Travaux de recherche

présentés

devant l’Université de Paris 6

pour obtenir

L’HABILITATION À DIRIGER DES RECHERCHES

par

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Titre :

Modulation de la production biologique par la turbulence océanique de mésoéchelle

à soutenir le 06/06/2006 devant le jury

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Acknowledgment

I would like to thank Bernard Barnier, Mick Follows and Jean-François Minster for their review of this work, together with Gurvan Madec, Patrice Klein and Vladimir Zeitlin for being part of this jury.

I am indebted to Patrice Klein who motivated me to write the proposal for the ACI "jeunes chercheurs" and taught me the concepts of Geophysical Fluid Dynamics. Working with him has been a very enriching experience.

I worked in the team of Laurent Memery (Modélisation biogéochimique) from 1993 to 2003. I am thankful for his support over all these years, and for offering me to be part of the POMME program.

Being now part of the team of Gurvan Madec (DYCOS : Dynamique et Couplage de l’Ocean de Surface) enables me to fit my research into broader perspectives. Most of all, I have the chance to benefit from his enthousiasm, disponibility and constructive remarks.

I am thankful to Jean-Michel André for having me involved in the collaboration between the LOCEAN and the NIO (National Institute of Oceanography, Goa, India). This manuscript has greatly benefited from his inputs.

I would like to take this opportunity to thank all of those who are or have been part of the ESOPA (Equipe Système Opa), INCAS (Ingénierie en calcul Scientifique), JIJI (Joyeux Informaticiens de Jussieu IPSL), RESO (équipe Système et Réseau) teams, the engineers from the "Pôle de modélisation de l’IPSL", Marie-Alice Foujols and Sébastien Masson. They develop high quality tools and ensure an up-to-date work environment. This work would not exist without them.
Résumé


Abstract

This document reviews the current state of knowledge on bio-physical interactions at mesoscale and at sub-mesoscale. It is focused on the mid-latitudes open ocean. From examples taken from my own studies or selected in the literature, I show how high-resolution process-oriented model studies have helped to improve our understanding. I follow a process-oriented approach; I first discuss the role of mesoscale eddies in moderating the nutrient flux into the well-lit euphotic zone. Then I address the impact on biogeochemistry of transport occurring on a horizontal scale smaller than the scale of an eddy. I show that submesoscale processes modulate biogeochemical budgets in a number of ways, through intense upwelling of nutrients, subduction of phytoplankton, and horizontal stirring. Finally, I emphasize that mesoscale and submesoscale dynamics have a strong impact on productivity through their influence on the stratification of the surface of the ocean. These processes have in common that they concern the short-term, local effect of oceanic turbulence on biogeochemistry. Efforts are still needed before we can get a complete picture, which would also include the far-field long-term effect of the eddies.
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Résumé étendu

A l’occasion de mon habilitation à diriger des recherches, il m’a semblé pertinent de présenter mes travaux sous la forme d’une revue de mon domaine. Peu de temps après avoir commencé cette revue, Antonello Provenzale m’a demandé d’écrire le chapitre d’un livre dans le contexte d’une école d’été «Transport in Geophysical flows : Ten years after » (Valle d’Aoste, Italie, 14-23 juin 2004). J’ai saisi cette opportunité pour publier cette revue ; elle est actuellement sous presse dans un numéro spécial de Lecture Notes in Physics.

Dans ce résumé étendu, la présentation est plus classique. J’ai choisi de revenir sur quatre de mes travaux les plus importants.

0.1 Introduction

Mes travaux de recherche portent sur les cycles biogéochimiques océaniques, et plus particulièrement sur le contrôle de ces cycles par la dynamique océanique. Ils visent à mieux contraindre les flux de carbone associés à la production de phytoplancton (production primaire) et à son devenir (export, remineralisation). La croissance du phytoplancton est limitée par la lumière et les sels nutritifs, qui sont abondamment présents au fond de l’océan, mais rapidement épuisés quand ils atteignent la surface. Le problème général auquel je m’intéresse concerne l’estimation de l’impact de la dynamique océanique via les flux advectifs et diffusifs de sels nutritifs et via la variabilité de la profondeur de la couche de mélange, qui module l’éclairement moyen vu par les cellules.

La dynamique liée à la turbulence méso-échelle et à sa structure fine, et celle liée aux mouvements de haute fréquence, sont particulièrement énergétique et de petite échelle (sub-mésoéchelle, typiquement 10 km, 1 à 2 jours). Ces petites échelles ne sont pas résolues par les modèles actuels de climat, ni par les modèles de bassin les plus performants. Elles ne sont pas non plus résolues par les mesures ponctuelles in situ. La prise en compte insuffisante de cette partie petite échelle du facteur dynamique, à la fois dans les modèles et dans les observations, est d’autant plus préoccupante que la réponse de la biogéochimie présente des comportements fortement
Impacts de la sub-mésoéchelle sur le bilan de production nouvelle

Ma philosophie d’approche est de mettre en évidence les processus de couplage entre la dynamique et la biogéochimie, d’étudier ces différents mécanismes non-linéaires qui impliquent des échelles équivalentes pour la dynamique et pour la biogéochimie, et d’estimer la contribution de chaque gamme d’échelle, depuis la grande échelle jusqu’à la sub-mésoéchelle. Les modèles sont mon principal outil d’investigation. J’utilise ces modèles pour conduire des études de processus, pour établir des bilans régionaux et pour analyser la variabilité que j’observe dans les données satellites de couleur de l’eau. Mon objectif général est de mieux comprendre et de rationaliser les processus qui ont lieu à petite échelle, d’évaluer leur impact sur les bilans de flux à plus grande échelle, afin d’être capable à terme de les paramétriser.

0.2 Impacts de la sub-mésoéchelle sur le bilan de production nouvelle

Les premières images de couleur de l’eau (Gower et al., 1980) ont mis en évidence une variabilité de la chlorophylle à l’échelle du premier rayon interne de déformation (Rd=20-100km, ou ”méso-échelle”), mais aussi à plus petite échelle (5-20km, ou ”sub-mésoéchelle”). Ces petites échelles de phytoplancton ont longtemps été considérées comme peu énergétiques, et résultant de la cascade turbulente bidimensionnelle (Abraham, 1998). La vision classique, confirmée par un certain nombre d’études de modélisation (McGillicuddy et al., 1998 ; Lévy et al., 1998 ; Mahadevan and Archer, 2000 ; Spall and Richards, 2000 ; Abraham, 1998), est que l’injection de nitrate dans la couche euphotique a lieu à méso-échelle (ou à plus grande échelle dans les cas d’un apport suite à un approfondissement de la couche mélangée), et que par cascade turbulente le phytoplancton s’organise en plus petites échelles, ce qui conduit à une décorrélation entre les zones de production et les zones de biomasse (Lévy et al., 1998 ; Spall and Richards, 2000). Cependant, la résolution horizontale utilisée dans ces études a rarement dépassé Rd/4, ce qui est suffisant pour bien résoudre la dynamique méso-échelle et les mouvements verticaux associés, mais qui filtre explicitement les processus sub-mésoéchelle. Or un certain nombre d’études dynamiques, basées à la fois sur des observations (Pollard and Regier, 1992) et des expériences numériques (Snyder et al., 1991), ont montrées que la dynamique sub-mésoéchelle est fortement agéostrophique, ce qui suggère que des injections importantes de nitrate peuvent avoir lieu à ces plus petite échelle.

C’est ce que nous avons montré et quantifié, dans le cadre d’une série d’expériences numériques représentatives d’un front barocliniquement instable dans l’Atlantique Nord-Est (avec Rd=30km). Dans ces expériences,
où la résolution horizontale atteint 2km (Rd/15), les apports de nitrates par les seuls processus sub-mésoéchelle constituent 1/3 des apports dynamiques totaux (i.e., ici en l’absence de vent, les apports dus à la fois à la méso-échelle et à la sub-mésoéchelle).

