLFE SAN JORGE (PATAGONIE, ARGENTINE) COMME CAS D'ETUDE

1.1 RÉSUMÉ

La région côtière de la Patagonie argentine est l'une des plus grandes aires productives du monde et elle est considérée principalement comme un puits de carbone atmosphérique. Le plancton marin joue un rôle fondamental dans le cycle global du carbone et de la pompe biologique, où la fixation du carbone se produit à travers la photosynthèse du phytoplancton et le zooplancton contribue à son transport vers le fond marin, comme un processus supplémentaire à la sédimentation des cellules du phytoplancton vivants et mortes et la sédimentation du détritus. Dans ce contexte, la migration verticale du zooplancton dans la colonne d'eau représente un processus qui affecte le flux de matière organique en profondeur, où le carbone finalement est séquestré dans les sédiments. Dans ce travail, nous avons étudié la dynamique de l'écosystème marin localisé dans la zone centrale du golfe San Jorge, en utilisant des simulations numériques idéalisées pour la migration verticale du zooplancton dans un modèle unidimensionnel couplé à un modèle physico-biogéochimique. Des comparaisons ont été faites avec des données obtenues pendant une mission océanographique (février 2014) et entre le modèle avec et sans l'addition de la migration verticale du zooplancton. Les résultats montrent que la production du phytoplancton et détritus sont affectés par la migration de ces organismes. Les concentrations de ces deux composantes ont augmenté en ajoutant la migration verticale du zooplancton au modèle comme conséquence de la diminution de la pression de prédation et la majeure disponibilité de matière organique sans être broutée proche au fond. Ce résultat contribue à mieux comprendre la distribution du phytoplancton observée *in situ*. Par contre, la concentration du zooplancton a montré une forte diminution quand la migration est présente dans le modèle. Cette basse concentration peut être expliquée par le décalage pendant le jour entre le zooplancton et le phytoplancton, comme conséquence du mouvement vers la profondeur de la part du zooplancton.

1.2 EFFECTS OF ZOOPLANKTON MIGRATION ON VERTICAL CARBON FLUXES: THE SAN JORGE GULF (PATAGONIA, ARGENTINA) AS CASE STUDY

Abstract: The Patagonian shelf is one of the most productive areas of the world and is mostly considered as a net sink of atmospheric carbon. Marine plankton plays a key role in the global carbon cycle and the biological pump, in which phytoplankton initiates carbon fixation and zooplankton greatly contributes to the vertical transport towards the seabed, as an added process to the sedimentation of living and dead cells and detritus. In this sense, the vertical diel migration of zooplankton in the water column is a significant process that can affect the downward flux of organic matter to deep layers, where carbon sequestration will further take place in sediments. Here we study the dynamics of the marine ecosystem in the center of the San Jorge Gulf using idealized numerical simulations, considering zooplankton vertical migration in a one-dimensional coupled physical-biogeochemical model. Comparisons with data obtained during a cruise (February 2014) and between the model without (control) and with the zooplankton migration were performed. Phytoplankton and detritus production are highly sensitive to diel vertical migration of zooplankton. Both positively increased when vertical migration is included in the model because of lower predation pressure on phytoplankton and more availability of ungrazed organic matter at the bottom. This effect could contribute to explain the phytoplankton distribution observed *in situ*. In contrast, zooplankton concentration decreased with the addition of migration when compared to the control simulation. This observed diminution can be explained by the decrease in zooplankton grazing on phytoplankton during daytime, when zooplankton move downward.

1.3 INTRODUCTION

Marine ecosystems play a key role in the global carbon cycle (Heinle and Slawig, 2013). Primary producers present in the ocean's surface transform the dissolved inorganic carbon into organic matter by means of the photosynthesis, which is then can be either transferred to higher levels in the food web or exported to the bottom. Along this path, organic matter can be fixed by organisms or modified, such as when carbon is exported downwards, which can be mediated by passive or active transport. The set processes by which carbon dioxide (CO_2) is transformed in the upper ocean by phytoplankton into particulate organic matter (POM) and exported to deeper waters is known as the biological pump (Turner, 2002). In coastal waters, a fraction (~ 15%) of primary production can leave the euphotic zone before being consumed and transformed (Smith and Hollibaugh., 1993). The bottom receives most of organic matter from surface layers, when it sinks down in the form of particulate matter and aggregates. It has been shown that around 9% of the particles leaving the euphotic zone in these environments is buried in the sediments, while the other part is consumed or respired (Smith and Hollibaugh., 1993).

The efficiency of the biological carbon pump in regulating the atmospheric concentration of CO_2 has been shown to be very sensitive to the vertical migration behavior of zooplankton and micronekton (Steinberg et *al.*, 2000; Steinberg et *al.*, 2002; Bianchi et *al.*, 2013). This is the greatest type of migration in the aquatic environment, in terms of biomass, and different strategies could be adopted within freshwater, where migration is mostly seasonal, and oceans, where it is mostly daily (Ringelberg, 2009). Marine zooplankton vertical migration plays a central role in the active transport of dissolved and particulate organic matter to depth (Ducklow et *al.*, 2001; Ringelberg, 2009). Its behavior could vary depending on environmental characteristics, ontogeny and biological conditions. Diel vertical migration (DVM) occurs among most zooplankton species with either the nocturnal or twilight pattern most commonly observed (Ringelberg, 2009). Zooplankton typically descends hundreds of meters at dawn and rise toward the surface at dusk, mainly to evade predators and to search for food (Pearre, 2003), but there may be other causes for this behavior such as intraspecific competition, temperature and irradiance (Ringelberg, 2009). Even if the effect on carbon flux depends on the biomass and type of migrating community, the excretion and respiration (e.g. Steinberg et *al.*, 2000), fecal pellets production (e.g. Laurenceau-Cornec et *al.*, 2015), death and molt (Morales, 1999; Zhang and Dam, 1997) of zooplankton have been documented to provide high quantities of nutrients below the euphotic zone. This is also the case of the “lipid pump”, described as the vertical transport of lipids accumulated in the surface waters and after metabolized by overwintering zooplanktonic migrating species at depth (diapause), which can contribute to carbon sequestration similar to sinking POC (Jónasdóttir et *al.*, 2015). Organic material downward displacement by secondary producers is referred to as active transport, in contrast with the gravitational flux of particles, referred to as passive transport, and could represent significant amounts of carbon export in some areas of the world's ocean (Honjo et *al.*, 2008).

Coastal seas and shelves are considered areas of great importance due to their high productivity and human activities (Holt et *al.*, 2009). The Southwestern Atlantic Ocean (40° to 60°S) is considered as a CO_2 sink to carbon flux, mostly during summer and fall (Bianchi et *al.*, 2005; Schloss et *al.*, 2007). Moreover, the Atlantic Argentinian shelf has been classified as a Class 1 Large Marine Ecosystem (LME) showing a primary productivity (PP) higher than 300 g C m^{-2} yr^{-1} (Bisbal, 1995). Some specific areas such as the SJG present even higher values (Rivas et *al.*, 2006). In this area, there is not primary production local data (Carreto et *al.*, 1995) as well as the amount and quality of sinking particles and on carbon flux (Bianchi et *al.*, 2005). Data on zooplankton composition, abundances and behavior are scarce (Sabatini et *al.*, 2004), while information about upper trophic level predators and fisheries are in constant increase (e.g. González-Zeballos et *al.*, 2007; Yorio et *al.*, 2015). However, the connection and relations among them, and the role of primary production and zooplankton in the net downward carbon flux are poorly understood.

The SJG is a shallow basin (~ 100 m) with a wide entrance (~ 250 km) where westerly winds and large semi-diurnal tides (~ 6 m) are distinctive characteristics. No riverine inputs or significant rainfall (<250 mm) take place (Akselman, 1996). Water masses are mainly influenced by the offshore circulation and currents from the Argentinean shelf. Depth-average currents in the central area of the Gulf are around 2.5 cm s^{-1} towards the coast (Palma et *al.*, 2004; Palma and Matano, 2012), coastward in the deeper portion of the Gulf and offshore in the direction of the dominant winds in the upper layer. Considering the size $L \sim 10^5$ m of the Gulf and a typical current speed $U \sim 0.02$ m s^{-1}, particles or organisms traveling up and down in the water column can remain in the Gulf area over a period as long as $T = L/U \sim 5 \times 10^6$ s ~ 60 days. Because the biological processes under study here occur on equivalent or shorter time scales (see 1.6 Simulation results), the influence of advective transport can be neglected, allowing the use of one-dimensional water column models that assume horizontal homogeneity.

Numerical biogeochemical models are useful tools for studying dynamics of complex ecosystems (Fasham et *al.*, 1990; Dippner, 2006) in a relative simple and realistic framework representation (Heinle and Slawig, 2013). Some models consider the relation with turbulence in the marine environment where biogeochemical physical processes are incorporated and coupled (Kuhn and Radach, 1997; Burchard et *al.*, 2006). Models can help to elucidate the complex interactions between physical environmental dynamics and biological processes such as primary production, distribution and sinking of organic matter (Stow et *al.*, 2009). Furthermore, ecosystem models allow obtaining significant results by simplifying ecosystem interactions (Dippner, 2006). When gathering field data is difficult to obtain, models can contribute with information that otherwise will need significant technological or economical efforts (Franks, 1995; Arhonditis et *al.*, 2006). Therefore, the application of models in the San Jorge Gulf enables a useful insight to answer some basic questions related to the carbon export and its possible sequestration.

The aim of the present study is to incorporate zooplankton migration in an Eulerian NPZD (Nitrate-Phytoplankton-Zooplankton-Detritus) model to determine whether this process affects the patterns and magnitude of carbon fluxes in the San Jorge Gulf, Patagonia, Argentina. It was not intended to reproduce *in situ* observations, but rather to establish relations and insights on ecosystem interactions under the hypothesis that zooplankton vertical migration will increase carbon export in the gulf. Some observations and results from the mission of the *R/V Coriolis II* in the SJG (February 2014) were used in this study.

1.4 PARAMETERIZATION OF DIEL VERTICAL MIGRATION (DVM)

To date, many studies have been done to determine and/or represent the causes and consequences of zooplankton DVM (Williamson et *al*., 2011; Hays, 2003; Morales, 1999; Dodson, 1990) and represent/include the results in models (Bianchi et *al*., 2013; Maps et *al*., 2011; Richards et *al*., 1997). Even if results vary among regions and the group of zooplankton represented, most of them agree that species undergoing DVM should be considered in the estimation of total carbon flux and ecosystem interactions.

Different approaches have been followed to represent vertical migration, considering zooplankton ontogeny or physiological approaches (Maps et *al.*, 2011; Aita et *al.*, 2003; Batchelder et *al.*, 2002). In these studies, factors such as temperature, salinity, irradiance, development time or physiological state were at the center of discussion for parameterization of zooplankton displacements in the water column. In the present work, prior to the formulation of DVM, we analyzed different biological and environmental factors, which later allowed us parameterizing DVM. Instead of focus on DVM causes, we looked at its possible effects and contributions on carbon fluxes in the water column. In order to explore the simplest but still representative mechanisms, inspired by the work of Maps et *al.* (2011) we made some modifications to represent the average zooplankton assemblage (Eulerian approach) present in the SJG. The election of an Eulerian model rather than an individual based model allows for a lower degree of computationally complexity with still accurate results (Dippner, 2006).

In order to represent the main characteristics of zooplankton distributions observed in the GSJ, we choose two different factors influencing zooplankton swimming velocity: light intensity in the water column and phytoplankton concentration. We assumed that zooplankton migrate mainly to find refuge in the dark where predators are less abundant and cannot easily locate them through vision. Consequently, we set the vertical swimming speed of the zooplankton to a maximum when the local irradiance is high and to zero whenever the ambient light is sufficiently low, i.e. below a finite irradiance threshold value I_c. If ambient light is lower than I_c, zooplankton will swim upward until the depth of I_c is reached in the water column, otherwise it swims downward. An exception to this rule is that zooplankton would not swim if the local food abundance is high, which is set by a phytoplankton threshold concentration value ($P_{\min}$). This parameterization is shown by the following conditional equation with a saturating function:

$$w_z = \begin{cases} -w_z^{\max} \tanh(\zeta(I(z) - I_c)) & I(z) < I_c \quad \text{and} \quad P < P_{\min} \\ 0 & \text{otherwise} \end{cases} \tag{1.1}$$

where $w_z^{\max}$ is the positive maximum swimming speed value, which normally depends on the organism's physiological conditions and size, ζ is the slope coefficient, $I(z)$ is the irradiance intensity in the water column, I_c is the critical light irradiance intensity for zooplankton to move and $P_{\min}$ the minimum phytoplankton concentration needed as food. Figure 2 shows an example of how w_z varies with depth and time according to equation (1.1) with $\zeta = 0.05$ W^{-1} m^2, $I_c = 10$ W m^{-2}, and $w_z^{\max} = 320$ m d^{-1} during a typical diurnal cycle with maximum surface PAR at noon of 400 W m^{-2}.