D’autre part, nous avons montré que les apports de nitrates liés à la dynamique sub-mésoéchelle sont concentrés dans des filaments de vorticité dont la largeur n’excède pas 10km (Fig. 1.1c). Ce résultat est lié à la relation de phase particulière entre les forts gradients de vorticité et la vitesse verticale, associée aux processus de frontogénèse et de frontolyse à petite échelle, ainsi qu’au fait que les forts gradients de vorticité ne peuvent se développer que dans les zones d’étirement du courant (Fig. 1.1a et b). Dans ce cadre, la structuration à sub-mésoéchelle du phytoplancton résulte donc directement d’une structuration à sub-mésoéchelle des apports de nitrate et de la production nouvelle. Ce résultat est important car il suggère que la résolution spatiale nécessaire pour estimer la production nouvelle, que ce soit dans les modèles et ou dans les données, doit être bien plus élevée qu’elle ne l’est actuellement.

Ces expériences ont été les premières à suggérer que c’est essentiellement sur les bords des tourbillons et dans les filaments que les apports en nitrate sont les plus importants. Le centre des tourbillons, au contraire, est relativement bien isolé et enferme les conditions biogéochimiques de la zone de formation.

Ces expériences nous ont également permis de mettre en évidence une forte corrélation entre les zones de vorticité relative négative et les zones de forte production nouvelle, à l’échelle des tourbillons anticycloniques, mais aussi aux plus petites échelles. Cette corrélation résulte de la forte contraction des colonnes d’eau de vorticité négative lorsqu’elles traversent un front du sud vers le nord (du fait de la conservation de la vorticité potentielle), contraction qui est associée à une remontée de sels nutritifs. Ainsi, contrairement au processus proposé par McGillucuddy et al. (1998), basé sur un enrichissement en nutritifs au centre des tourbillons cycloniques par diffusion le long des isopycnes, dans le cas d’un front baroclimiquement instable qui sépare deux masses d’eau aux propriétés biogéochimiques similaires, les zones anticycloniques sont les plus productives.

Par ailleurs, ces expériences ont mis en évidence des liens forts entre dynamique mésoéchelle et dynamique sub-mésoéchelle. En particulier, les vitesses verticales importantes associées à la mésoéchelle se trouvent piégées, près de la surface, dans des structures filamentaires. D’autre part, cette étude suggère que la variabilité mésoéchelle ne peut être correctement appréhendée que si la sub-mésoéchelle est elle-même résolue. Une mauvaise représentation de la sub-mésoéchelle est responsable dans le cas étudié d’une forte sous-estimation de l’énergie cinétique turbulente et du temps de vie des tourbillons. La raison principale est que les filaments de vorticité
**FIG. 1** – a/ Vorticité relative à la surface, b/ vitesse verticale à 100m (zoom en couleur, lignes de vorticité), c/ phytoplancton dans la couche 0-120m d/ phytoplancton dans la couche 120m-240m. D’après Lévy et al. (2001a).
qui entourent les tourbillons agissent comme des barrières dynamiques qui vont permettre le maintien (ou la destruction) de la cohérence de ces structures (Mariotti et al., 1994). Les résultats de ces études ont été résumés dans un article (Lévy et al., 2001).

0.3 Impacts de la distribution de sels nutritifs

Sous la couche euphotique, la distribution de nutritifs dans l’océan résulte de l’équilibre entre le mélange le long des isopycnes et la reminéralisation de la matière organique. De ce fait, la distribution de nitrate ne présente pas nécessairement les structures frontales que la densité peut présenter. Par exemple, le Gulf Stream apparaît clairement comme un front entre deux provinces biogéochimiques très contrastées, avec d’un côté les eaux du large très oligotrophes, et de l’autre les eaux côtières très productives. Par contre, les eaux sont oligotrophes de part et d’autre du front des Açores. Ces éléments montrent qu’il existe un gradient méridien important en nitrates au niveau du Gulf Stream, et qu’au niveau du front des Açores, il existe essentiellement un gradient vertical en nitrates.

Dans cette étude (Levy, 2003), j’ai mis en évidence et rationalisé ces deux situations extrêmes (Fig. 2.1, Exp 1 et 2). Sur la base d’expériences numériques, et en faisant varier les conditions initiales en nitrates, j’ai montré que :

1/ par phénomène de cascade directe, un gradient grande échelle en nitrate dans la couche euphotique va alimenter une variabilité à mésoechelle puis à sub-mésoechelle, ce qui explique le contraste qu’il peut exister entre l’intérieur et l’extérieur de certains tourbillons, et

2/ la variabilité de la distribution de nitrate sous la couche euphotique a par contre peu d’influence directe sur la variabilité du phytoplancton dans la couche euphotique, car elle influe peu sur la valeur du gradient verticale.

0.4 Généralisation au cas d’un champs de tourbillon

Pour comprendre et quantifier l’impact de la variabilité dynamique sur la variabilité biogéochimique, nous avons mis au point une série d’expériences numériques longues correspondant à des situations de turbulence en équilibre statistiquement stationnaire.

Sur la base de ces expériences, nous avons montré que (Levy et Klein, 2003) :
Impacts de la distribution de sels nutritifs

Fig. 2 – a) Front initial de température dans les expériences de Lévy (2003). b) Front de température après un mois de simulation (C : cyclone, AC : anticyclone). c) Concentration initiale de nitrate dans l’expérience 1. d) Concentration finale de nitrate dans l’expérience 1. e) Concentration initiale de nitrate dans l’expérience 2. f) Concentration finale de nitrate dans l’expérience 2. g) Représentation schematique de la formation des tourbillons au cours des expériences 1 et 2.
1/ La variabilité basse fréquence associée à la dynamique méso-échelle permet d’expliquer une part importante de la variabilité observée des spectres de phytoplancton et de zooplankton (Fig. 3.2),

2/ Les résultats obtenus dans le cas d’une turbulence libre dans Lévy et al. (2001), à savoir que la production nouvelle est majoritairement augmentée dans les filaments de vorticité négative, sont statistiquement confirmés dans le cas d’une turbulence entretenue (Fig. 3.1), et

3/ les différences de pentes de spectres entre phytoplancton et zooplankton dépendent de la dynamique de basse fréquence (Fig. 3.2).

Fig. 3 – Vorticité relative, densité (anomalie), phytoplancton et zooplankton après 1600 jours de simulation. D’après Lévy and Klein (2004).
Fig. 4 – Evolution temporelle des pentes de spectre de Fourier de la vorticité relative, densité (anomalie), phytoplancton et zooplankton. D’après Lévy and Klein (2004).
0.5 Étude régionale : l’Atlantique Nord-Est (POMME)

Un des objectifs du programme POMME est de comprendre le rôle des tourbillons sur les propriétés biogéochimiques des eaux qui subductent au niveau de la zone de discontinuité de la couche de mélange dans l’Atlantique nord est. Trois campagnes en mer ont eu lieu en 2001 (P1, P2 et P3), durant lesquelles un nombre important de paramètres physiques et biologiques ont été mesurés. Ces campagnes ont permis de fournir une image à peu près synoptique de la zone durant trois périodes bien distinctes (hiver, bloom, et été). La résolution spatiale des mesures (environ 50 km dans les réseaux) ne permet pas de conclure sur le rôle et la contribution de la mésoéchelle et des échelles inférieures sur la production primaire. Or le signal associé à ces petites échelles apparaît sur les images satellites de couleur de l’eau dans cette région. De plus, la forte variabilité du forçage atmosphérique d’un jour à l’autre rend difficile de distinguer entre variabilité spatiale et variabilité temporelle dans les mesures. Dans ce cadre, mes objectifs scientifiques étaient :

1/ de fournir une vue synoptique et intégrée de l’évolution de la zone entre P1 et P2, des distributions de traceurs et des flux à méso-échelle, afin entre autres de restituer dans le temps et l’espace les mesures effectuées, et de suivre la composition de traceurs des eaux de surface,

2/ d’effectuer des bilans de flux régionaux et de suivre leur évolution,

3/ d’analyser la variabilité dynamique de mésoéchelle et sub-mésoéchelle susceptible d’avoir un impact sur la production et l’export de matière organique (vitesses verticales, couche de mélange) et les processus dynamiques en jeu,

4/ d’analyser les différents processus de couplage à mésoéchelle entre la dynamique et la croissance du phytoplancton, et leur importance relativement à distribution du plancton et aux bilans régionaux,

5/ de quantifier l’impact de la mésoéchelle et des forçages haute-fréquence par des études modifiant la résolution spatiale du domaine et temporelle des flux de forçage.

Pour cela, j’ai mis au point une simulation réaliste, couplée dynamique/biologie, haute-résolution (5 km avec certains tests à 2.5 km sur l’horizontale) et basée sur l’utilisation d’OPA, qui a permis d’aborder une variabilité à plus petite échelle que celle observée, et de répondre aux objectifs. Cette simulation a été validée par les mesures P1 et P2.

Les principaux résultats sont les suivants (Fig. 4.1) :

1/ les paramètres dynamiques importants pour la biologie (couche de mélange, vitesses verticales) ont des échelles spatiales inférieures à la mésoéchelle

2/ la variabilité sub-mésoéchelle de la production est essentiellement
forcée par la variabilité sub-mésoéchelle de la profondeur de la couche de mélange (MLD),

3/ la variabilité sub-mésoéchelle de la MLD résulte de la cascade turbulente et de l’inhomogénéité du forçage atmosphérique sur des échelles de l’ordre de 100-200km.

4/ Les vitesses verticales sont faibles (inférieures à 5m/j) et ne semblent pas jouer un rôle important. Les structures petite échelle de phytoplancton ne résultent pas de la dynamique verticale associées à la dynamique sub-mésoéchelle, mais de la cascade directe. La situation observée durant P1 et P2 est proche de celle décrite par Abraham (2000) : forçage à grande échelle et cascade. Ce résultat suggère que la dynamique de moyenne et petite échelle ne modifie pas les bilans régionaux des flux de production durant le bloom dans cette zone où l’activité tourbillonnaire, bien que présente partout sur le domaine, n’est pas très intense.

Ces résultats font l’objet de deux publications (Lévy et al., 2005a, Paci et al., 2005)
Fig. 5 – a) SSH (en cm), b) flotabilité (in w/m²), c) couche de mélange (en m), d) phytoplancton (in mmoleN/m²). D’après Lévy et al., 2005b.
Impacts de la distribution de sels nutritifs
Foreword

Over the last ten years, I had the chance to witness remarkable advance in oceanic biogeochemistry. For instance, it is now widely accepted that the comprehension of biogeochemical cycles has to involve not only the mean state of the dynamics of the ocean, but also its variability. Recent investigations concern the role of processes ranging from the short-term impact of mesoscale eddies to the longer term impact of inter-annual climatic changes. Another example regards the role of micro-nutrients in the structuration of the ecosystem and the fate of organic material. A natural consequence of this awakening is that the complexity of ocean biogeochemical models has increased tremendously. Nowadays, with the unprecedented advent of computer power, multi-nutrients multi-species ecosystem models are runned routinely at high-resolution (AGU-OS, 2006, Hawaii). This is amazing given that the first ecosystem models were run in coarse resolution ocean models only about ten years ago.

My contribution to this general advance mainly regards the role of mesoscale turbulence in the modulation of biological production. My work is only a part of the building and it is closely connected to the work of others. This is why I thought it would be more interesting to review my field rather than to limit this document to a personal work report. I hope that I have succeeded to outline our current knowledge, to bring to light the uncertainties that remain, and at the same time to synthesize my personal contribution.

Soon after I started to work on this review, Antonello Provenzale asked me to write a book chapter in the context of the summer school «Transport in Geophysical flows : Ten years after » (Valle d’Aoste, Italie, 14-23 juin 2004). I took this opportunity to have it published ; it is now in press in a special issue of Lecture Notes in Physics.
Impacts de la distribution de sels nutritifs
Chapitre 1
Introduction

The photosynthesis of phytoplankton represents roughly half of the biological production on the planet. This Primary Production (PP) supports almost all marine life. It plays a key role in the global carbon cycle because phytoplankton growth, and subsequent death and sinking, transports vast quantities of carbon out of the surface layer where it can be sequestered for long times (Longhurst, 1991; Holligan, 1992; Shaffer, 1993). Phytoplankton require nutrients for growth and reproduction. PP occurs in the sunlit surface layer of the ocean where photosynthesis can take place. In this well-lit euphotic layer\(^1\) available nutrients are rapidly assimilated. Then, it is generally the supply of new nutrients from deeper water that limits productivity in the ocean. The dynamical mechanisms that control this supply occur over a large range of temporal and spatial scales. On the planetary scale, and for time scales beyond the year, the transport of nutrients is controlled by the thermohaline and the wind-driven circulations. These circulations regulate the subsurface nutrient distribution (Williams and Follows, 2003). On the seasonal time-scale, the convective supply of nutrients is strongly modulated at mid and high latitudes (de Boyer-Montégut et al., 2004). At shorter time scales, vertical advection is controlled by the three dimensional circulation associated with baroclinic eddies (Pollard, 1983; Shearman et al., 2000; Martin and Richards, 2001) and by the processes of frontogenesis and frontolysis (Pollard and Regier, 1990; 1992; Davis-Jones, 1991; Wang, 1993; Spall, 1997), an effect that can be crucial in subtropical gyres, i.e. over large areas of the ocean (Williams and Follows, 1998b). The relative importance of these different processes for the PP is still under debate (Oschlies, 2001; 2002a; 2002b; McGillicuddy et al., 2003). There is however growing evidence that PP occurring both at the scale of eddies (the mesoscale) and at the scale of frontogenesis (the submesoscale) contributes significantly to the global budgets.

From an observational point of view, direct PP measurements are

\(^1\)The euphotic layer is generally defined by the 1% light level
Introduction

sparse because they involve long incubations and heavy isotope techniques (Hitchcock, 1986; Dandonneau and Le Bouteiller, 1992). However, satellite retrieved ocean color\(^2\) (Platt and Sathyendranath, 1988) and continuous measurements of other related parameters such as fluorescence or carbon dioxide partial pressure (pCO\(_2\)) make clear that ocean productivity is highly variable at the (sub-)mesoscale\(^3\) (Gower et al., 1980; Yoder et al., 1993a; Watson et al., 1991; Dickey et al., 1998; Hood et al., 1999). Jenkins (1988) has also suggested that the discrepancy between the large rates of export of organic matter estimated from biogeochemical budgets in the oligotrophic North Atlantic subtropical gyre compared with the lower rates of measured productivity could be explained by the undersampling of eddy induced PP.

PP is a process where dynamics, bio-geochemistry, and radiation play equal roles and interact strongly. It is only since the early 90’s that models have been developed where all these processes are coupled together (Nutter et al., 1991; Sarmiento et al., 1993). To develop such models, the first natural step is to introduce in dynamical Ocean General Circulation Models (OGCM) conservative schemes for the transport of minor species, the second is to introduce into those models realistic biogeochemical schemes for the life cycle of phytoplankton. Mostly because of computational limitations, most of the OGCMs today use rather coarse horizontal grids (1/2° to 2°). Some preliminary modeling studies suggest that such a resolution can result in errors near 30% in the estimation of PP (Lévy et al., 1998, Oschlies and Garçon, 1998; Mahadevan and Archer, 2000; McGillicuddy et al., 2003). Some simulations at even higher resolution show that incorrect representation of submesoscale frontogenesis can result in even larger errors (up to 50%, Lévy et al., 2001).

The growing evidence that the (sub-)mesoscale variability of PP is large is a challenge for the measurement networks and for the OGCMs used to study the climate: none of them resolve those scales. Therefore, there is an imperative need to understand the mechanisms by which the (sub-)mesoscale physical dynamics are reflected by the biological processes. Providing we can predict the (sub-)mesoscale dynamics from the larger scale dynamics, this should enable the development of parametrizations of the (sub-)mesoscale biophysical interactions for application to large scale models. The ultimate goal is to better predict the evolution of the oceanic

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\(^2\)Due to the absorption properties of chlorophyll-a (the primary photosynthetic pigment), measures of solar light retrodiffusion by the ocean in the green and blue wavebands by optical sensors onboard earth viewing platforms provide an accurate estimate of the concentration of chlorophyll-a at the surface, the 'color' of the sea.

\(^3\)The terminology (sub)-mesoscale is used in this paper to define the scale range including both the submesoscale and the mesoscale. Approximately, the mesoscale covers the range 20-100 km, the submesoscale covers the range 2-20 km, and thus the (sub)-mesoscale the range 2-100 km.
carbon cycle at climatic scales.