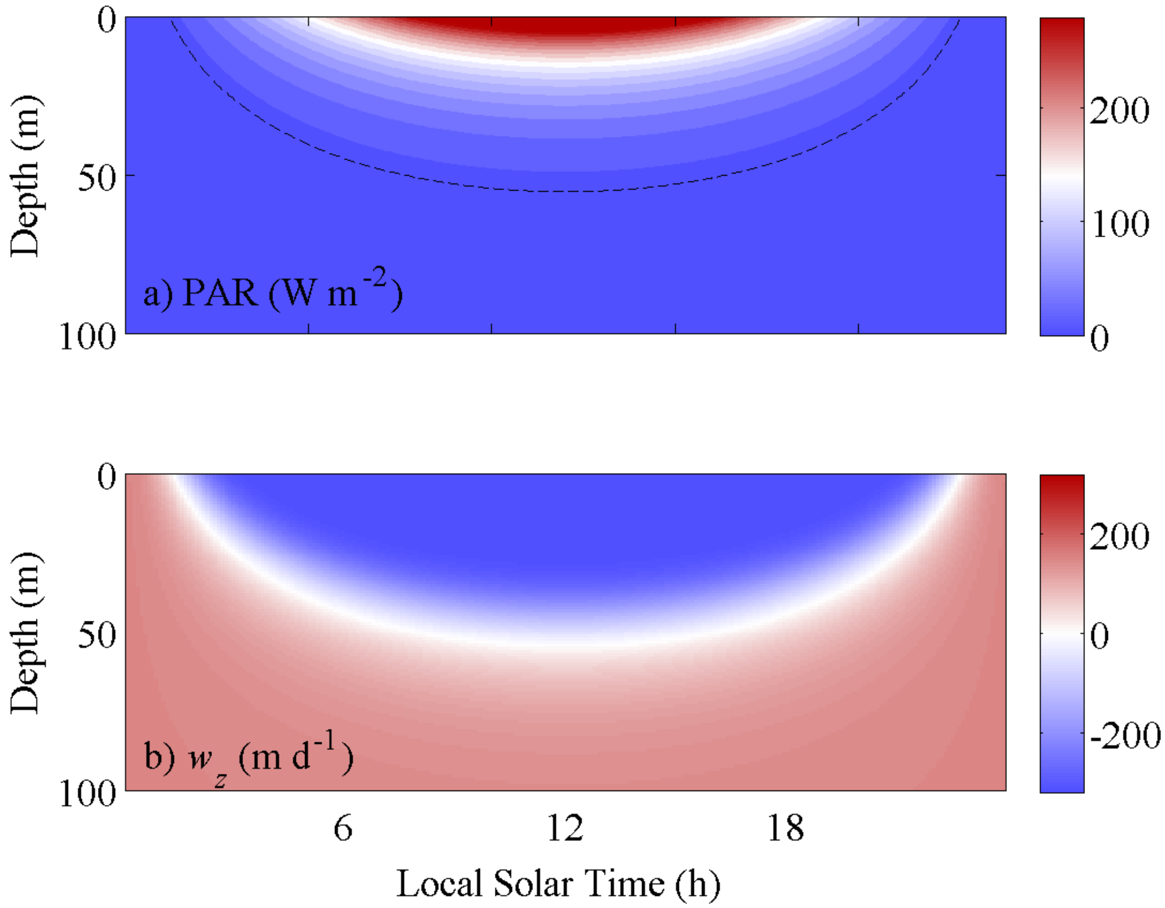

Figure 2. a) Photosynthetically available radiation (PAR) as a function of depth during a 24 h cycle, used to compute b) the vertical migration velocity of the mesozooplankton using the parameterization of equation 1.1 with $\zeta = 0.05$ W^{-1} m^{2}, and $w_z^{\max} = 320$ m d^{-1}. The critical irradiance $I_c = 10$ W m^{-2} is indicated by the dash line in the top panel.

1.5 MODEL DESCRIPTION

The biogeochemical NPZD model was adapted from Burchard et *al.* (2006), which is based on the biological model proposed by Kühn and Radach (1997). It represents a nitrogen-limited planktonic system, including nitrogen recycling by the microbial loop, as well as primary and secondary productions. The model includes seven state variables, usually expressed as concentrations of the different ecosystem components either as dissolved chemicals (e.g. nitrate) or as particulate matter (e.g. phytoplankton). In Figure 3, DVM was added to the model and illustrates the coupling intensity anticipated between primary producers, grazers and detritus when considering the diurnal migration. Nitrate (NO_3^-) is the only limiting nutrient considered in this model. Primary production is provided by one phytoplankton group (PHY) that corresponds to the structural base of the model food web, which grows and reproduces depending on the nutrient compartment and environmental conditions (light, temperature, turbulence, etc.). This group represents phytoplankton larger than 10 μm up to 200 μm, which corresponds to the optimal food size for copepods (Sabatini et *al.*, 2012).

Secondary production was parameterized for mesozooplankton (ZOO). This functional group in our case represents copepods, the most common zooplankton in the ocean (Turner, 2004) and the most abundant one in the San Jorge Gulf (Sabatini et *al.*, 2004). Copepods are well known as migrators in several areas (Longhurst, 1991), showing a DVM behavior, spending the daytime at the surface waters looking for food and at depth during the night to evade predators (Fig. 3). While microzooplankton could represent an important part of the ocean daily feeding percentage in comparison with mesozooplankton (70% against 20%, Longhurst, 1991), mesozooplankton is the most abundant grazer in the SJG, although in terms of biomass the krill could be more representative (Sabatini et *al.*, 2004; Gimenez et *al.*, in prep).

A part of phytodetritus, dead zooplankton, remainings of grazing and fecal pellets are undifferentially included in a detrital compartment (DET). The excretion and respiration of organisms can re-enter elements to the biogeochemical model through recycling processes by the microbial loop. This recycling process includes three state variables: bacteria (BAC), ammonium (NH_4^+) and labile dissolved nitrogen (DON).

The seven state variables in the model are expressed in nitrogen concentrations (mmol N m $^{-3}$), which are latter converted to carbon units (mg C m $^{-3}$) assuming a constant carbon-nitrogen ratio (see Annex I).

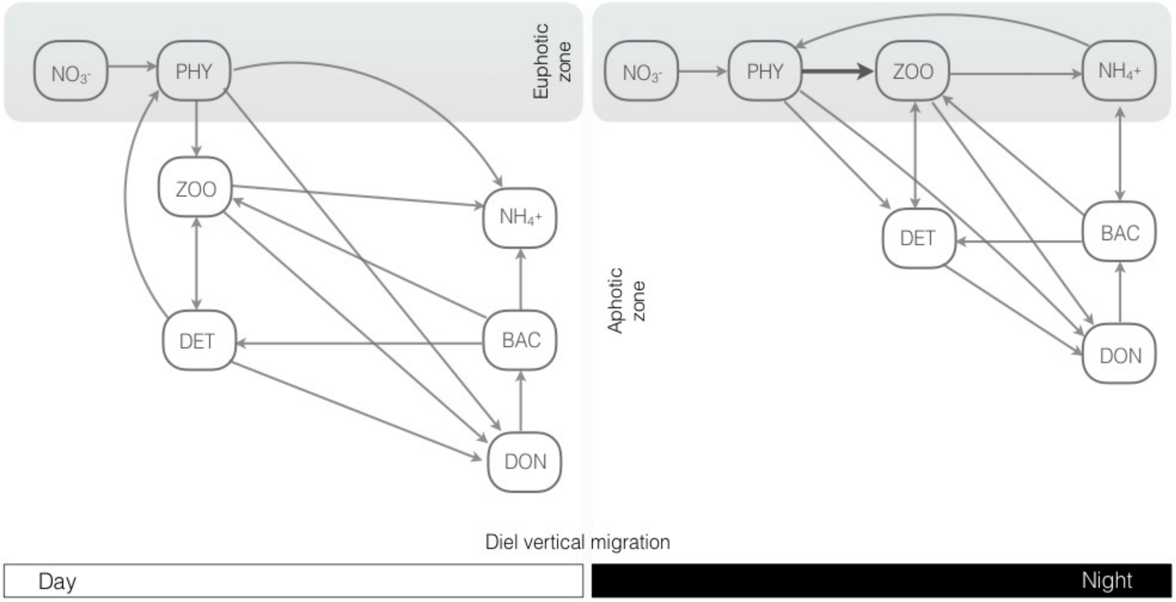

Figure 3. Conceptual model with seven state variables (see text) adapted from Burchard et *al*. (2006) with the inclusion of diel vertical migration for the zooplankton group. Modeled food web and interactions are shown during the day (left panel) and at dusk (right panel). The thick arrow represents a strong relation between compartments.

All compartments were parameterized with the ecologically nearest estimation found in the literature (Table 1), when information was not present. Some approximations were made to represent *in situ* observations in February 2014 from an echo-sounder during the mission of the *R/V Coriolis II* in the San Jorge Gulf (Southern Argentina, MARES project). Figure 4 shows that zooplankton organisms detected by the echosounder migrate down near a depth of 80 m during daylight and come back near the surface during the night, in phase with our parameterization. Discrepancies in the vertical velocity, daytime rest depth and vertical distribution during the night between model simulations and observations can be explained by the difference between the same size of zooplankton we try to simulate and the one that is observed and turbulent transport. A list of all parameters closely related with the carbon flux is described in Table 1, while the rest of model parameters used are shown in the Annex II.

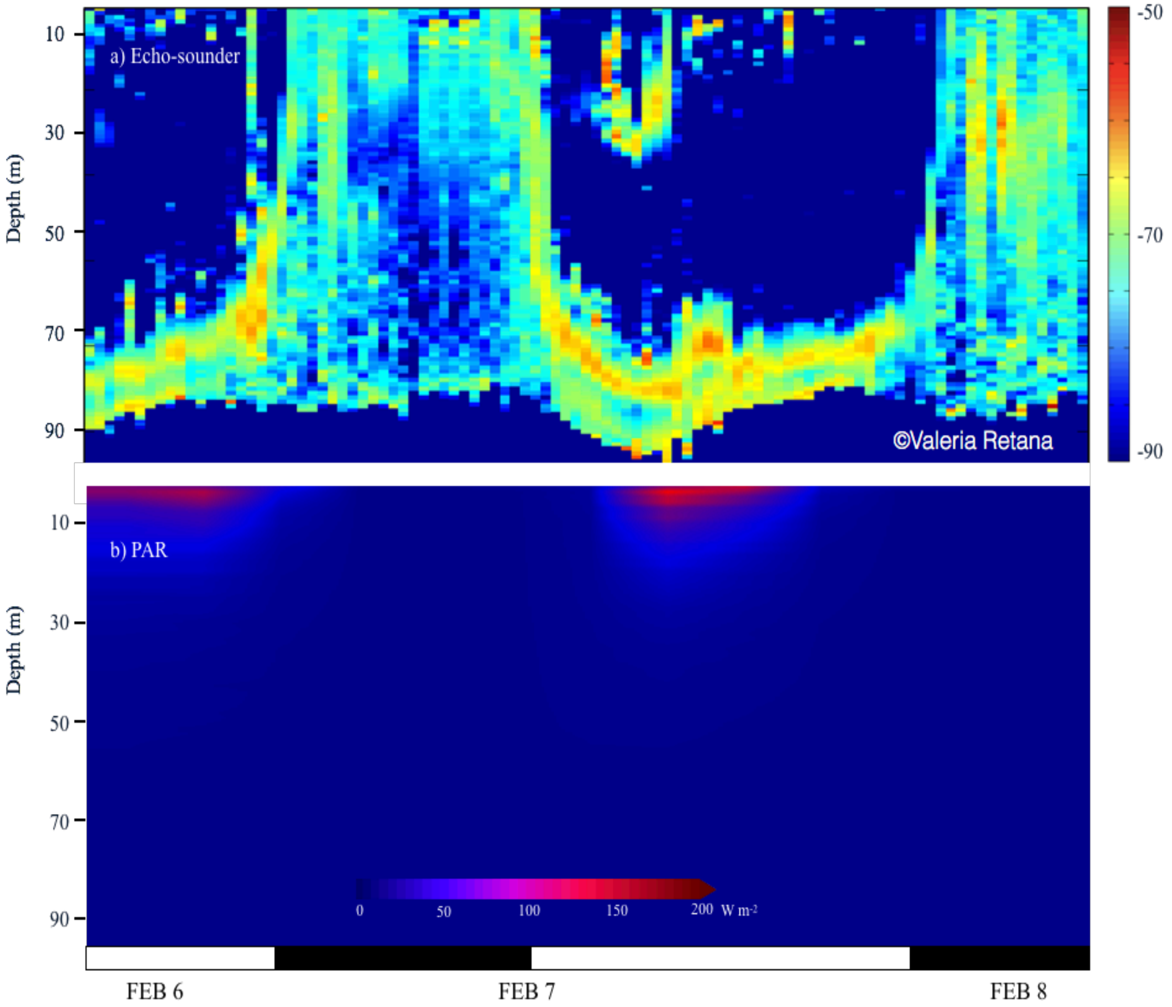

Figure 4. a) Echogram (EK 60, 120Hz) for organisms larger than 1 cm (e.g. krill) in the SJG central area, showing migration behavior during the day (white bars) and at dusk (black bars). Colors indicate the volume backscattering strength during summer (36 hours, February 2014). b) Photosynthetically active radiation (PAR) *in situ* for the same time period.

Table 1. Description and value of parameters directly involved in carbon flux.

Symbol	**Value**	**Unit**	**Description**
γ	0.05		exudation fraction[a]
μ_1	0.05	d^{-1}	phytoplankton mortality rate[a]
$P_{\min}$	0.7	mmol N m^{-3}	minimum phytoplankton concentration[c]
w_p	-0.38	m d^{-1}	phytoplankton settling velocity[a]
μ_2	0.03	d^{-1}	zooplankton loss rate[a]
δ	0.1		fraction zooplankton to LDON[a]
ε	0.7		fraction zooplankton to ammonium[a]
$w_z^{\max}$	320	m d^{-1}	maximum zooplankton swimming speed[b]
μ_4	0.02	d^{-1}	detritus breakdown[a]
w_d	-5.0	m d^{-1}	detritus settling velocity[a]
ζ	0.05	W^{-1} m^2	slope coefficient for the DVM
I_c	10	W m^{-2}	critical irradiance[c]

[a] Burchard et *al.*, (2006)

[b] Maps et *al.*, (2011)

[c] Observations from echo-sounder (MARES project)

The biogeochemical model (Fig. 3) is coupled with the General Ocean Turbulence Model (GOTM, Burchard et *al.*, 1999), a physical one-dimensional (1D) water column model, which integrates the most important hydrodynamic and thermodynamic processes related to mean and turbulent vertical transport in the ocean, given initial and boundary conditions. The numerical grid has 50 vertical levels with a 2 m resolution from the surface to the bottom at 100 m. Atmospheric forcing data were taken from the ERA-Interim Reanalysis datasets (http://www.ecmwf.int/research/era).

We run the 1D model to test the diel vertical migration parameterization (Fig. 2) and its impacts on carbon export in the ecosystem. The model represents the conditions prevailing in the center area of the San Jorge Gulf, Patagonia, Argentina (66°W, 46°S) enclosed within the 90 m isobath line, and excluding the shallowest southeastern portion, which is highly influenced by tidal mixing (Fig. 5). Two different numerical experiments have been carried out: 1) a control model run without DVM for the mesozooplankton; and 2) a DVM model run, where migration is simulated. Different specific simulations were performed for primary production, secondary production and detritus for both experiments from June 2013 to August 2016 (Table 2). The period considered in the simulations was chosen to encompass the mission of the *R/V Coriolis II* (February 2014). To stabilize the model variables, we start the runs half a year before (2013) and we let the model continue running until 2016 in order to compare inter-annual.

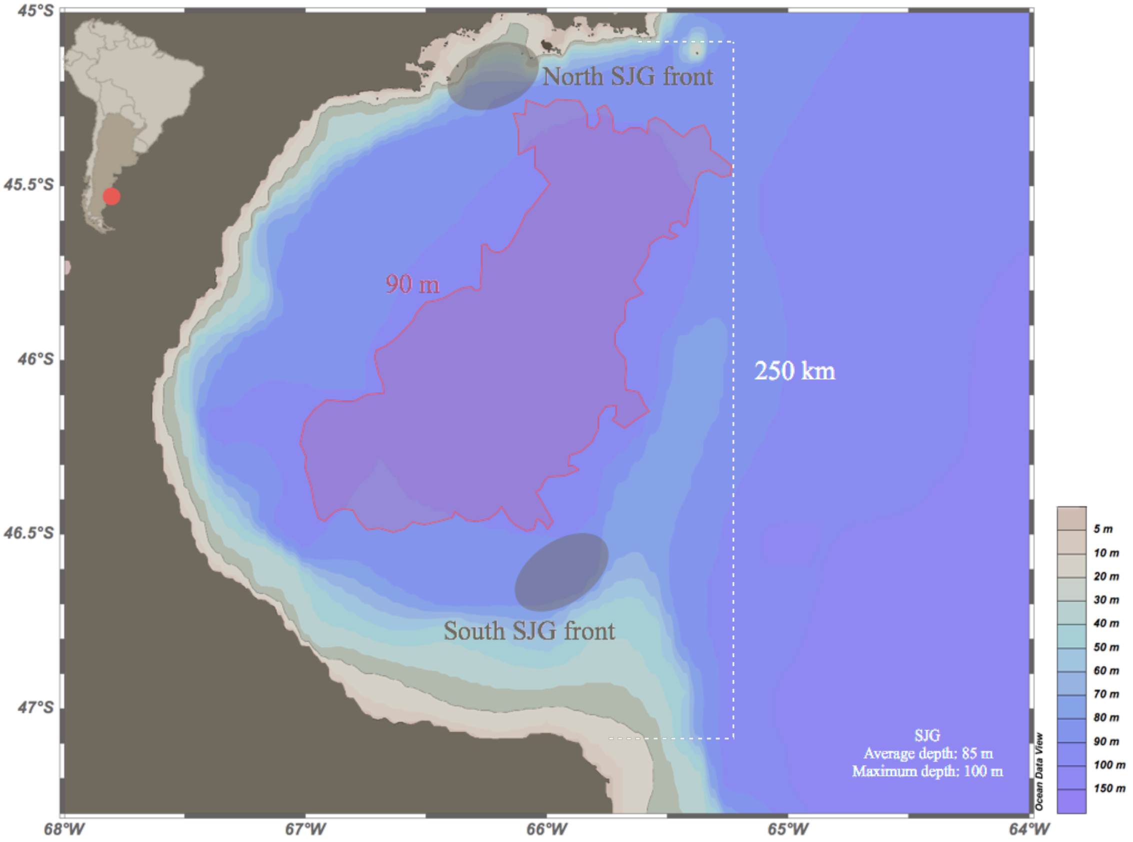

Figure 5. Map of the San Jorge Gulf showing the bathymetry and the central region deeper than 90 m (red line) that the model represents.

Table 2. Summary of figures for all numerical simulations performed in this study.

		PHY	ZOO	DET
June 2013 to August 2016	Control model	5a & 5c	6a	7a & 7c
	DVM model	5b & 5d	6b	7b & 7d

1.6 SIMULATION RESULTS

The simulated interannual cycles of physical variables (wind, temperature and salinity) for the three simulation years are shown in Figure 6. Average wind speeds were weaker in 2016 (0.09 N m^{-1}) than over the period 2013-2015 (~1.2 N m^{-1}, Fig. 6a). However, maximum wind speeds were recorded in different months for the studied period: in July 2013 (0.94 N m^{-1}), in June 2014 (0.71 N m^{-1}), in March and June 2015 (0.65 and 0.63 N m^{-1} respectively) and in July 2016 (0.54 N m^{-1}). In summary, the strongest winds were found during fall but mostly in winter. The SJG is seasonally stratified. During winter, the water column is homogeneous (Fig. 6*b*), with temperature values around 9 to 7°C. Vertical thermal stratification starts to develop during October and lasts until April, being more pronounced during January-February, with a temperature maxima of 17°C occurring in February (2015 and 2016). In summer, a thermocline is evident at 30 m water depth and during winter it vanishes due to mixing. In the case of salinity (Fig. 6*c*), its evolution follows a temporal pattern similar to that of temperature, even if value ranges are narrower (33.35–33.42 psu). The water column shows a less salty upper layer (0–30 m) during winter, which becomes saltier during October-May, for the three simulations years. This low variability in salinity values lets infer that water column stratification in the SJG is controlled by temperature.

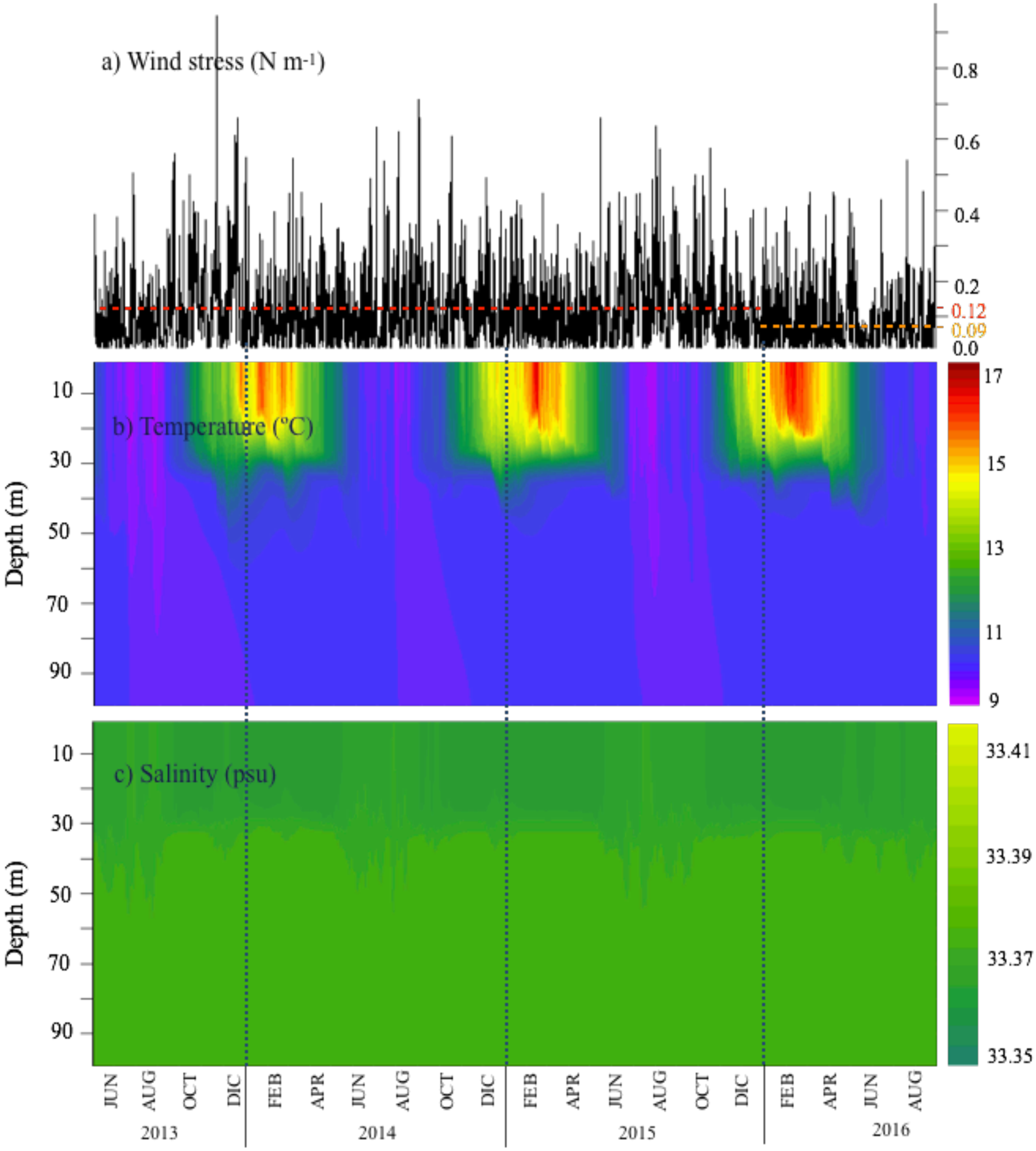

Figure 6. Annual cycle of a) wind, b) temperature and c) salinity for the SJG during the three simulation years for the two numerical experiments (see text).

Interannual variability for biological variables was less accentuated in comparison with differences between model experiments (Table 3). Only the two complete years (2014 and 2015) were considered in this evaluation. Total annual primary production for 2014 and 2015 was 1.25 and g C m^{-2} y^{-1} for the control model, while for the DVM model was 2.79 and 2.78 g C m^{-2} y^{-1} respectively. Zooplankton production presented similar values for 2014 and 2015 in the control model (1.19 and 1.17 g C m^{-2} y^{-1}, respectively), but a significant reduction was present for the DVM model during both years, with values threefold lower, corresponding to 0.32 and 0.30 g C m^{-2} y^{-1}. Notable differences in detritus production were observed when experiments are compared, but low interannual variation was detected with a slight decrease in 2015 for the control model (2.22 to 2.07 g C m^{-2} y^{-1}) and DVM model (7.79 to 7.12 g C m^{-2} y^{-1}).

Table 3. Summary of annual average and its standard deviation for primary, secondary and detritus vertically-integrated concentrations in both experiments (g C m^{-2} y^{-1}).

		PHY	ZOO	DET
Control model	2014	1.25 (±0.39)	1.19 (±0.44)	2.22 (±0.75)
	2015	1.25 (±0.41)	1.17 (±0.49)	2.07 (±0.90)
DVM model	2014	2.79 (±0.82)	0.32 (±0.23)	7.79 (±2.99)
	2015	2.78 (±1.18)	0.30 (±0.27)	7.12 (±3.63)

The zooplankton compartment, which was modified in the model, was examined to evaluate its evolution with the addition of DVM. Not only zooplankton concentrations were higher in the control model, but also the temporal pattern distribution over the water column showed differences between simulations (Fig. 7*a*, *b*). In the control experiment, zooplankton accumulates near the seabed, feeding on sinking detritus. In this model, zooplankton concentrations generally increased with depth (Fig. 7*a* and 7*c*). For the DVM model, maximum concentrations were observed in deeper waters during the summer (December-February) when compared to the rest of the year, matching with the highest irradiance in the surface layer (see equation 1.1, section 1.4). A two-month lag was observed when comparing both models for maximum integrated zooplankton abundances: for the DVM model, they were reached during the period from October to November while for the control model the peaks were high between January and March. However, concentrations differ fourfold (0.4 g C m^{-2} and 1.6 g C m^{-2}, for the control and DVM model, respectively).

Figures 7*c* and 7*d*, show the simulated diurnal vertical pattern for three-day zoom in February 2014 during MARES mission. Maximum concentrations were found at 30-40 m during half of the daytime, while when dusk arrives higher zooplankton concentrations were located near the surface. The control model showed the same distribution for the zooplankton concentrations day-by-day, with higher values at the bottom and less variability during the day. During this same period, two environmental variables that influenced vertical migration displacement were analyzed (Fig. 7*e* and 7*f*). Photosynthetically active radiation (PAR) presented high values (~200 W m^{-2}) near the surface during daytime with decreasing values below the 20 m and reaching cero values at night. Turbulent diffusivity resulting from the surface wind stress influences roughly the top 30 m of the water column and goes down rapidly to the background value (10^{-6} m^{-2} s^{-1}) with depth.