The purpose of this paper is to give an overview of the current state of knowledge on the (sub)-mesoscale bio-physical interactions. It complements previous review papers: Lewis (2002) presented the discussions about the observed discrepancy between the rate of PP of organic matter and its export; Flierl and McGillicuddy (2002) reviewed the impact of mesoscale and submesoscale physics on biological dynamics; Williams and Follows (2003) focussed on the transport processes regulating nutrient distribution in the global ocean; Martin (2003) discussed the patchy distribution of phytoplankton at mesoscale and submesoscale from an observational and theoretical point of view.

The present review is focused on the mid-latitudes open ocean. Section 2 (‘Generalities’) introduces some basic ingredients of the oceanic biogeochemical cycles, of the turbulent motion in the ocean and of the influence of the latter on the former. Section 3 (‘Modelisation of bio-physical interactions’) describes the models that are used to analyze these interactions. It includes a discussion of the transport equations for plankton and how the physical dynamics enter the equations. Then, we adopt a process oriented approach, and review our current knowledge of the biogeochemical interactions with the mid-latitudes turbulent oceanic eddy field, jets and the isolated vortices in the open ocean. Using few examples, we will show how high-resolution process-oriented model studies improve our understanding. Given that the primary source of variability of PP is due to variations in nutrient input, section 4 (‘Transport by mesoscale eddies’) will discuss the role of mesoscale eddies in moderating the nutrient flux into the well-lit euphotic zone. In section 5 (‘Transport by submesoscale dynamics’), we discuss the impact on biogeochemistry of transport occurring on a horizontal scale smaller than the scale of an eddy. We will show that submesoscale processes modulate biogeochemical budgets in a number of ways, through intense upwelling of nutrients, subduction of phytoplankton, and horizontal stirring. In section 6 (‘Bio-physical interactions through changes in stratification’), we show that mesoscale and submesoscale dynamics have a strong impact on productivity through their influence on the stratification of the surface of the ocean. I will conclude with some insight on the remaining way to go before a complete understanding of the impact of oceanic mesoscale turbulence on phytoplankton productivity and, more generally, on ocean biogeochemical cycles, is established.
Introduction
Chapitre 2

Generalities

2.1 Interplay of transport and biology

2.1.1 Role of phytoplankton in the carbon cycle

Phytoplankton play a major role in the oceanic carbon cycle and these floating, microscopic single-cell plants are the foundation of the marine food web. Like land plants, phytoplankton fix carbon through photosynthesis, making it available for higher trophic levels. Phytoplankton generally have limited or no swimming ability and are advected through the water by currents ("plankton" is actually derived from "πλακτόν", "to wander"). Also as in terrestrial plants, the chlorophyll pigment in the phytoplankton absorbs light, which is used as an energy source to fuse water molecules and carbon dioxide into carbohydrates. The major environmental factors that influence phytoplankton growth are light (Marra, 1978) and inorganic nutrients (Dugdale and Wilkerson, 1992). When favorable conditions are encountered, phytoplankton can undergo rapid population growth usually referred to as "blooms" (Riley, 1942). However, most of the time phytoplankton growth is either light limited (e.g. in winter at high latitudes) or nutrient limited (e.g. in the subtropical gyres). Because light attenuates dramatically with depth, phytoplankton growth is restricted to the euphotic layer. Limiting inorganic nutrients such as nitrogen and phosphorus are constantly removed from the surface waters by the growing phytoplankton. Dissolved inorganic carbon is also consumed by phytoplankton. It is exchanged at the sea surface and always plentiful in the surface layer, contrary to limiting nutrients (Fig. 2.1).

Most of the phytoplankton are consumed locally by zooplankton, so that the nutrients comprising their biomass are regenerated at the surface and made available for another round of production. The Regenerated Production (RP) is that portion of PP fueled by the limiting inorganic nutrients remineralized within the euphotic zone (Eppley and Peterson, 1979). The
**Fig. 2.1** – Schematic representation of the biological pump in the ocean.
Export Production (EP) is the fraction of PP that finds its way to the deep sea through the settling of dead cells and detritus, through zooplankton diel migrations, and sometimes by downwelling or mixing. Most of the EP is ultimately assimilated by bacteria, which regenerate it into inorganic forms (end-product of respiration and excretion). At steady state and at large scale, the biotically mediated downward flux of organic matter is balanced by an upward return flux of inorganic nutrients that fuels the New Production (NP).

The collective action of this so-called 'biological pump' (Longhurst and Harrison, 1989) is to create a sharp vertical gradient of nutrients. Minimum nutrient concentrations are found at the surface due to photosynthetic consumption and maximum concentrations between 500m and 1000m due to remineralization. This pump plays a central role in the global carbon cycle. It sequesters carbon away from the atmosphere in the deep sea.

2.1.2 Transport modulation of biotic rates

Transport modulates NP, RP and EP in various ways. Primarily, the flow transports the biological actors, i.e. phytoplankton, zooplankton, bacteria, dissolved and particulate organic matter. When this transport is directed out of the euphotic zone, it directly contributes to EP. Secondly, the flow transports inorganic nutrients, providing them to the euphotic layer through vertical diffusion or upwelling. Thirdly, the ocean physics can also modulate the rates of the biological processes. The most common manifestation is due to the vertical movements which displace phytoplankton within the light gradient and thereby affect phytoplankton growth rate (Marra, 1978). Also, zooplankton growth rate depends on the encounter rate between zooplankton and its prey, which is partially controlled by the transport (Kiørboe and MacKenzie, 1995). Note also that phytoplankton retroacts on transport : large concentrations of phytoplankton significantly alters the penetration of solar radiation, which in turn modulates density, and transport through the thermal-wind balance (Murtugudde et al., 2002; Oschlies, 2004). This effect is often neglected in models.

2.2 The oceanic turbulence

The (sub-)mesoscale oceanic turbulence has similarities with two-dimensional turbulence. It is characterized by the presence of interacting vortices, usually referred to as mesoscale eddies (analogous to atmospheric weather systems). Eddy scales are strongly correlated with the first-mode Rossby radius of
deformation\textsuperscript{1} (Stammer, 1998), suggesting that baroclinic instability is the primary eddy source term (Wunsch, 1997). This is also consistent with the high levels of mesoscale energy that are found along boundary currents at mid-latitudes, and along frontal structures and current systems (Stammer, 1997) while minima are found in the interior of gyres. However, a variety of eddy formation processes have been reported (i.e. Aristegui et al., 1994; Pichevin and Nef, 1996; Herbette et al., 2003; Di Lorenzo et al., 2005, ... ) that can result in eddies of different scales.

Oceanic turbulence is also characterized by the presence of elongated submesoscale filaments (Dubos et al, 2001; Dubos and Babiano, 2002). The large scale action of these submesoscale filaments is complex. Some of the submesoscale movements generate turbulent diffusion (Pasquero et al., 2001). Others act as dynamical barriers; they locally inhibit diffusion and reinforce the coherence of mesoscale eddies (Mariotti et al., 1994; Pasquero et al., 2006). Reciprocally, submesoscale structures are guided by the rotation and strain fields of the eddies. Submesoscale activity has strong spatial variability, related to the variability of the strain and rotation fields, and the recent works by Hua et al. (1998) and Lapeyre et al (1999; 2001) provide ways of partitioning flows into poorly dispersive rotation and highly dispersive strain dominated regions.

Besides these 2D-characteristics, oceanic turbulence is also characterized by its vertical structure. Baroclinic mid-ocean eddies often have vertical structure of the first baroclinic mode (cyclones characterized by doming isopycnals in their core, and anticyclones by shoaling isopycnals). Actually, oceanic mesoscale eddies are better described by quasi-geotrophic dynamics than by 2D-turbulence. They are associated with vertical velocities (w) of the order of 1 to 10 m/d. The typical w distribution in the quasi-geostrophic (QG) approximation is a multipolar structure with alternate upwellings and downwellings along meandering fronts (with upwelling occurring downstream of the trough and downwelling occurring downstream of the ridge, Woods, 1988) and around the eddies (Pollard, 1983; Davies-Jones, 1991; Shearman et al., 2000; Martin and Richards, 2001). These patterns, which extend down to the zero-crossing of the first baroclinic mode (i.e. approximately 1000m), are induced by the curvature and by eddy-eddy interactions.