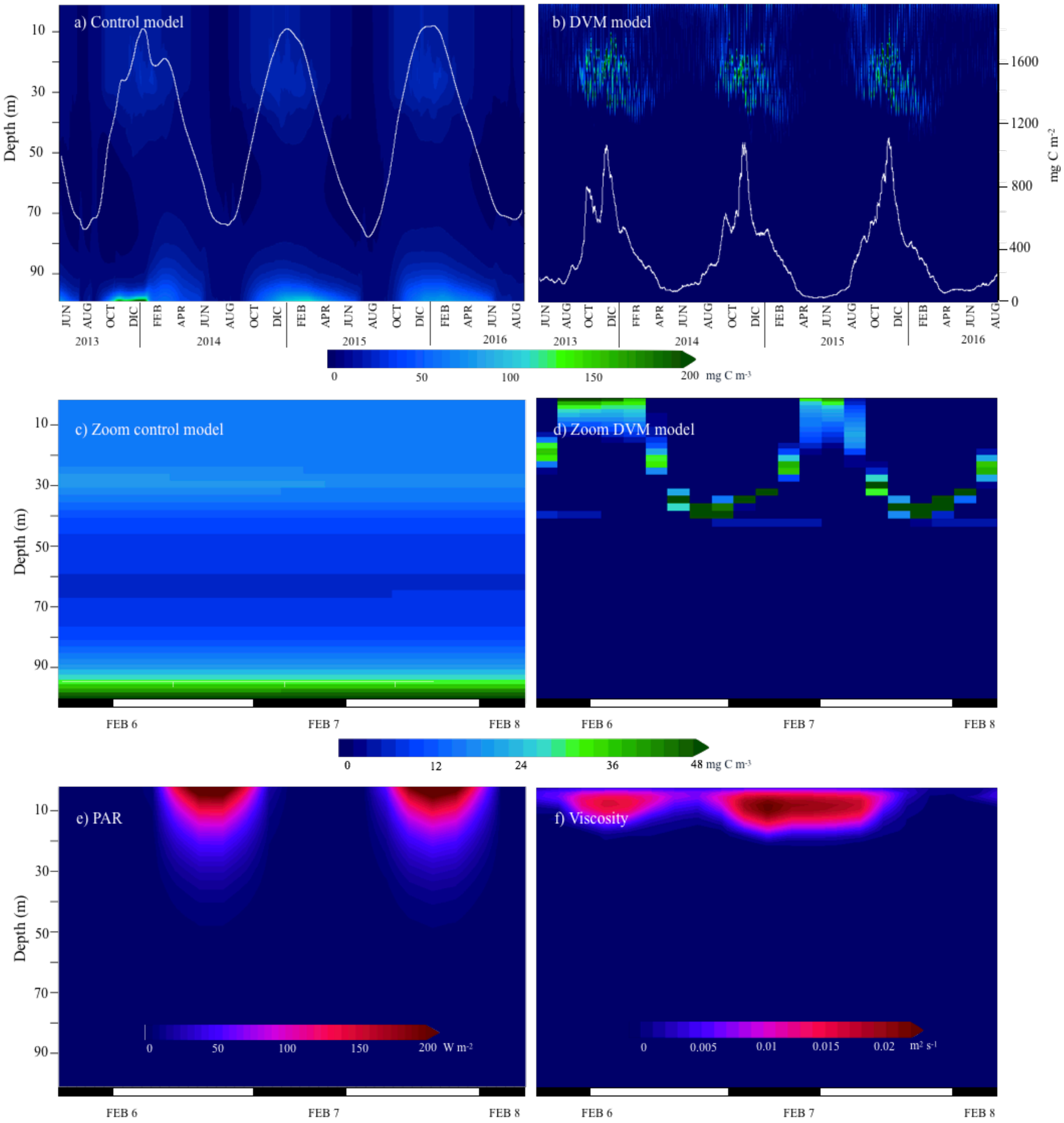

Figure 7. Evolution of zooplankton concentration in the water column (mg C m^{-3}) for a) the control model and b) the DVM model. The white lines show depth-integrated zooplankton concentration (mg C m^{-2}). Panels c) and d) show a three-day zoom in February 2014 for the control and DVM model, respectively, evidencing the diel migration pattern. Panels e) and f) show the same three-day zoom for PAR and viscosity (turbulent diffusivity), respectively.

To compare DVM behavior obtained from the model and observations made with the echo-sounder during the cruise, we analyzed the three-day zoom with data availability for the sounder (6-8 February 2014). Zooplankton displacement registered with the echo-sounder (Fig. 4a) shows a fast movement after dusk, with organisms moving from 80-60 m up to the surface in three hours. They remain at the surface after the sunrise, to move downward until reach the previous depth by 7 am. During the ascent, a distribution mostly homogeneous appears in the water column above the 80 m. The same pattern is observed the following day. In contrast, the model result (Fig. 7*d*) presents a shorter distance displacement by organisms, initiated at lower depth (30-40 m) with a progressive movement upwards. During daytime, a dispersed concentration is found up to 25 m in depth, which concentrates and moves downward after midday. The organisms represented in the model spend almost fourfold to reach the surface compared with *in situ* observations.

To study the influence of the DVM on the system we additionally evaluated the evolution of primary producers. Phytoplankton concentrations in the control model were highest than the rest of the years from October to February in the three simulated years, presenting maximum values in the upper 30 m (Fig. 8*a*). Lower concentrations of phytoplankton were present during the winter, especially in July, no matter the simulation year. In the DVM model, phytoplankton concentrations were higher and lasted longer during the same period compared to the control model (Fig. 8*b*). In addition, maximum concentrations (October-November for the three simulation years) occurred in the surface layer. It is also evident a second phytoplankton peak, between January-February, but it is deeper in the water column (between 30 and 60 m). Integrated concentrations along the simulations showed a difference of almost three times the values (2.5 versus 6 g C m^{-2}) between experiments. Peak maximum values correspond to the end of November (2016) in the DVM model, while for the control model peaks are equal for the entire time simulation.

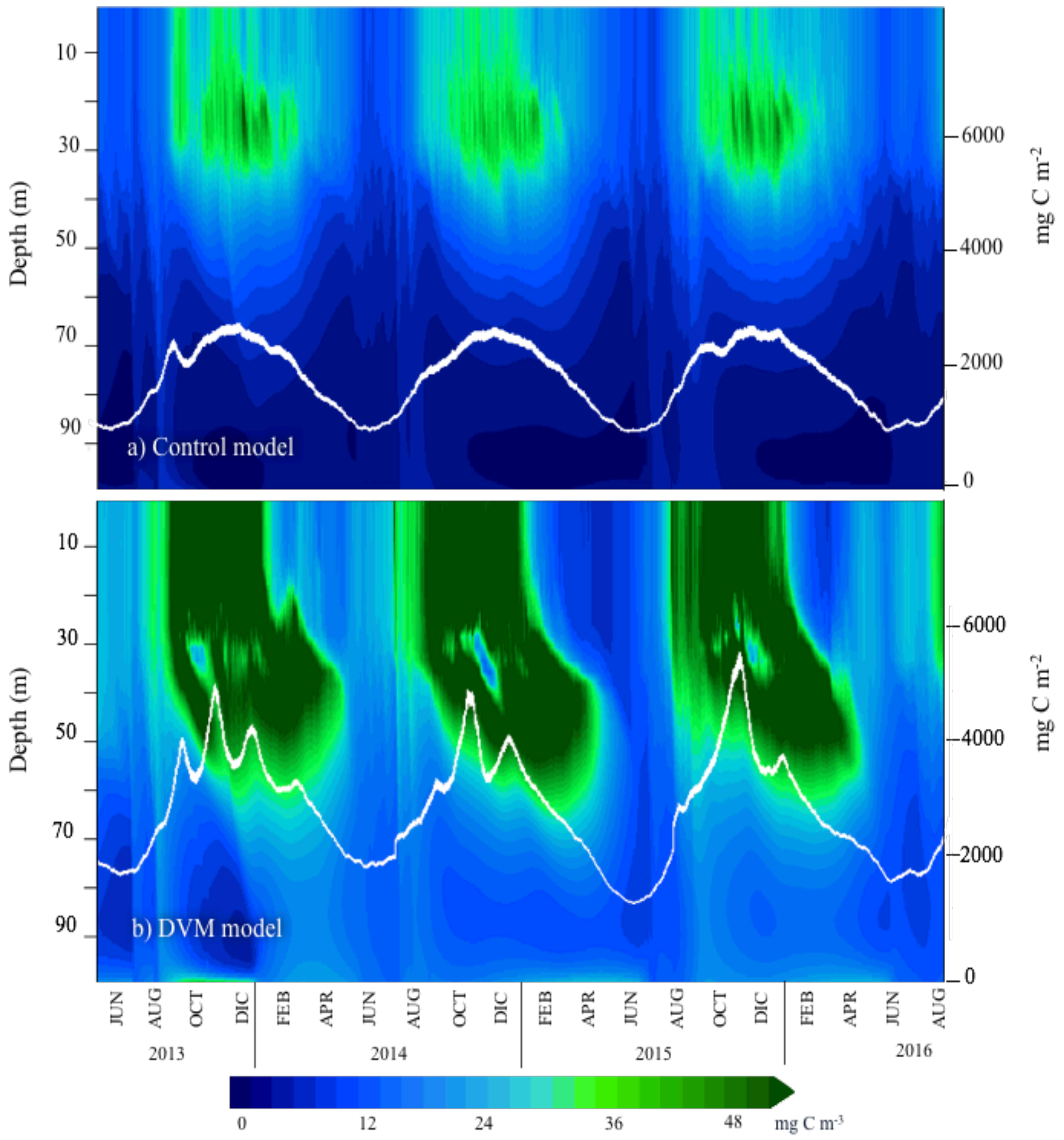

Figure 8. Evolution of simulated phytoplankton concentrations (mg C m^{-3}), white curves correspond to depth-integrated values (mg C m^{-2}) for a) the control model, and b) the DVM model.

Model simulations showed a significant increase of detritus production when vertical behavior is added to the biological model (Fig. 9). Maximum concentration values in the control model were observed from January to March (2014) and from October to March (2015 and 2016), mostly located below 30 m depth (Fig. 9*a*). Integrated values for the same model showed peaks around 3 g C m^{-2} for the same periods. For the DVM model, highest detritus concentrations were observed in the bottom, but it was also possible to distinguish some concentrations in the entire water column during summer months. Integrated values are four times the concentrations obtained in the control model, with peaks reaching more than 12 g C m^{-2} (Fig. 9*b*) in the most productive year (2016).

When the detritus compartment was studied in more detail (Fig. 9*c* and 9*d*), the highest concentrations were found below 40 m in both simulations. The largest differences between concentrations were found for the DVM model when comparisons between layers were made. Zooplankton migration seems to facilitate the sinking of organic matter, particularly to deep zones, and at the same time prevents zooplankton to graze detritus near the seabed. The production of detritus becomes more evident during the summer in comparison with the rest of the year, especially between February and March.

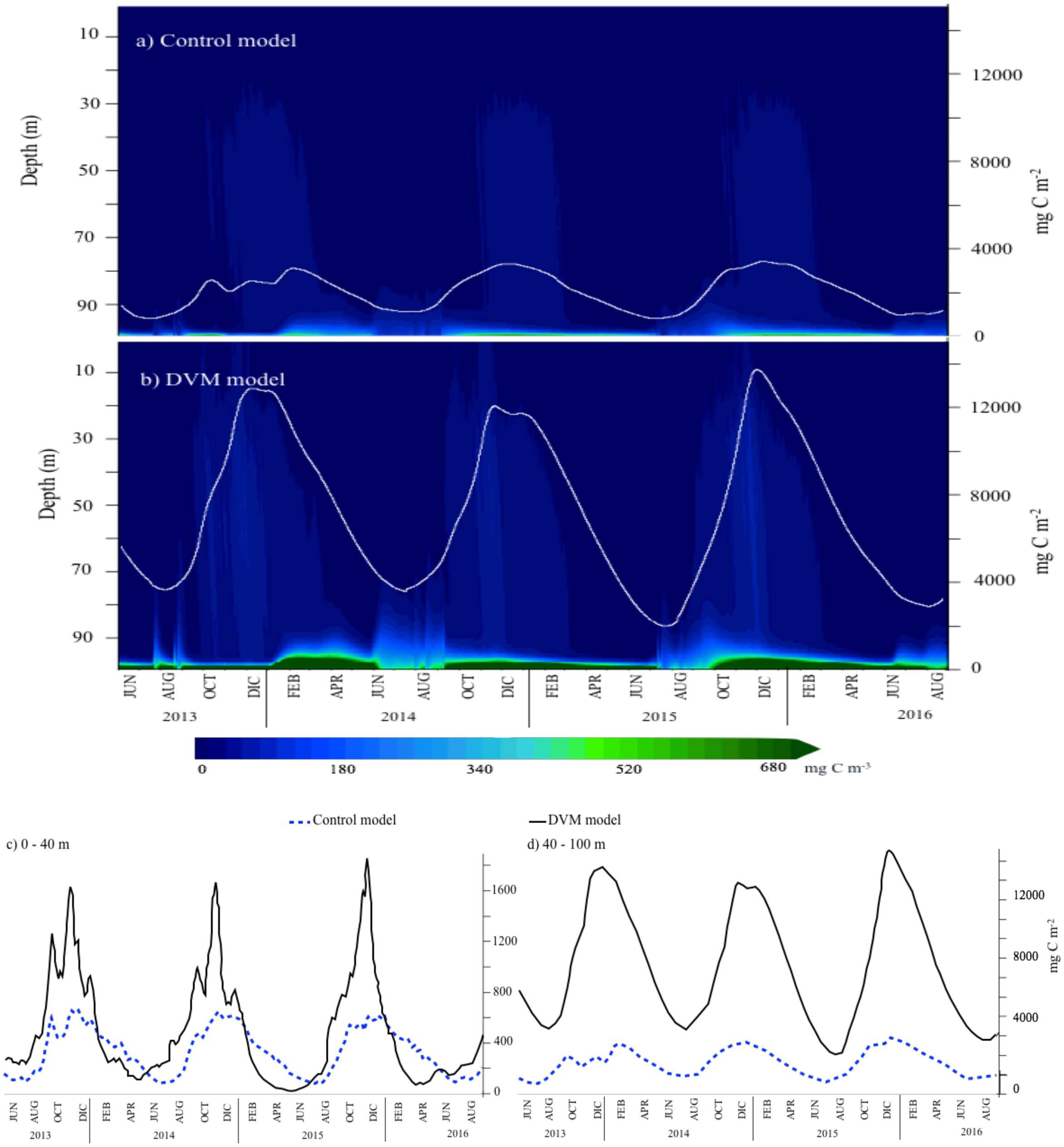

Figure 9. Evolution of detritus concentrations (mg C m^{-3}) for a) the control model and b) the DVM model. The right axis corresponds to depth-integrated values for the same period (mg C m^{-2}). Depth-integrated detritus concentrations c) above and d) below 40 m (mg C m^{-2}) are shown for the control model (blue dashed line) and the DVM model (black line).

1.7 DISCUSSION AND CONCLUSION

The numerical model applied here shows a good agreement with the known environmental characteristics in the SJG. It further provides information where data is lacking. Physical variables (wind, temperature and salinity) in the simulation show a dynamic that is in accordance with the available references such as Cucchi-Colleoni and Carreto (2001), who described that water column structure in the central zone of the SJG as controlled by the thermocline. In addition, the values obtained of salinity (33.3–33.6 psu) in their work were similar to those from the model at the same depth (~30 m). A few studies focused on the properties of the water column throughout time (e.g. Louge et *al*., 2004; Cucchi-Colleoni and Carreto, 2001; Akselman, 1996). Information about physical variables is scarce in the region, especially for winter. However, similarities (see Annex III) such as the range of salinity and temperature, depth of the thermocline and water column structure along the year, allows simulating longer temporal scales, since the ecosystem model is driven by simple physical representations of the environment. Lower values obtained by Louge et *al*. (2004) for temperature and salinity are related with a southern water mass intrusion less salty and colder. In this context, the biogeochemical model can be reasonably applied to the central area of the SJG, given its relatively homogeneous characteristics and low hydrodynamics, in contrast with coastal and frontal areas (Fig. 4; Akselman, 1996).

The parameterization chosen for mesozooplankton migration (section 1.4) allows us to represent a behavior pattern that is not fully consistent with the echo-sounder observations made in the SJG (Fig. 4). In both cases, diel vertical migration was present showing low zooplankton abundances near the surface for daily hours (after midday for model results), while the opposite was observed during the nighttime for the same layer. However, differences were found when depth was considered. Modeled zooplankton never presented high concentrations below 50 m (Fig. 7b), which contrasted with the echo-sounder signal, which showed that zooplankton could reach 80 m. These differences can be explained considering swimming speed, which is strictly related with organisms' size (Mann and Lazier, 2013) and light horizon chosen. It should be noted that the acoustic echogram wavelength set during the R/V *Coriolis* II cruise is mostly efficient for organisms larger than 1 cm, while our model focused on copepods, which size range is 200–2000 µm. The size difference between both zooplankton groups relates to maximum swimming velocities that individuals can reach, being on average 50 cm s^{-1} for krill (e.g. Antarctic krill in Kils,1979) and 0.035 cm s^{-1} for copepods (e.g. Batchelder et *al.*, 2002), which corresponds to approximately a few body lengths. This differential swimming capacity allows bigger organisms the possibility of traveling longer distances and reaching deeper waters faster. Anti-predator tactics also indicate that diel migration ranges are in relation with body size, becoming the distance covered wider as the animal's size increase (Dam et *al*., 1993).

When simulating zooplankton dynamics, we found that the control model produces a significant quantity of demersal zooplankton. This unusual behavior is no longer present in the DVM model, which is more consistent with classical observations and descriptions from the literature for mesozooplankton (e.g. Hays, 2003; Longhurst, 1991), in which zooplankton as member of the pelagic community is usually not found close to the bottom. On the other hand, the lower zooplankton concentrations in the DVM model can be interpreted because of the limitation imposed in terms of food. When migrating, the zooplankton accumulates at preferential depths, sometimes reducing proximity to phytoplankton and increasing competition for food, as opposed to the control model where zooplankton follows phytoplankton.

Environmental characteristics, such as turbulence, can modify migration behavior (Visser et *al*., 2001). Increasing prey encounter and homogenizing phytoplankton concentration translates in higher metabolism rates (Alcaraz et *al*., 1994; Kiørboe, 1993) and they represent only two examples on how water column structure can modify zooplankton vertical distribution (Visser and Stips, 2002). There is also evidence that copepods move downward to avoid high turbulence values found in surface waters, which at the same time reduce ingestion rates as a consequence of leaving the euphotic zone (Visser and Stips, 2002). Zooplankton concentration for the three-days zoom showed, for the DVM model, agreement with light penetration, avoiding surface waters during daytime and moving upward once radiation is minimum. On the other hand, zooplankton disperse distribution could be explained by average intensity turbulence, reaching deeper when its increase in intensity, around 10 m and 30 m, respectively.

When adding DVM, greater phytoplankton concentrations were simulated with a different vertical distribution pattern. Annual phytoplankton cycles showed two different blooms, a stronger one during springtime and a weaker one in early fall. These results are in agreement with remote sensing data from the SJG (Rivas et *al*., 2006; Glembocki et *al*., 2015) and provide more information about its probable distribution in depth in the water column, which is not possible to be obtained with remote sensing. Zooplankton grazing pressure on phytoplankton was reduced in the DVM model because of its lower residence time in the surface layer, which allows phytoplankton to growth and reproduce in the absence of predators during daytime, coinciding with favorable light conditions. In turn, the increase in primary production can modify the export and the fraction of phytoplankton loss by sinking, and its effects can be even greater in high primary productivity marine ecosystems (Aksnes and Wassmann, 1993; Baines et *al*., 1994). Furthermore, Dagg and Walser (1986) demonstrated that high concentrations of food availability can positively modify the size and composition of fecal pellets (compaction) in some copepods species, facilitating the carbon export. However, some modelling results showed that increasing complexity and additional phytoplankton and zooplankton functional groups can negatively affect primary productivity and carbon export (Aita et *al*., 2003).

Zooplankton migration also favors the increase of detritus. The zooplankton zonation allows phytoplankton to increase, which results in a more non-grazed phytoplankton contribution to the detritus pool. At the same time, zooplankton spends less time at the bottom to feed on detritus present there. This behavior will restrict the consumption, repackage and excretion of non-living matter, and consequently reducing the feedback re-entering nutrients to the water column. As result, zooplankton concentration was lower in the DVM model than in the control.

From an ecosystem perspective, the generation of larger detritus amounts leaves more organic matter available in the water column (near the bottom) and mostly for benthic organisms, altering the passive carbon flux. High concentrations of organic matter in deep layers can promote their availability as food before its long-term sequestration of a small fraction in the sediments, which represents the final step in the biological pump process. Ariza et *al*. (2015) demonstrated that carbon flux in the water column could be underestimated if DVM is not considered, with zooplankton derived particles representing ~29% of the carbon active transport leaving the euphotic zone. Other authors have demonstrated that zooplankton activities in deeper waters, such as gut flux and fecal pellets production, can contribute to the carbon transport by 10-30% in different areas of the ocean (Hidaka et *al*., 2001; Bianchi et *al*., 2013). Consequently, the inclusion of zooplankton vertical migration into numerical models provides a more accurate representation of ecosystem production and carbon export.

Zooplankton is, as a migrant component of the ecosystem, one way by which the organic matter could be removed from the ocean surface and transported to the water column interior (Longhurst, 1991). The flux of total organic matter to the deep ocean can be affected by changes in the relative abundance of zooplankton functional groups. In this sense, zooplankton can modify the primary production and composition, aggregation and sedimentation rate of sinking organic particles (Ducklow et *al*., 2001; Turner, 2002; Honjo et *al*., 2008).

Our model has proven to be a useful tool to study the relationships between ecosystem dynamics and physical aspects in the SJG central area. Understanding the distribution, abundance and fluctuations of different system components may allow answering further inquiries. The model showed that the inclusion of more realistic events, like zooplankton diel vertical migration, can modify interactions and results obtained at the food web level. However, the missing information about zooplankton life cycle (e. g. diapause, rates), species-specific behavior, causes of DVM and each development stage reactions, among others, represent limitations to our approach. We conclude that more information, such as physiological local rates for zooplankton and swimming speeds among others, is needed for a better understanding of their effects on organic matter transport and its capacity to modify the carbon fluxes in the region. *In situ* measurements and experimental studies should be a priority for future research as well as an important step in order to calibrate and test (sensitivity analysis) the model for a more accurate study of the biological pump in the SJG.

CHAPITRE 2

CONTRIBUTION DES DIFFERENTS TYPES DE DETRITUS SUR LE FLUX DU CARBONE DANS LE GOLFE SAN JORGE (PATAGONIE, ARGENTINE)

2.1 RÉSUMÉ

La pompe biologique est une série de processus majeurs qui transforment le carbone inorganique de l'atmosphère en carbone organique à l'intérieur d'une série d'interactions dans la colonne d'eau. Elle contribue de manière significative aux flux de carbone et à son transport vers la profondeur. Le détritus est un élément clé dans ce processus, et cela plus particulièrement dans les régions côtières hautement productives. Le golfe San Jorge (GSJ), localisé en Patagonie argentine, est reconnu comme une zone avec une productivité primaire élevée. Dans ce travail, nous avons utilisé un modèle conceptuel idéalisé du type NPZD pour étudier la contribution de la matière organique particulaire au flux vertical de carbone dans cet environnement, avec une emphase sur la dynamique du *pool* de matière organique détritique. On a divisé le compartiment détritique en quatre sous-compartiments (variables d'état) en fonction de l'origine et de la taille des particules qui les composent. Ces nouveaux compartiments sont affectés par différentes vitesses de sédimentation et diverses interactions avec l'écosystème. Le modèle, basé sur celui de Fasham et *al*. (1990) qui possède sept compartiments, présente maintenant dix variables d'état, en incluant le phytodetritus, le zooplankton mort et les pelotes fécales, qui peuvent contribuer à la formation des agrégats marins tels que la neige marine. Ce modèle biogéochimique a été couplé avec un modèle unidimensionnel de l'océan (GOTM) pour évaluer l'évolution des compartiments. Les résultats préliminaires du modèle ont démontré que le phytodetritus contribue en moyenne de manière plus significative au flux de carbone dans la colonne d'eau en comparaison avec le zooplancton mort et les pelotes fécales.

2.2 CONTRIBUTION OF DIFFERENT DETRITUS TYPES TO THE CARBON FLUX IN THE SAN JORGE GULF (PATAGONIA, ARGENTINA)

Abstract: The marine biological pump is a series of major of processes transforming atmospheric inorganic carbon into organic carbon by means of interactions in the water column. It contributes significantly to vertical organic carbon fluxes and its final sequestration in the seabed. Detritus represents one component that enhances this carbon flux. Productive coastal regions are more susceptible to produce detritus material. The San Jorge Gulf (SJG), in the Argentinian Patagonia, is recognized as a highly productive area. Here we used an idealized conceptual NPZD model to study the contribution of particulate organic matter to vertical carbon flux in the SJG, with an emphasis on the detrital component. We separated the detritus compartment in four new state variables, according to particles' origin and size. These compartments are then affected by different sinking speeds and ecosystems interactions. The ten-compartment model includes phytodetritus, dead zooplankton and faecal pellets groups, which can contribute to the formation of marine aggregates such as marine snow. The biogeochemical model is coupled to a one-dimensional atmospheric and ocean physical model (GOTM) to evaluate organic carbon pathways. Our results show that phytodetritus contribute in a greater way to carbon flux in the water column and near sediments in comparison with dead zooplankton and faecal pellets.

2.3 INTRODUCTION

Marine ecosystem processes are important determinants in ocean biogeochemistry (Le Quéré et *al*., 2005). The biological pump is a major process in these environments that involves the production and sinking of particulate organic matter (POM, Lam et *al*., 2011; Longhurst and Harrison, 1989). Organic matter is produced by photosynthesis in the ocean surface and can be exported into deeper layers during the carbon cycle (Stemmann et *al*., 2004), although a significant proportion (~80%) of this carbon will be transformed and consumed in mesopelagic waters, during the downward export (de la Rocha and Passow, 2007). A small fraction (~15%) of the organic matter produced in the euphotic zone will reach the seabed (Ducklow et *al*., 2001; Smith and Hollibaugh, 1993).

The non-living organic matter, known as detritus, includes dissolved materials and particles of different sources, sizes and chemical compositions, which all play different and important roles in marine ecosystems (Moore et *al*., 2004). The general definition that is widely accepted by the scientific community involves a wide variety of forms, including autotrophs' tissue, animal tissue and molts, dead microbes, faecal pellets as well as products secreted or exuded from organisms (e.g. phytoplankton exudates and dissolved organic carbon by zooplankton; Turner, 2002). While small particles tend to sink very slowly, are consumed and disappear as the result of trophic interactions, larger particles sink at higher velocities and can reach the bottom within hours or days depending of their characteristics and depth (Alldredge and Jackson, 1995). Consequently, large particles like faecal pellets and aggregates contribute significantly to the organic carbon sequestration and mineralization in sediments (Gooday and Turley, 1990).

In marine ecosystems, the quantity and quality of detritus vary from one pelagic environment to the other, which may affect the system differently. The particulate and dissolved forms of detritus affect light penetration and temperature through light absorption within the water column (Moore et *al*., 2004). From a trophic perspective, detritus may constitute reservoirs of supplementary energy that are usually considered to rely only on living organisms (Moore et *al*., 2004), representing an extra food source.