Submesoscale structures are particularly intense close to the surface (above 200m approximately). They are strongly ageostrophic, their relative vorticity can be of the order of the planetary vorticity. They can be

\textsuperscript{1}The first mode Rossby radius of deformation $R_d$ is the length scale at which rotation effects become as important as buoyancy effects. $R_d$ decreases from 300 km at the equator to a few kilometers at high latitudes, and ranges between 30 and 50 km at mid-latitudes (Chelton et al., 1998). Within the approximation of homogeneous buoyancy, $R_d = NH/f$, with N the buoyancy frequency, f the Coriolis parameter and H the depth
described by the dynamics contained in the Primitive Equations (PE). Associated with the strong submesoscale vorticity gradients, the vertical velocities are one order of magnitude stronger than the vertical velocities of QG dynamics (Halliwell and Cornillon, 1989; Pollard and Regier, 1992; Wang, 1993; Spall, 1995, 1997). These vertical velocities are characterized by dipolar structures astride the vorticity gradients (Hoskin and Bretherton, 1972; Spall, 1997; Lévy et al., 2001a; see also Fig. 5.2). When the flow in the filament of vorticity accelerates, a secondary circulation develops across the filament leading to upwelling on the anticyclonic side and downwelling on the cyclonic side. When the flow decelerates, a secondary circulation of opposite sign is formed.

Numerical simulations (Lévy et al., 2001a) suggest that submesoscale vertical velocities are maximum at around 100m depth where they take over mesoscale QG vertical velocities, which are maximum at around 1000m depth.

2.3 Observed variability of phytoplankton

2.3.1 Basin scale variability of phytoplankton

The production patterns at basin scale are strongly constrained by the wind-driven vertical circulation (Ekman pumping). The general features of this Ekman transport are upwelling in subpolar gyres, at the equator and at eastern boundaries and downwelling in subtropical gyres. Sea-color satellite images reveal the signature of the Ekman transport on the distribution of phytoplankton (Yoder et al., 1993b). Fig. 2.2a shows a climatology of the surface chlorophyll distribution in the North Atlantic. Strong spatial inhomogeneities of the phytoplankton distribution are revealed, with maxima located in regions of ascendance (at the equator, in the subpolar gyre and at the coasts) and minima in regions of subsidence (in the center of the subtropical gyre). The maintenance of different levels of phytoplankton production by these dominant oceanographic features enables the division of the world’s oceans in so-called ‘biogeochemical provinces’ (Longhurst, 1998).

2.3.2 Seasonal cycles of phytoplankton production

Seasonal variations of winds and solar radiation drive seasonal cycles of phytoplankton production. These variations are mediated through the mixed-layer (ML) seasonal cycle. For instance, from 30°N to 50°N in the northeast Atlantic, three different seasonal regimes can be distinguished, depending on the strength of winter mixing (Lévy et al., 2005a). These regimes and their boundaries exhibit an intense variability from one year
Fig. 2.2 – a) Climatology of sea surface chlorophyll from space (Classic CZCS scene, from NASA Web site). b), c) and d) Typical seasonal cyclings of sea-surface chlorophyll versus mixed-layer depth in the northeast Atlantic (from Lévy et al, 2005a). The grey line shows the seasonal cycle of the mixed-layer depth, and the black line the seasonal cycle of the surface chlorophyll concentration. e) and f) High-resolution snapshot of sea surface chlorophyll from space (e : classic CZCS scene, NASA Web site ; f : Lehahn,pers. comm.). Locations of the cyclings and of the high-resolution images are indicated on the climatological map.
to the next, which are driven both by the synoptic and and by the lower frequency variability in the atmosphere (Dutkiewicz et al., 2001; Follows and Dutkiewicz, 2002; Lévy et al, 2005a). Nevertheless, general patterns can be drawn:

When the winter ML is deeper than twice the euphotic layer depth (Ze) (Fig. 2.2b), Sverdrup’s (1953) conditions are encountered: production is inhibited, cells being continuously mixed below the euphotic layer for periods greater than their doubling time. At the same time, this deep mixing efficiently supplies the surface with nutrient, thus enabling an intense spring bloom to occur as soon as the mixed-layer stratifies in spring. The rapid exhaustion of nutrients leads to an oligotrophic situation in summer. The deepening of the ML in fall leads to an entrainment bloom. This cycle is encountered in the subpolar gyre of the North Atlantic.

When the winter ML never exceeds Ze (Fig. 2.2d), nutrient limitation prevails. The seasonal cycling is characterized by a single weak entrainment bloom, that starts with the deepening of the ML, peaks when the ML is at its deepest, and ends with the exhaustion of nutrients (Menzel and Ryther, 1961).

When the winter ML is comprised between Ze and 2Ze (Fig. 2.2c), the seasonal cycling is characterized by a single bloom that lasts longer than any other bloom and corresponds to the merging of the subpolar spring bloom with the subpolar fall bloom. This bloom is initiated in fall by the deepening of the ML (as the entrainment bloom), and peaks after restratification (as the spring bloom) (Levy et al, 2005a).

A general feature of these different cyclings is the alternation between periods of light limitation and periods of nutrient limitation. When light limitation prevails, PP is controlled by the ML depth. Phytoplankton concentration is maximum in the ML and decreases below. When nutrient limitation prevails, PP is controlled by the supply of nutrients. The distribution of phytoplankton is characterized by a subsurface maximum, located at the base of the nutricline (Longhurst and Harrison, 1989). As we will see, the impact of mesoscale turbulence on biological production depends on which situation prevails, and therefore varies both regionally and seasonally.

2.3.3 Observations of mesoscale and submesoscale variability of phytoplankton

The development of towed vehicles and the advent of sea-color remote sensing now permits us to observe the distribution of phytoplankton at high resolution. These observations have revealed considerable variability in the (sub-)mesoscale range (Gower et al., 1980; Yoder et al., 1993a; Longhurst, 2001; McGillicuddy et al., 2001; Santoleri et al., 2003), as shown for example in the sea-color snapshots of Fig. 2.2e and f. In situ observations
Fig. 2.3 – Observations from Bermuda Testbed Mooring deployment 3 during the summer 1995. Upper panel, temperature records at various depths; lower two panels, nitrate concentration at 80m, chlorophyll fluorescence at 71m. All signals have been filtered via a six-day moving average. From McGillicuddy et al. (1998).
complement the sea-color view and enable the association of plankton variability with specific hydrologic structures such as fronts, meanders, eddies and filaments.

In the 80’s, most of such observations were concerned with Gulf Stream ”warm core rings” (Joyce, 1985; Wiebe and McDougall, 1986; Hitchcock et al, 1985; 1987). In 1991, Falkowski et al. reported an enhancement of production by a cyclonic eddy in the subtropical Pacific. Since then, the number of in-situ observations at the mesoscale has kept increasing. Allen et al. (1996) measured PP within and outside a cyclonic eddy, and found that photosynthetic rates near the edge and at the center of the eddy were approximately 50% higher, than outside the eddy. Mooring data in the Sargasso Sea (McGillicuddy et al., 1998; McNeil et al., 1999) provide evidence of waters rich in nutrients and chlorophyll within a cyclonic eddy (Fig. 2.3). Other striking correlations between the presence of eddies and the chlorophyll distribution also been reported by Robinson et al. (1993) during NABE (North Atlantic Bloom Experiment), by Aristegui et al. (1997) around the Canaria Islands, by Letelier et al. (2000) in the North Pacific subtropical gyre, by Moran et al. (2001) in the Algerian Basin, by Barth et al. (2001) in the Antarctic polar front and by Garcia et al. (2004) in the Brazil-Malvinas Confluence region, among others.

Correlations between chlorophyll and dynamical features have also been observed at the submesoscale. For instance, Hitchcock et al. (1993), during a series of transects across the Gulf Stream, identified a maximum of chlorophyll at the periphery of a warm core ring. Strass (1992), using a towed, undulating vehicle in the open North Atlantic during summer revealed patches of high chlorophyll concentration of scales 10-20 km. These patches were located on the warm side of a temperature front. Perez et al. (2003), during a summer oceanographic cruise in the Azores front region, located with good accuracy maximum chlorophyll concentrations on the South side of the front and at the border of an anticyclonic eddy. Other examples of submesoscale variability have been observed in the Gulf Stream (Lorenz et al., 1993), in the Almeria-Oran front (Prieur and Sournia, 1994) and in the Antarctic Circumpolar Current (Strass et al., 2002a).