Dissolved detritus can be transformed into particles via coagulation and aggregation, driven by turbulent mixing which increases the encounter probabilities, and small particles can be built up into larger detrital forms (Alldredge et *al*., 1990). Marine gels enclose a wide size spectrum from colloids to particles of hundred's, where their composition can determine chemical and physical characteristics like porosity, volume and structure

(Verdugo, 2012; Verdugo et *al*., 2004). The size classification has separated gels into colloidal nanogels, micro and macrogels. The first two type, have dissolved organic carbon (DOC) polymers assemble as precursor, which are stabilized by entanglements and cations bonds, and both gel types are interconnected in reversible processes (annealing and fragmentation; Verdugo, 2012). On the other hand, macrogels such as transparent exopolymer particles (TEPs) play a key role in sedimentation processes due to their size, being critical for the formation of marine snow and the aggregation of diatom blooms (Verdugo et *al*., 2004; Alldredge et *al*., 1993). TEPs are composed of acid polysaccharides produced by phytoplankton and bacteria exudation with high stickiness properties (Passow et *al*. 2001, Passow 2002). Marine snow and other macroscopic aggregates are constituted and enriched by faecal pellets, abandoned larvacean houses, phytodetritus, protozoans, dinoflagellate flocs, minerals and aggregates of detritus (e.g. Turner, 2002; Alldredge et *al*., 1993). Large marine snow macroflocs form under phytoplankton blooms and low wind speeds conditions, being dissipated by wind-induced turbulence (Riebesell, 1992). Some authors have demonstrated the importance of aggregates as additional food for the pelagic community, where organisms like zooplankton can profit and graze from small particles aggregations that otherwise are not available due to their size (Alldredge and Jackson, 1995; Lampitt et *al*., 1993). Marine gels have a high nutrient content, representing a strong advantage for bacteria to colonize them (Verdugo, 2012). This, in turn, modifies the spatial and temporal dynamics of nutrients sustaining the microbial community in the water column (Wells, 1998).

The vertical carbon flux in the sea is highly variable and depends on multiple factors. However, three components of the biological pump have been identified to play a significant role in organic matter transport and recycling: phytoplankton sinking (live and dead), sedimentary flux of faecal pellets and marine snow formation (Turner, 2002). These processes not only affect water column interactions and composition, but also have a great influence on benthic communities (Silver and Gowing, 1991).

Organic carbon reaching the sea bottom can be consumed, respired or finally remineralized in the sediments (Ducklow et *al*., 2001). Generally, benthic organisms' biomass and distribution are good indicators of the quality and quantity of organic matter bioavailable in deep layers (Gooday and Turkey, 1990). This organic matter input could vary between seasons, and organism's assimilation response would be faster in shallower marine environments (Lampitt et *al*., 1993), with the different forms of detritus being transported at different rates and across different spatial scales (Moore et *al*., 2004).

Continental margins are biogeochemically active environments (Gruber et. al, 2006) and particularly productive coastal regions are susceptible to generate larger amounts of detritus (Wassmann, 1985). The Atlantic Argentinian shelf is a region with high primary productivity (>300 g C m^{-2} yr^{-1}; Bisbal, 1995), and particularly the San Jorge Gulf (SJG, 45° to 47°S) appears from remote sensing images as a region with elevated levels of chlorophyll-*a* (Glembocki et *al*., 2015; Rivas et *al*., 2006). The most relevant characteristics of the SJG include a shallow bottom (~ 100 m), dominant westerly winds, semi-diurnal tides (~ 6 m) and no riverine and low rainfall water inputs (Akselman, 1996). Therefore, nutrients and organic matter provision in the water column and for the benthos are either produced locally or arriving the region by currents from the Argentinean shelf. Furthermore, in the SJG human activities can add organic carbon to the water column, in many cases resulting from marine fisheries discard waste (González-Zeballos et *al*., 2007). In this area, information and relation about processes producing detritus components and formation of aggregates do not yet exist. According to Fernández et *al*. (2007), the seasonal variability of physical conditions, like water column stratification, can modify the vertical carbon flux in the SJG. There are evidences of a stronger flux during winter when the water column is well mixed, which allows for amounts of organic matter to reach the sediments (Fernández et *al*., 2005). However, there are no studies about how detritus is transformed in the upper or middle water column and the possible pelagic-benthic coupling. The connection between these processes and the vertical carbon flux in the Gulf are little known and their role in ecosystem dynamics is scarcely understood.

Detritus distribution in the water column is far from homogeneous, but is rather highly variable in form and concentration depending on spatial and temporal scales. Moreover, this variability has implications for marine organisms, food webs and ecosystems. The inclusion of detritus dynamics in models allows for ecological products and interactions to be considered. The principal aim of this study is to build a framework that will allow for a better representation of the detrital production, transformation and sedimentation in numerical ecosystem models. The conceptualization of the corresponding biogeochemical model is proposed as a first step towards its implementation and future use in the study of complex marine systems, and more specifically the carbon cycle dynamics.

2.4 BIOGEOCHEMICAL MODEL MODIFICATIONS

The NPZD model used as a basis for this work is the DVM model presented in Chapter I. Some modifications are proposed to evaluate the effect of the detritus compartment, which in the original model was conceived as the sum of different sources of non-living organic matter. The model proposed here includes ten state variables (Fig. 10), expressed as concentrations of the different ecosystem components (Table 4) each representing either dissolved chemicals (e.g. ammonium) or particulate matter (e.g. faecal pellets). Figure 10 represents the conceptual model with the division of the detritus compartment and Figure 11 shows their specific new interactions. The model is nitrogen-based (Fasham et *al*., 1995), since the sole limiting nutrient is nitrate (NO_3^-). Primary (PHY) and secondary (ZOO) producers are represented by one group each, namely phytoplankton of size > 10-200 µm and mesozooplankton, respectively.

Detritus is divided into four compartments according to the major components of the biological pump in the organic carbon vertical flux presented in the introduction (section 2.3). Some decisions have been taken in relation with particle sources and sinking speeds to regroup these compartments. The phytodetritus (DPH) compartment includes dead phytoplankton and bacteria, as well as remains of zooplankton grazing on phytoplankton and bacteria. Zooplankton fecal pellets (FCP) as well as dead zooplankton (DZO) are represented in separate compartments. Finally, the marine snow compartment (MAS) is composed of particles of different sizes and origins as above (phytodetritus, faecal pellets and dead zooplankton). Equations for the processes described above are listed in section 2.5 and the parameters involved are presented in Table 5.

The microbial loop includes three state variables: bacteria (BAC), ammonium (NH_4^+) and labile dissolved nitrogen (DON). The recycling process allows the elements to re-enter the systems by means of bacteria excretion and respiration.

Vertical sinking speeds affect all particulate compartments, except for zooplankton, which is able to swim and migrate vertically. It is important to note that phytodetritus sinking speed will be influenced by the sinking speed range of particles such as phytodetritus (<1-510 m d^{-1}), phytoplankton fragments (1.5-26 10^3 m d^{-1}) and bacteria (~0.06 m d^{-1}) (Smayda, 1971, 1969; Pedrós-Alió et *al*., 1989).

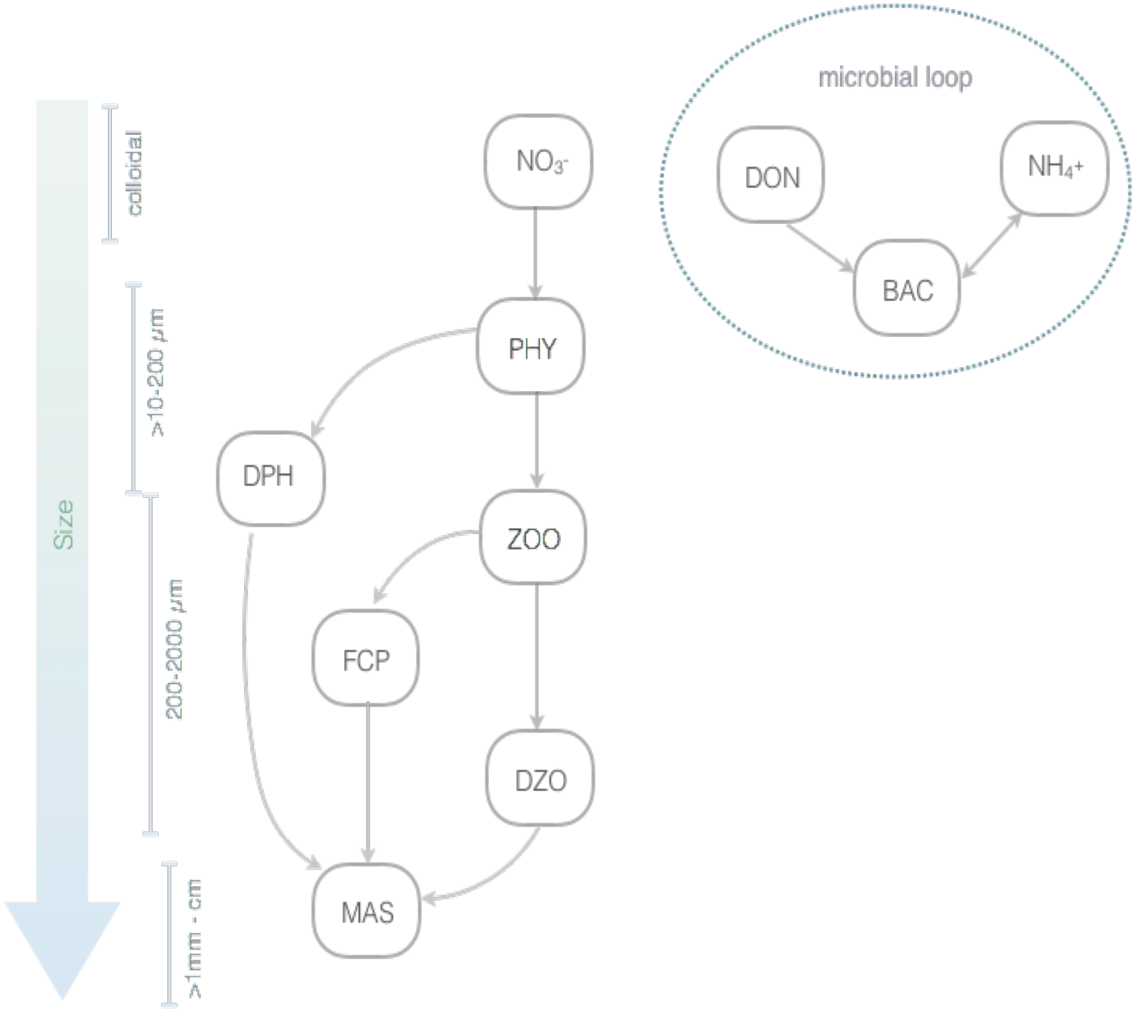

Figure 10. Biogeochemical conceptual model with ten state variables adapted from Fasham et *al*. (1990) with the division of the detritus compartment in phytodetritus (DPH), faecal pellets (FCP), dead zooplankton (DZO) and marine snow (MAS). The microbial loop is present in the model, but its relations are excluded to emphasize the changes made. Size spectrum for different compartments will be translated in differential sinking speeds (see Table 4).

Table 4. Biogeochemical model original and modified (bold italic) state variables.

Variable	Symbol	Description	Dimension
c_1	NIT	Nitrate	mmol N m^{-3}
c_2	PHY	Phytoplankton	mmol N m^{-3}
$\boldsymbol{c_3}$	***DPH***	***Phytodetritus***	***mmol N m^{-3}***
c_4	ZOO	Zooplankton	mmol N m^{-3}
$\boldsymbol{c_5}$	***FCP***	***Faecal pellets***	***mmol N m^{-3}***
$\boldsymbol{c_6}$	***DZO***	***Dead zooplankton***	***mmol N m^{-3}***
c_7	BAC	Bacteria	mmol N m^{-3}
c_8	AMM	Ammonium	mmol N m^{-3}
c_9	DON	Labile Dissolved Nitrogen	mmol N m^{-3}
$\boldsymbol{c_{10}}$	***MAS***	***Marine snow***	***mmol N m^{-3}***

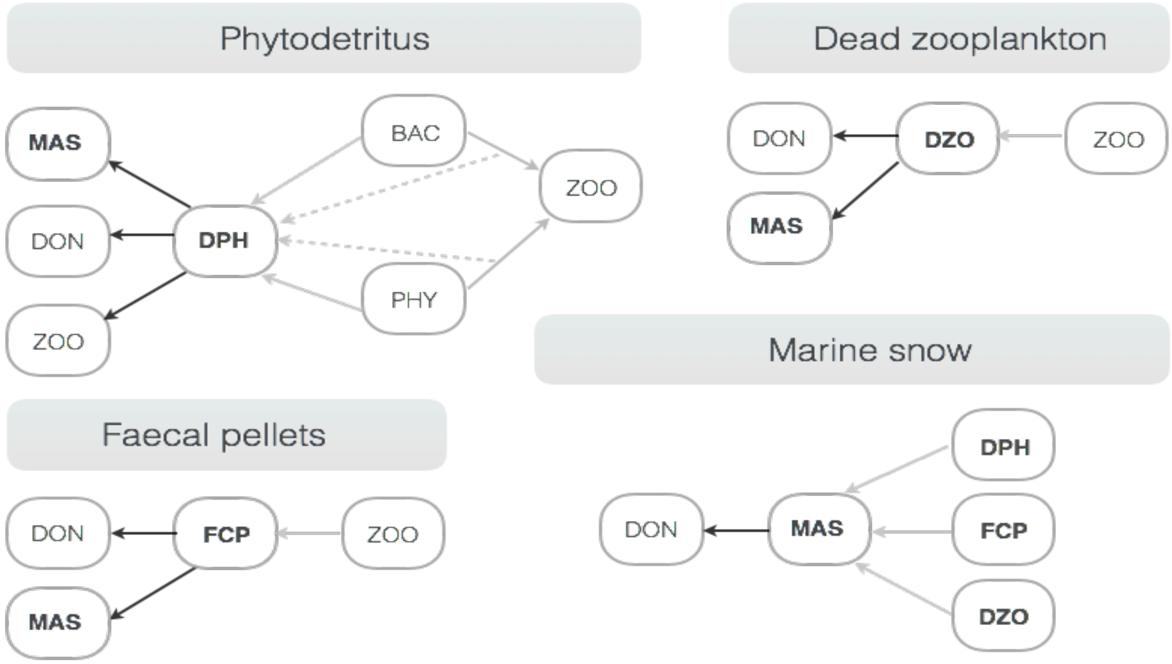

Figure 11. Modified interactions for the new four state variables (bold), showing with grey and black arrows their gains and losses, respectively. Dashed lines show remains of phytoplankton and bacteria after zooplankton grazing.

2.5 MATHEMATICAL FORMULATIONS

The system of first order ordinary differential equations governing the ecosystem evolution follows the formulation and notation of Fasham et *al*. (1990) to which modifications are made. We adopt the same notation to simplify the reader's understanding, inviting him to refer to Fasham et *al*. (1990). The following sections present the evolution equation for three new state variables, namely phytodetritus (DPH), faecal pellets (FCP) and dead zooplankton (DZO), respectively, and a theoretical approach to be computerized in the future for the marine snow compartment (MAS). Parameters description used in the biogeochemical model are presented in Table 4.

2.5.1 Phytodetritus (DPH)

This detritus compartment was defined including natural mortality of phytoplankton, which is represented by the two terms in eq. 2.1*a*.

$$\frac{dDPH}{dt} = \mu_2 \mathrm{PHY} + \mu_7 \mathrm{BAC} \tag{2.1a}$$

The next terms added to this equation are in relation with zooplankton grazing on different groups (eq. 2.1*b*). Fasham et *al* (1990) proposed zooplankton grazing preferences on different preys (phytoplankton, phytodetritus and bacteria, β_2, β_3 and β_7, respectively), considering that small parts of them are not consumed. Thus, the remains of zooplankton grazing on phytoplankton and bacteria will be incorporated to the phytodetritus compartment represented by

$$\frac{dDPH}{dt} = (1-\beta_2)G_2 + (1-\beta_3)G_3 + (1-\beta_7)G_7 \tag{2.1b}$$

where G_i are Michaelis-Menten limitation functions of the grazed compartments, as in equation 10 of Fasham et *al*. (1990).

Finally, two more terms represent phytodetritus compartment losses (eq. 2.1c), by further assuming that phytodetritus can be recycled within the mixed layer by breakdown into dissolved organic nitrogen (DON) and the subsequent uptake by bacteria. The breakdown of detritus to DON may be partly purely chemical leaching and partly due to bacterial activity. In addition, a fraction of exudates will end in the marine snow compartment, allowing the structural base to form aggregates, due to their stickiness characteristics.

$$\frac{dDPH}{dt} = -\mu_3\mathrm{DPH} - \mu_8\mathrm{DPH} \tag{2.1c}$$

2.5.2 Faecal pellets (FCP)

The first term in equation 2.2 refers to the rate for zooplankton faecal pellets production, which at the same time will depend on their grazing preference on phytoplankton and bacteria, respectively. In this model, we did not consider coprophagy, as we did not represent smaller zooplankton groups that could generate little feces. The second term represents faecal pellets breakdown rate to DON that will be later degraded by means of bacteria interactions. The last term involves faecal pellets contribution to marine snow, which we know can represent a great percentage of organic matter in some marine food webs.

$$\frac{dFCP}{dt} = (1 - \beta_2 - \beta_3)\,\mu_4\,\mathrm{ZOO} - \mu_5\mathrm{FCP} - \mu_9\mathrm{FCP} \tag{2.2}$$

2.5.3 Dead zooplankton (DZO)

Part of the dead zooplankton becomes detritus (first term eq. 2.3), and is then subsequently broken into dissolved organic nitrogen (DON, second term eq. 2.3), which will be afterwards degraded by bacteria. The other portion will sink out of the mixed layer and a small fraction can remain attached to marine snow (third term eq. 2.3). It is important to highlight that in the original model (Fasham et *al*., 1990) zooplankton mortality included natural mortality causes and indirect losses by higher level predators, even if they were not explicitly taken into account, an assumption that we kept.

$$\frac{d\mathrm{DZO}}{dt} = \mu_4\,\mathrm{ZOO} - \mu_6\mathrm{DZO} - \mu_{10}\mathrm{DZO} \qquad (2.3)$$

2.5.4 Marine snow compartment (MAS)

Coagulation efficiency in marine aggregates could be modulated by features such as particle composition, structure, phytoplankton species, shape, porosity, stickiness and compactness (Laurenceau-Cournec et *al*., 2015; Iversen and Ploug, 2010).

Some authors have attempted to include marine aggregates in models under the theories of coagulation (e.g. Logan et *al*., 1995) and Stokes sinking rate (e.g. Laurenceau-Cournec et *al*., 2015; Fisher and Karakas, 2009; Gruber et *al*. 2006), sometimes dividing the compartment depending on sinking rates into two big particles assemblages: small and big nuclei (e.g. Ploug and Stevens, 2002). However, chemical characteristics, particularly stickiness, and physical environmental conditions such as turbulence, can be as much important as aggregates origin and composition (e.g. Laurenceau-Cournec et *al*., 2015; Schmittner et *al*., 2005) and they are needed to be incorporated in models to improve the knowledge of marine snow dynamics. In general, biogeochemical models leave this high complexity aside, and so we do here, in order to prioritize the understanding of the role of some of the main components in the formation of marine snow.

We assumed that the marine snow compartment is mostly constituted by three main fractions: phytodetritus, dead zooplankton and faecal pellets (Fig. 12 *a*, *b* and *c*). Losses relate only with the breakdown to DON and have, as in the other compartments representing particulate matter, an associated sinking speed.

Table 5. Description and value of parameters involved in the new detritus state variables.

Symbol	**Value**	**Unit**	**Description**
$\beta_2=\beta_3=\beta_7$	0.75		zooplankton assimilation efficiency on PHY,DPH and BAC[a]
γ	0.05		phytoplankton exudation fraction[a]
μ_2	0.05	d^{-1}	phytoplankton mortality rate[a]
w_p	-0.38	$m\ d^{-1}$	phytoplankton settling velocity[a]
μ_3	0.05	d^{-1}	phytodetritus breakdown to dissolved organic nitrogen[a]
w_{dph}	-10	$m\ d^{-1}$	phytodetritus settling velocity[b]
μ_4	0.05	d^{-1}	zooplankton mortality rate[a]
μ_5	0.05	d^{-1}	faecal pellets breakdown to dissolved organic nitrogen[a]
w_{fcp}	-112	$m\ d^{-1}$	faecal pellets settling velocity[b]
μ_6	0.05	d^{-1}	dead zooplankton breakdown to DON[a]
w_{dzo}	-30	$m\ d^{-1}$	dead zooplankton settling velocity[c]
μ_7	0.05	d^{-1}	bacteria mortality rate[a]
μ_8	undefined	d^{-1}	fraction phytodetritus loss to marine snow
μ_9	undefined	d^{-1}	fraction faecal pellets loss to marine snow
μ_{10}	undefined	d^{-1}	fraction dead zooplankton loss to marine snow

[a] Fasham et *al.*, 1990

[b] Turner, 2002

[c] Smayda, 1969 (sinking speed for dead copepods and molts)

2.6 RESULTS AND DISCUSSION

Simulations were run for three detritus compartments (DPH, FCP and DZO) to evaluate their concentrations values and patterns in the water column (Figure 12). Numerical simulations were performed during almost three years (June 2013 to August 2016) to enclose the *R/V Coriolis II* cruise (MARES, February 2014) and allow for some comparisons with *in situ* observations and known literature for the San Jorge Gulf (Patagonia, Argentina).

Highest concentrations were estimated for 2016 for the three detritus compartments (Table 6) than for the previous simulated years. When comparing among seasons, summer represents the highest values for phytodetritus, faecal pellets and dead zooplankton, while lower values are found in winter, except for faecal pellets in 2013, when the minimum value was present in spring. The response of the three detritus compartments were similar when we look the general pattern, with higher concentrations in depth, mostly below 90 m (Fig. 12; but see the different concentrations scale values between compartments).

Phytodetritus (Fig. 12*a*) shows highest concentrations in the water column below 30 m in 2013, lasting from October to June 2014. During years 2014 and 2015 the patterns start with a peak in October near the surface, gradually decreasing until June. High concentrations of phytodetritus are evidenced at the bottom during the entire simulation. Similar patterns were found for dead zooplankton (Fig. 12*b*) and faecal pellets (Fig. 12*c*), for which in 2013 the highest concentrations are present below 30 m (October-June), presenting a surface peak in October (2014 and 2015) diminishing until April when the distribution in the water column becomes less evident. These observations are consistent with post bloom scenarios, which leave available significant amounts of organic matter in the water column.

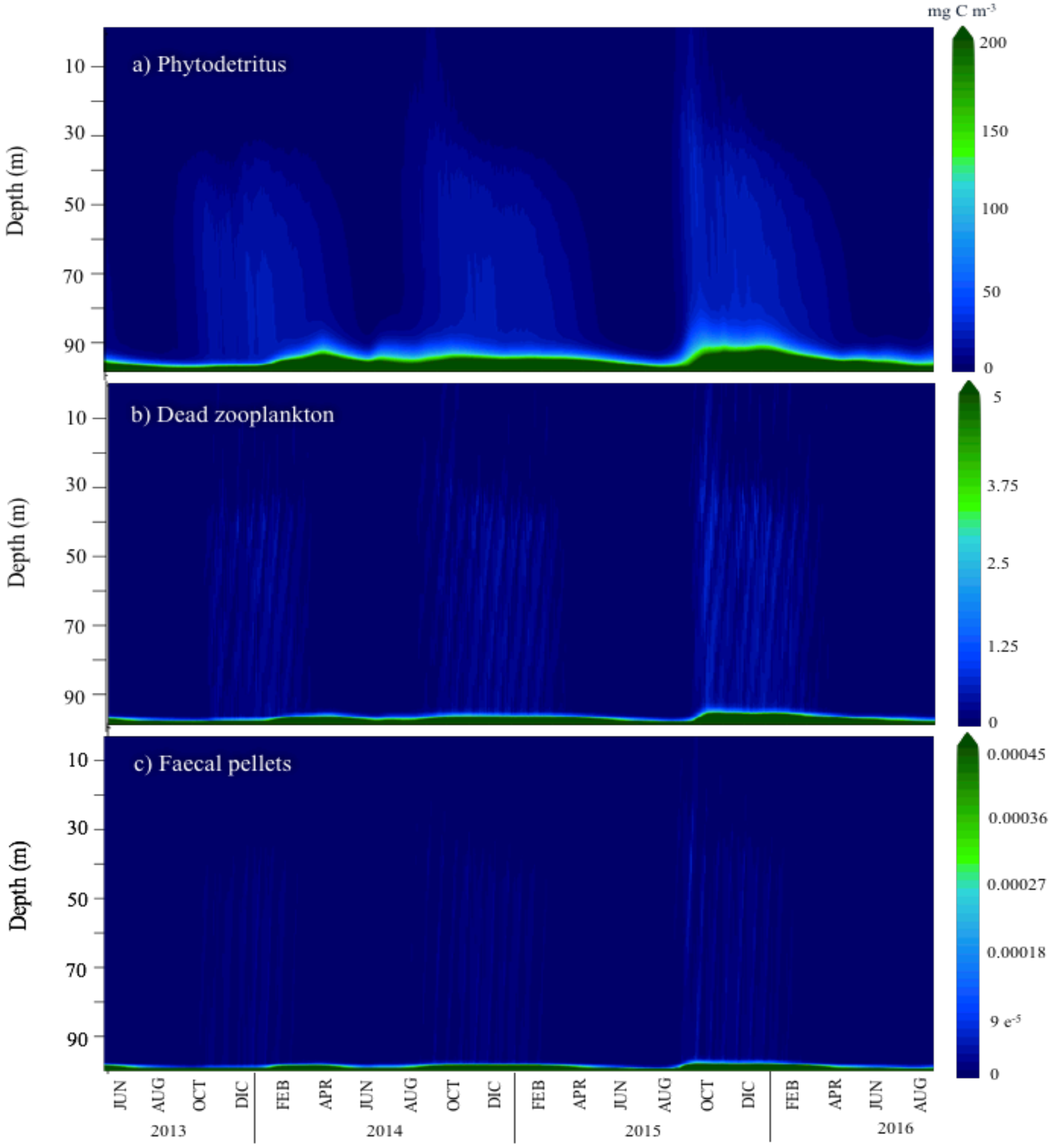

Figure 12. Evolution of a) phytodetritus, b) dead zooplankton and c) faecal pellets concentrations (mg C m^{-3}) simulated with the ten state variables model.

In coastal waters, mass sedimentation of phytoplankton blooms plays an important role in carbon and nitrogen vertical flux (Turner, 2002). If cells can finally arrive to the sediments, this can also provide a way for certain species, e.g. diatoms and other cyst forming organisms, to persist and proliferate in the next season (Smetacek, 1985). In nearshore areas, there is a direct relationship between organic matter deposited in the seabed and the intensity of the processes occurring in the water column (Wassmann, 1985). Fernández et *al*. (2005) described the organic matter present in sediments in the SJG and reported values for C:N ratios corresponding to phytoplankton origin, during autumn and wintertime. In contrast, high abundances of organic matter in spring and summer were attributed to local accumulation processes, rather than allochtonous inputs, since that in the SJG there are not important contributions of riverine or rainfall (Akselman, 1996).

Zooplankton faecal pellets can play a significant role in the vertical carbon flux (Honjo et *al*., 2008; Turner, 2002; Ducklow et *al*., 2001; Wassmann et *al*., 2000). This type of particle has a high sinking speed, which enhances the contribution of organic matter to the benthos, avoiding its consumption and decomposition by epipelagic organisms (Eppley and Peterson, 1979). In the past, zooplankton mortality loss at depth was considered negligible compared with passive particulate organic carbon (POC) flux, but nowadays it has been estimated to be of similar magnitudes than POC flux (Kobari et *al*., 2008; Kobari et *al*., 2003; Bradford-Grieve et *al*., 2001). In the SJG no studies exist that focused on these two types of particle fluxes and the effects they could have in the ecosystems dynamics. However, a first approach made by Massé-Beaulne (2016) measuring carbon flux with sediment traps stressed the importance of faecal pellets contribution to carbon flux in the central region of the gulf, but no estimations were done in relation with the possible effects of dead zooplankton and its molts.