There is also some evidence of (sub-)mesoscale variability in zooplankton and in bacteria (Ashjian et al., 1994; Huntley et al., 1995; Karrasch et al., 1996; Labat et al., 2002; Velez-Belchi et al., 2002; Mackas et al., 2005), and in particle fluxes (Newton et al., 1994). Watson (1991) provided the first evidence of the impact of (sub)-mesoscale dynamics on oceanic pCO2, which has been confirmed by drifting buoys observations (Hood et al., 1999). Section 4 will present theories that attempt to explain the impact of oceanic (sub-)mesoscale turbulence on the biological pump.
Generalities
Chapitre 3

Modelisation of bio-physical interactions

In this section, we present the basis for the modelisation of the interaction between biogeochemical cycles and ocean dynamics.

3.1 Transport

The description is restricted to transport occurring on space scales much larger than the cell distribution scale. In this case, plankton are described as the continuous concentration (in space and time) of a constitutive element. Nitrogen provides a natural currency for biological quantities. A planktonic population, like any tracer $T$ expressed for instance in $nmoleN/m^3$, is then assumed to obey the transport equation, which reads, in its eulerian form:

$$\frac{\partial}{\partial t} T = -\vec{\nabla} \cdot (T \vec{v}) + B(T)$$

(3.1)

where $\vec{v}$ is the velocity field and $B(T)$ is the budget between the biological sources minus the biological sinks for tracer $T$. Advection is written here in a flux form assuming that the ocean is incompressible. Diffusion is negligible at the scale at which plankton population can be described as a concentration and has therefore been disregarded. Because biological tracers are positive quantities, often close to zero, the numerical resolution of the transport equation requires the use of positive advection schemes (Oschlies, 2000; Lévy et al, 2001b).

3.2 Biological source/sink terms

The biogeochemical schemes describe the interactions between the various forms of plankton, organic and inorganic material. They vary in com-
plexity from very simple models with one or two tracers (nitrate, or nitrate and phytoplankton), to much more complicated models with more than 20 tracers (Aumont et al., 2003). In these complex models, different species of phytoplankton are considered, as well as different limiting nutrients. A common trade-off in complexity is the use of models with 4 to 6 tracers (so called NPZD models, i.e. Lévy et al., 2004). Biogeochemical fluxes are exchanged by the tracers. These fluxes are empirical functions (parametrizations) of the biological variables, often non-linear, and sometimes of other environmental conditions such as light or temperature, derived from laboratory experiments (i.e. Michaelis and Menten, 1913). The determination of the parameters used in these parameterizations is a difficult task and a large source of model error and uncertainties. Nowadays, inverse modeling is the most objective way of tuning parameters in biogeochemical models (Fasham et al., 1995; Spitz et al., 2001, Faugeras et al., 2003).

3.3 Reynolds equation

The Reynolds equation is derived by applying to the transport equation (3.1) an operator \( \bar{\mathbf{v}} \) defined as:

\[
\bar{\mathbf{v}} = \frac{1}{V} \int_V \mathbf{v} dv
\]  

(3.2)

where \( V \) is an element of volume of scale \( S \). In numerical models, the scale \( S \) is set by the size of the grid and the averaging is done over a grid cell.

Any variable (such as \( T \) or \( \mathbf{v} \)) can then be decomposed into the mean \( \overline{T} \), comprising the variability above the cut-off scale \( S \), and \( T' = T - \overline{T} \), the variability below the cut-off scale, which verifies \( T' = 0 \).

Thus averaging (3.1) with the linear operator (3.2), and then using, for simplicity, the notation \( T \) instead of \( \overline{T} \) and \( \mathbf{v} \) instead of \( \overline{\mathbf{v}} \), gives the Reynolds equation:

\[
\frac{\partial}{\partial t} T = -\nabla \cdot (T \mathbf{v}) + B(T) - \nabla \cdot \left( T' \mathbf{v}' \right) + B'(T)
\]  

(3.3)

Compared to equation (3.1), the Reynolds equation (3.3) has additional terms on the RHS (third and forth terms). These terms represent the impact that the scales below the cut-off (or sub-grid scales) have on the larger scales. The third term is the transport Reynolds term and represent the effects of motions on scales smaller than \( S \). The fourth term is the biological Reynolds term and represents the effects of the inhomogeneous distribution of the biological tracers within the grid.

To close equation (3.3), the effects of the sub-grid scales must be represented entirely in terms of large scale quantities. In the transport term,
these effects appear as the divergence of turbulent fluxes (i.e. fluxes associated with the mean correlation of small scale perturbations). To assume a turbulent closure is equivalent to chose a formulation (or parametrization) for these fluxes, usually called the subgrid scale physics.

Although much progress has been made in the parameterization of turbulent fluxes for ocean models (Gaspar et al., 1990; Gent and McWilliams, 1990; Blanke and Delecluse, 1993; Large et al., 1994; Gent et al., 1995; Visbeck et al., 1996; Treguier et al., 1997), there is still a long way to go before (sub)-mesoscale transport is correctly represented in coarse resolution or eddy-permitting models.

On the contrary, I am not aware of any reference regarding sub-grid scale biology. Practically, it is always omitted in models. Interestingly, an analogous problem concerns the chemical reactions in the stratosphere. For instance, Edouard et al. (1996) show that ozone depletion in the Artic is sensitive to filament-scale inhomogeneities in the distribution of reactant species because of the non-linearities in the chemical rate laws. There modeling study suggests that the effect is of the order of 40%. Another study by Vinuesa and Vila-Guerau de Arellano (2005) shows that heterogeneous mixing in the atmospheric boundary layer can slow down the reaction rates of ozone formation and depletion. Similar behaviors may be expected for biological species in the ocean, since the interactions are often non-linear.
Chapitre 4

Transport by mesoscale eddies

4.1 Vertical transport associated with coherent mesoscale eddies

The "eddy-pumping mechanism" (Yentsch and Phinney, 1985; Falkowski et al., 1991; McGillicuddy and Robinson, 1997; McGillicuddy et al., 1998) rests on the fact that within a cyclonic eddy isopycnals are deflected upward, pushing subsurface nitrate rich waters into the euphotic zone (Fig. 4.1). The same upward deflection applies to anticyclonic mode water eddies (McGillicuddy et al., 1999). Conversely, within an anticyclonic eddy the nutricline is depressed and so there should be no biological response (McGillicuddy et al., 1998). These vertical displacement are though to occur during events of eddy intensification, for example through eddy-eddy interaction.

This 1D-vertical view on the scale of the eddy is based on observed distributions of nitrate or chlorophyll across cyclones which highlight the surfacing of nutrient-rich waters within cyclones and which suggest that the surfacing nutrients come from upwelling (McNeill et al., 1999; McGillicuddy et al., 1998, 1999, 2001, see also Fig. 2.3).

This idea led to various estimations to the contribution of eddies to the nitrate supply to the euphotic layer from satellite altimetry (Siegel et al., 1999). These estimates should be handled with care, since they strongly depend on the efficiency of the pumping (Martin and Pondaven, 2003) and of its recurrence time.

4.2 Eddy propagation.

The propagation of eddies with doming isopycnals on the beta-plane (north-westward for cyclones and south-westward for anticyclones) can cause upwelling that uplift nutrients to the euphotic layer (McGillicuddy
Fig. 4.1 – Schematic figure depicting the ecosystem response to an uplift and depression of the nutricline. When nutrient-rich isopycnals are raised into the euphotic zone, there is biological production. Conversely, when the nutrient-rich isopycnals are pushed into the dark interior, there is no biological response. In order for the transient upwelling to persist, there needs to be a process maintaining the nutrient concentrations in the thermocline, which might be achieved by remineralisation of organic fallout, diapycnal transfer or a lateral influx of nutrients from the time-mean or time-varying circulations. After Williams and Follows (2002).
Transport by mesoscale eddies

et al., 1995; Flierl and McGillicuddy, 2002; Martin and Pondaven, 2003). In the limit of linear propagation, this transport mechanism can be interpreted as a propagation flux; the passing of an eddy can be thought as a wavelike upward displacement of the isopycnals, resulting in an injection of nutrients in the euphotic layer (Kahru, 1983). Moreover, recent satellite observations of Rossby waves and sea-color anomalies propagating in subtropical gyres have suggested that wave-induced upwelling could stimulate photosynthesis (Uz et al., 2001; Cipollidi et al., 2001). Thus, Rossby waves would act as a "rototiller" by lifting nutrients to the euphotic layer as they propagate (Siegel, 2001). A different interpretation involves the convergence near the surface of organic floating particles generated by the ecosystem which could be mistaken for phytoplankton by sea-color algorithms (Dandonneau et al., 2003). In this case, the Rossby waves would act as "marine hay rakes". The interpretation of Dandonneau et al. (2003) is supported by the fact that the sea-color anomalies are co-located with convergence and positive sea surface temperature anomalies. Killworth (2004) pertinently points out that this organic detritic material cannot be durably trapped in the convergences if the wave speed of the Rossby waves is larger than the current anomalies generated by the waves. The debate underscores the need for in-situ observations of floating material (Dandonneau et al., 2004).

4.3 Horizontal transport by coherent mesoscale eddies

If the eddy exhibits a strongly non-linear behavior, trapping waters within it for long periods, it is a coherent feature. Its passing can be visualized as the translation of a solid obstacle which moves surrounding waters around it. Observations of eddies traveling for several months and over hundreds of kilometers, while maintaining the chemical characteristics of their source waters, have been reported (Richardson, 1993; McDonagh and Heywood, 1999). Provenzale (1999) shows that this horizontal transport by coherent barotropic vortices is possible because they are highly impermeable to inward and outward particle fluxes.

Lévy’s (2003) numerical experiments illustrate such a case: a cyclone C and of an anticyclone AC are formed by baroclinic instability of a density front (Fig. 4.2a and b), as schematized on Fig. 4.2g. The raised isopycnals of C are not the signature of upwelling as in the eddy-pumping mechanism. They result from the horizontal displacement of a water column into a warmer environment (Fig. 4.2g). This is all the more contrasting with the eddy-pumping mechanism than the formation of C is associated with a downward stretching of the water column. Indeed, as put forward by Williams and Follows (2003), the conservation of potential vorticity (defi-
Fig. 4.2 – a) Initial temperature front in the experiments of Lévy (2000). b) Temperature front at the final state (after one month of simulation). The dashed lines delimit a cyclone C and an anticyclone AC that have been formed in the course of the simulation. c) Initial nitrate concentration in experiment 1. d) Nitrate concentration at the end of experiment 1. e) Initial nitrate concentration in experiment 2. f) Nitrate concentration at the end of experiment 2. g) Schematic representation of the formation of cyclone C and of anticyclone AC during the experiments.
nounced as $(\zeta + f)/h$, with $\zeta$ the relative vorticity, $f$ the Coriolis parameter and $h$ the thickness of an isopycnic layer), implies that the increase of $\zeta$ must be balanced by an increase of $h$ (which corresponds to the stretching).

Lévy (2003) carried two experiments where they varied the initial nitrate distribution. Experiment 1 (Fig. 4.2c and d) describes an oligotrophic front; nitrate is distributed along isopycnal surfaces below the euphotic layer, and drops to zero within the euphotic layer. Experiment 2 (Fig. 4.2e and f) describes a more productive front. As in experiment 1, nitrate is distributed along isopycnal surfaces below the euphotic layer. Within the euphotic layer, nitrate concentrations are low but not null. Due to biological consumption, they have departed from a purely linear regression with density. Fig. 4.2d and f show that the nitrate distribution in AC and C depend very much on the initial situation.

In the case of Exp. 1, nitrate is depleted in C with respect to the surrounding waters down to 200m depth. In Exp. 2, nitrate is on the contrary increased in C at the same depth. In the two experiments, there is actually a competition between the effect of downward stretching and the effect of horizontal transport. In Exp. 1, the horizontal transport in the euphotic layer is nul because there is no horizontal nutrient gradient. The downward stretching prevails. In Exp. 2, there is an important nutrient gradient within the euphotic layer, and horizontal transport prevails. As for temperature, in Exp 2 the raised nitrate concentrations within C result from the horizontal displacement of C. Similar arguments can be drawn for AC.

Interestingly, the (mostly horizontal) mechanism illustrated by Exp 2 is in agreement with the same type of observations (i.e. Fig. 2.3) as the (vertical) eddy pumping mechanism. Clearly, this reveals that distinguishing between horizontal and vertical transport requires knowledge on the eddy formation process and history.

The importance of the horizontal mechanism is supported by large scale modeling studies. Oschlies (2002b) regional budgets computed from an eddy-permitting North Atlantic basin biogeochemical model experiment, show that horizontal nitrate supply to the oligotrophic gyre is larger than vertical transport. These budgets show that vertical eddy advection is the strongest near western boundary currents, where turbulent eddy energy is the highest, whereas eddies supply nutrients predominantly via horizontal advection near the quieter southern and eastern margins of the subtropical gyre. The above works led Williams and Follows (2003) to propose a generalized version of the scheme of McGillicuddy and Robinson (1997), including horizontal as well as vertical transfer (Fig. 4.1). The recent observations of the impact of eddies on chlorophyll distribution by Aristegui et al. (1997) around Gran Canaria and by Crawford et al. (2005) in the Gulf of Alaska support this idea of a combination of vertical and horizontal transport processes.
Transport by mesoscale eddies
Chapitre 5

Transport by submesoscale dynamics

5.1 Vertical advection at the submesoscale

5.1.1 Upwelling of nutrients in filaments

In order to explore vertical advection of nutrients at scales smaller than the eddies, Mahadevan and Archer (2000) report the change of primary production induced by the change of horizontal resolution in a model (Fig. 5.1). They explore the range of resolution from 10 km to 40 km in a model representing a limited area of the ocean where PP is limited by the availability of nutrients. They show a tremendous increase in PP (up to a factor three) in response to increasing model resolution. The increase is related to a better representation of the mesoscale range; increasing the model resolution results in more undulation of the isopycnal surfaces and in an increased length of the frontal zone (or isopycnal outcropping).

Lévy et al. (2001a) follow a similar approach and increase their model resolution up to 2 km in order to resolve the submesoscale features. They report a factor two change in PP when changing the resolution from 10 km to 2 km. This increase is due to the resolution of intense vertical velocities, captured within filaments of strong vorticity gradients which surround the eddies or which are ejected by the eddies (Fig. 5.2a and b). This strongly ageostrophic surface dynamics cannot be captured in the frame of the QG approximation, since it involves strong surface density gradients. This explains why it is not seen in modeling studies using QG models (Flierl and Davies, 1993; Yoshimori and Kishi, 1994; McGillicuddy et al., 1995; Smith et al., 1996; McGillicuddy and Robinson, 1997), nor in modeling studies based on primitive equation models but where the horizontal resolution is not sufficient enough to accurately resolve these gradients, and the associated submesoscale vertical transport (Oschlies and Garcon, 1998;...
Fig. 5.1 – The density and nitrate distribution plotted at the base of the euphotic zone alongside the depth of a particular isopycnal. In each column, fields from (a) 0.4°, (b) 0.2° and (c) 0.1° model resolution are shown. The pattern of new production is very similar to the nitrate distribution pattern. From Mahadevan and Archer (2000).
Fig. 5.2 – a/ Relative vorticity at the surface, b/ vertical velocity at 100m (zoom, in color, superposed on vorticity lines), c/ phytoplankton within the euphotic layer (0-120m) and d/ export of phytoplankton below the euphotic layer (120-240m), simulated with a primitive equation model with a horizontal resolution of 2 km. The initial state is an unstable baroclinic front and the fields shown are after 22 days of simulation. From Lévy et al. (2001a).
As the submesoscale vertical velocities are in phase with the vorticity gradients, regions of nutrient input coincide with regions of elevated strain. This results in phytoplankton distribution being concentrated and elongated in filaments, either isolated filaments or filaments around eddies (Fig. 5.2c). First obtained in a simulation of decaying turbulence (Lévy et al., 2001a), this result has then been generalized to the situation of forced turbulence (Lévy and Klein, 2004, Fig. 5.3).

A more careful examination of the fields in Fig. 5.2 and in Fig. 5.3 reveals that phytoplankton mainly develop in filaments of negative vorticity within the euphotic layer. Moreover, the spectral slope of phytoplankton, zooplankton and vorticity are close to -1.5 while the density spectrum is steeper with a slope close to -3 (Fig. 5.4).