Organic matter in sediments influences the distribution of different commercially important species, e.g. peneids (Fernández et *al*., 2007). Even if particles size can bring an important feature for the distribution of these species, as refuge e.g. in rocky reefs, there is a significant correlation between seabed organic carbon content and their abundances (Fernández et *al*., 2007). At the same time, increased organic matter availability in the water column and sediments can promote the proliferation of opportunistic species, such as *Munida sp.*, for which the role is not yet known in the SJG (Vinuesa and Varisco, 2007).

Table 6. Seasonal production of phytodetritus, faecal pellets and dead zooplankton for three years' simulations, maximum (bold) and minimum (italic) concentration per year, respectively (DPH= dead phytoplankton, FCP= faecal pellets, DZO= dead zooplankton).

		DPH ($g\ C\ m^{-2}$)	FCP ($mg\ C\ m^{-2}$)	DZO ($g\ C\ m^{-2}$)
2013	Winter	*2.08 (±0.34)*	0.021 (±0.0089)	*0.07 (±0.02)*
	Spring	3.02 (±0.81)	*0.019 (±0.0078)*	0.13 (±0.07)
2014	Summer	**5.32 (±0.35)**	**0.041 (±0.0036)**	**0.34 (±0.03)**
	Autumn	4.22 (±0.79)	0.017 (±0.0077)	0.16 (±0.07)
	Winter	*2.27 (±0.22)*	*0.008 (±0.0029)*	*0.06 (±0.02)*
	Spring	4.30 (±0.81)	0.032 (±0.0089)	0.26 (±0.07)
2015	Summer	**5.72 (±0.01)**	**0.046 (±0.0034)**	**0.40 (±0.02)**
	Autumn	3.98 (±0.90)	0.017 (±0.0083)	0.16 (±0.07)
	Winter	*1.58 (±0.33)*	*0.004 (±0.0014)*	*0.03 (±0.01)*
	Spring	4.56 (±1.16)	0.044 (±0.0130)	0.35 (±0.10)
2016	Summer	**6.52 (±0.24)**	**0.059 (±0.0067)**	**0.51 (±0.05)**
	Autumn	4.26 (±0.96)	0.021 (±0.0099)	0.19 (±0.09)

2.7 CONCLUSION AND FUTURE WORK

The variation in particle characteristics across different production systems is an issue that biogeochemical models should address (Fisher and Karakas., 2009). Numerical modeling efforts have been mainly focused on investigating the upper levels of planktonic systems, such as primary and secondary productions. However, lower levels (e.g. detritus) have not been given as much attention in their formulation (de Young et *al*., 2004), although the importance to investigate and include organic particles fluxes, as detritus, in models has been highlighted already (Evans, 1999). Some work has been however done (e.g. Fisher and Karakas, 2009; Gruber et *al*., 2006; Logan et *al*., 1995), but while previous research focused on individual particle transformations mechanisms in the water column, the present study highlights the relative contribution of different detritus sources and their interaction with the other ecosystem components.

Phytodetritus concentrations availability simulated by the model in the water column, with the future inclusion of exudates by phytoplankton and bacteria, opens the door to further inquiries about the marine aggregates formation and their role in SJG ecosystem dynamics. Furthermore, particle aggregation can considerably modify the residence time of organic matter and its accessibility in the water column. On the other hand, this suspended material will alter the water column physical characteristics (e.g. transparency and light penetration), as its might be present in high concentrations in some cases (phytodetritus). This represents a new perspective regarding physical interactions at the ecosystem level, since in their original model, Fasham et *al*. (1990) proposed phytoplankton as the only factor modifying light penetration. The addition of other sources will possibly be a next step for improving the model responses.

In this study, mesozooplankton faecal pellets production did not contribute significantly to the detritus pool. There has been thought that zooplankton faecal pellets are an important clue to carbon vertical flux, however more recent evidence indicates that only macrozooplankton, micronekton and fish large faecal pellets are important components to this flux (Turner, 2002; Alldredge, 1993). This difference lies in the faecal sinking speeds, while large pellets can reach fast the bottom, lower sinking speed for mesozooplankton pellets allows the possibility of consumption and degradation in the water column avoiding benthos destination (Turner and Ferrante, 1979). Sediment tramps installed during the *R/V Coriolis II* mission in the SJG presented significant quantities of large faecal pellets, probably from the crustacean *Munida sp*., but not important contribution was evident for the smaller ones (Massé-Beaulne, 2016). Nevertheless, Roy et *al*. (2000) found that in the Gulf of St. Lawrence with high mesozooplankton abundances through the year, copepods faecal pellets can represent an important contribution (50% on average) to the carbon flux, even if this can vary within seasons, depending on primary production of non-algae origin.

Dead zooplankton and molts production represented intermediate contributions when comparing with a phytodetritus and faecal pellets simulation results. Zooplankton and micronekton carcasses can be converted into aggregates by microbial heterotrophy (Honjo et *al*., 2008). There is evidence that dead zooplankton can play a substantial role as interstitials dissolved organic carbon (DOC) in aggregates, being a source of particulate organic carbon (POC) and being degraded by processes related to the enzymatic activity of microbes (Alldredge, 2000; Noji et *al*., 1999).

Furthermore, the impact of microorganisms (e.g. bacteria) on biogeochemical cycles and on detritus must further be considered. Even if in the present model the microbial loop was included and implicitly interacts with the other ecosystem components, no special attention was made on the possible effect in the organic carbon recycling path and its role in re-entering organic and inorganic elements into the system. In addition, the model considers only the free-living bacteria, while attached bacteria are probably more representative components acting in the detritus compartments due to its relation and aggregation to particulate organic matter (Azam and Malfatti, 2007; Pmeroy and Wiebe, 1988; Pace et *al*., 1984). To make useful predictions about how marine ecosystems can respond to particulate matter inputs, incorporating microbial processes is indispensable (Azam and Malfatti, 2007).

Combining the approaches on particle aggregations, differential sinking speeds and ecosystem interactions on detritus particles offers a powerful tool to understand the factors controlling particulate organic carbon (POC) flux and to predict this flux in the SJG.

However, modeled cycles of detritus compartments and the extent of their seasonal production cannot be validated due to sparse observations and scarce literature in the region. Future research should focus on the quantification, composition analysis and the role of aggregates as microhabitats as well as food sources for marine organisms in the water column. In this manner, more *in situ* observations and experiments are required to better parameterize and validate the model for this particular area.

CONCLUSION GÉNÉRALE

Les principaux objectifs de ce mémoire, présenté en deux chapitres, étaient d’étudier, à l’aide d’un modèle numérique couplé physique-biogéochimique 1D, les effets des divers processus sur le flux vertical de carbone dans la zone centrale du golfe San Jorge par : 1) l’inclusion de la migration verticale diurne du mesozooplankton (MVD) et 2) la considération des différents types du détritus en fonction des caractéristiques comme l’origine et la vitesse de sédimentation sur un modèle du type NPZD dans un contexte physique turbulent.

Les comparaisons du modèle avec des résultats publiés de télédétection et les observations *in-situ* obtenues de la mission MARES à bord du navire *R/V Coriolis II* ont montré que le modèle est capable de bien reproduire les caractéristiques moyennes à meso-échelle du système (en excluant les zones des fronts et côtière). Le phytoplancton présente deux périodes d’accumulation, une plus intense au printemps et une autre moins intense au début de l’automne, typique des eaux côtières en milieu tempéré. En même temps, le modèle a permis l’extraction d’information des caractéristiques physiques dans les cas où les données ne sont pas disponibles. La colonne d’eau a montré une forte stratification pendant les mois d’été, tandis que le milieu était bien mélangé durant l’hiver, la stratification de la colonne d’eau étant principalement contrôlée par la température.

La réponse du phytoplancton et des détritus à l’addition de la migration verticale diurne zooplanctonique a été positive dans les deux cas (Chapitre I). L’accumulation de la biomasse du phytoplancton a été trois fois plus élevée (2 g C m^{-2} vs 6 g C m^{-2}) lorsque la MVD est activée, alors que la concentration de détritus a quadruplé (3 g C m^{-2} vs 12 g C m^{-2}). L’augmentation de la concentration du phytoplancton est attribuable à une diminution de la pression de prédation pendant le jour, quand le zooplancton migre vers la profondeur et celle des détritus est liée à la forte production primaire couplée à l’absence du zooplancton près du fond marin qui pourrait les consommer. Par contre, la concentration du zooplancton a diminué, comme résultat de l'incorporation de la MVD. Ceci suggère que la MVD facilite la disponibilité de nourriture pour une période plus courte au zooplancton, particulièrement quand il est capable de nager vers la surface pendant les heures de moindre incidence lumineuse.

Le modèle conceptuel proposé dans ce travail (Chapitre II) fait d'abord une synthèse des études récentes publiées à ce sujet et permet d'explorer l'évolution des différents types de détritus selon leur source, qui auparavant étaient toutes englobés dans un seul compartiment. Les résultats montrent une variation interannuelle (juin 2013 - juillet 2016) des concentrations en augmentant en fonction du temps. Les productions simulées étant plus élevées durant l'été 2016 pour les trois compartiments, c'est le compartiment phytodetritus qui a contribué le plus significativement : phytodetritus (6.52 g C m^{-2}), zooplancton mort (0.51 g C m^{-2}) et pelotes fécales (0.059 mg C m^{-2}). Il est admis depuis longtemps que l'export de carbone vers l'intérieur de l'océan est modulé par la sédimentation du phytoplancton (vivant ou mort), des pelotes fécales du zooplancton et des agrégats marins. Représenter ces types de processus dans les modèles numériques permettra d'étudier et d'évaluer, dans des études subséquentes, leurs effets dans l'écosystème et ses rapports avec les flux de carbone. Cependant, peu de comparaisons ont été faites pour le GSJ, dû à la faible disponibilité des données dans cette région.

PERSPECTIVES

La dynamique des cycles élémentaires et la manière dont ils modulent l'amplitude et la production biologique, et conséquemment le flux de carbone organique, sont relativement peu connus dans le GSJ. Plus d'exploration dans la région devrait se faire pour recueillir des informations et élucider le fonctionnement de cet écosystème hautement exposé aux risques de l’exploitation humaine. Il existe un manque important de données pour le GSJ, tels que la vitesse de sédimentation pour des particules organiques, la composition de la communauté zooplanctonique migratoire, les taux d’excrétion, d’exsudation, etc. Pourtant, il serait utile d’amplifier la fréquence d’échantillonnage dans le golfe, ainsi que la réalisation des expériences en laboratoire, ce qui donnera plus d’information pour mieux paramétrer le modèle et le valider.

Pour les futures simulations, il serait important de considérer le rôle des bactéries, surtout celles attachées aux agrégats marins, comme décomposeurs de la matière particulaire organique et son lien avec la rentrée d’éléments dans le système. Il serait aussi intéressant d’approfondir les possibles effets que les processus physiques, tels que la turbulence, ont sur les organismes et sur la disponibilité de la matière organique dans la colonne d’eau. L’effet de la turbulence dans ce mémoire a été peu étudié, notamment en conjonction avec la migration verticale du zooplancton, et les effets sur le phytoplancton (ex. éloignement de la zone euphotique) et sur le détritus (ex. homogénéité de nourriture) restent encore à être évalués.

Les nouvelles hypothèses sur l’effet de la pêcherie dans le flux de carbone, ainsi que les possibles contributions de la poussière d’origine terrestre sur la production primaire dans la zone du GSJ, pourraient être des lignes du travail à explorer afin d’être incorporées dans le modèle numérique.

ANNEXES

ANNEX I. Conversion factors table for N to C concentrations values from Redfield's ratios.

Variable	**Molar ratio (C:N)**	**C relative atomic mass**	**N relative relative mass**	**Conversion Factor (m mol N m^{-3} to mg C m^{-3})**
Phytoplankton	106 : 16	12	14	79.5
Zooplankton	7 : 1	12	14	84
Detritus	106 : 16	12	14	79.5

ANNEX II. Parameters used in biogeochemical model simulations.

Symbol	**Value**	**Unit**	**Description**
α	0.065	$m^2(Wd^{-1})$	slope of the PI-curve
β	0.625		grazing efficiency
η	0.0		uptake ratio ammonium: DON
μ_3	0.15	d^{-1}	bacteria excretion rate
$\rho 1$	0.55		grazing preference phytoplankton
ρ_2	0.40		grazing preference bacteria
ρ_3	0.05		grazing preference detritus
c_1^{min}	0.0	mmol N m^{-3}	minimum phytoplankton conc.
c_2^{min}	0.0	mmol N m^{-3}	minimum bacteria conc.
c_4^{min}	0.0	mmol N m^{-3}	minimum zooplankton conc.
g	1.2	d^{-1}	max. ingestion rate
K_1	0.2	mmol N m^{-3}	half saturation constant nitrate uptake
K_2	0.8	mmol N m^{-3}	half saturation constant ammonium uptake
K_3	1.0	mmol N m^{-3}	half saturation constant ingestion
K_4	0.5	mmol N m^{-3}	half saturation constant bacteria uptake
K_5	0.2	mmol N m^{-3}	half saturation constant phytoplankton mortality
K_6	0.2	mmol N m^{-3}	half saturation zooplankton loss
Vb	1.2	d^{-1}	maximum bacterial uptake rate
Vp	1.2	d^{-1}	maximum phytoplankton uptake rate

Burchard et *al*., (2006)

ANNEX III. Comparison of physical variables between bibliography and model results.

			Physical variables		
			T (ºC)	S (psu)	Thermocline
	Study period	Data type	Min-Max	Min-Max	Min-Max
Louge et *al*., 2004	1995-2000	observation (discrete)	6,5-16	33,1-33,8	30-50 m
Present model results	2013-2016	simulation (continuous)	9-17	33,35-33,41	30-50 m

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