These results (Lévy et al., 2001a; Lévy and Klein, 2004) can be explained with the rationalization of Klein et al. (1998) regarding the density field: to prevent a thermal-wind imbalance, the physical system locally organizes the vertical and horizontal velocity fields such that sub-mesoscale vertical and horizontal advection of density tend to compensate each other. This phase relationship between vertical and horizontal advection of density explains why very few small-scale features are present in the density field (slope close to -3). It is also consistent with motions being almost parallel to the isopycnals. This local compensation between horizontal and vertical advection holds for any tracer forced by the same large-scale vertical and horizontal gradients than density. However, it does not hold for a tracer forced by either the horizontal or the vertical gradient. In the last two cases, small scales will develop. Moreover, due to this compensation, a tracer forced by a large-scale horizontal gradient will have its small scales strongly anticorrelated to those of a tracer forced by a large-scale vertical gradient.

Vorticity and nitrate have their isopleths almost orthogonal (and therefore both inclined to the isopycnals), since potential vorticity (close to relative vorticity in the surface layers) is forced by a large-scale horizontal gradient and nitrate by a large-scale vertical gradient. This favors the development of small scales for vorticity and for nitrate (slope close to -1.5). Moreover, small scales of vorticity should be strongly anticorrelated to those of nitrate, and ultimately to those of phytoplankton.

5.1.2 Subduction of phytoplankton in filaments

The simulations of Lévy et al. (2001a) and Lévy and Klein (2004) also evidence that downwelling velocities associated with vorticity filaments are responsible for an export flux out of the euphotic zone. This export is
Fig. 5.3 – Surface relative vorticity, density anomaly, phytoplankton and zooplankton simulated with a primitive equation model on the beta-plane with a horizontal resolution of 6 km. Fields shown are after 1600 days of simulation. The domain is periodic in longitude and turbulence is forced by restoring to a background density gradient. From Lévy and Klein (2004).
**Fig. 5.4** – Time evolution of the spectral slope of surface relative vorticity, density, phytoplankton and zooplankton, in a primitive equation model of forced turbulence (same simulation as that shown on Fig 5.3. Adapted from Lévy and Klein (2004).
located in filaments of positive vorticity (Fig. 5.2a and d), for the same reasons as developed above regarding nutrients and vorticity (the vertical phytoplankton gradient has a sign opposite to that of the vertical nutrient gradient). In-situ observations with high-resolution towed vehicles confirm such patterns of localised submesoscale subduction (Prieur and Sournia, 1994; Nurser and Zang, 2000; Strass et al., 2002a). Nevertheless, they are too sparse to provide a number for the magnitude of this export compared with more traditional form of export like the sedimentation of detritus (Boyd and Newton, 1999) or the convective export of organic matter (Koeve et al., 2002).

5.1.3 Net impact of submesoscale structures on PP

In oligotrophic situations, phytoplankton undergoes two antagonistic effects of (sub-)mesoscale transport: production is favored through the inputs of nutrients within the euphotic layer, and is inhibited through the removal of phytoplankton cells from the euphotic layer. Phytoplankton production is favored in filaments of negative vorticity and is inhibited in filaments of positive vorticity. Its development in a turbulent field therefore requires that its growth is fast enough to balance the losses.

In order to get some further insight on this balance, we compare the experiment of Levy et al. (2001) (LKT experiment) with the experiment in Levy and Klein (2004) (LK experiment). Both experiments are run with the same biological model, the same model parameters and the same initial condition for nitrate (a nutricline located at 100 m depth). The experiments differ in their horizontal resolution (6 km in LK versus 2 km in LKT) and in their forcing (decaying turbulence in LKT, forced turbulence in LK). They also differ in the size of the domain, the duration of the experiment and the width of the unstable front that forces turbulence. These differences all together result in vertical velocities one order of magnitude lower in LK (maxima around 10 m/d) compared with LKT (maxima around 100 m/d). One interesting contrasting result is that mesoscale turbulence increases PP by a factor 3 in LKT, but does not significantly change PP in LK. This indicates that the supply of nutrients prevails over the subduction of phytoplankton in the LKT experiment, while the two effects compensate in the LK experiment.

One possible explanation lays in the different order of magnitude of the vertical velocity field in the two experiments. A linear increase in upwelling velocities results in an exponential increase of the phytoplankton growth rate. Indeed, upwelling displaces the phytoplankton subsurface maximum and the nutricline closer to the surface (Levy et al., 2001) and the phytoplankton growth rate increases exponentially with decreasing depths in response to the exponentially increasing light. On the other hand, phyto-
plankton decrease through subduction responds in a linear manner to a linear change in downwelling velocities because the expression of advection is linear in $w$. Hence, with increasing vertical velocities, and assuming a comparable range of change for upwelling and downwelling velocities, phytoplankton production should increase more rapidly than phytoplankton subduction. This view suggests that vertical velocities must be large enough to have a positive influence on the increase in phytoplankton, and the experiments suggest that they should be larger than 10m/d. This view is in agreement with Smith et al. (1996), who found that the net effect of eddies on the rates of primary production is small in their QG simulation (QG vertical velocities are below 10m/d).

Let’s now consider a water parcel below the euphotic layer, which is advected up to the euphotic layer and back below it. The parcel is initially loaded with nutrients. The parcel will induce a net flux of nutrients into the euphotic layer which will have an effect on phytoplankton only if the time it spends in the euphotic layer is long enough to enable nutrient uptake by phytoplankton. Otherwise, the parcel will pass through the euphotic layer with no net effect. Typically, phytoplankton growth rate is of the order of one to two days and the euphotic layer is 100m depth. If the vertical velocity of the water parcel is less than 100m/day, then its journey in and out of the euphotic layer will last more than two days: nutrients will be consumed during that period. Vertical velocities must therefore be less than 100m/d to induce a net nutrient flux to the euphotic layer. Faster vertical velocities, for instance those associated with convective plumes (of the order of 1000m/day) are likely not to induce a net transport: nutrients do not remain long enough in the euphotic layer to be consumed.

Vertical velocities associated with submesoscale activity, typically 10-100 m/day, fall in the range imposed by the two above constrains. Those associated with mesoscale activity (1-10 m/day) have a more marginal impact, because the growth of phytoplankton that they induce is not strong enough to balance the loss of phytoplankton through subduction that they also induce.

In bloom situations, nutrients are plentiful in the euphotic layer. Submesoscale transport mainly acts as a sink for phytoplankton and tends to decrease primary production.

### 5.2 Horizontal transport at submesoscale

#### 5.2.1 Stirring

Another aspect concerns the ability of phytoplankton distribution to be stirred by mesoscale turbulence. This ability depends on the ratio between the tracer decay rate and the advection time scale of the flow (Mahade-
FIG. 5.5 – Snapshots at the end of a high-resolution model run. a) Carrying capacity (the equivalent for nutrients). b) Phytoplankton. c) Zooplankton. The strip at the left shows the zonally varying distributions the populations would have in the absence of advection while the bar on the right gives the values associated with the different colours. From Abraham (1998).
van and Campbell, 2002). Phytoplankton decay rate is approximately one month (the mean time-lag between mid-latitude phytoplankton and zooplankton blooms). This is long compared to the transport time within a filament, typically 2 to 10 days. It is therefore reasonable to expect phytoplankton to be stirred by the flow.

Production of small-scale filaments of phytoplankton in the ocean by horizontal stirring has been evidenced by in situ experiments, such as NATRE (North Atlantic Tracer Release Experiment; Ledwell et al., 1993) and SOIREE (Southern Ocean Iron RElease Experiment; Abraham et al., 2000). To rationalize this stirring, Abraham (1998) proposes a mechanism based on the production of smaller and smaller tracer scales by mesoscale eddies, which is the classical direct tracer cascade. This mechanism is evidenced in a 2D numerical experiment where nutrients are injected at large scales within the euphotic layer and are subsequently affected by the direct cascade process (Fig. 5.5). In this experiment, the spatial variability of phytoplankton involves more energetic small scales than for nutrients (in other words, the phytoplankton spectrum slope is less steep than that of nutrients), and the variability of zooplankton involves even smaller scales than phytoplankton. This behavior is due to the fact that the e-folding time of the phytoplankton growth rate (one to two days) is usually smaller than the cascade time scale (approximately 10 days in the ocean, Klein and Hua, 1990). Since nutrients are injected at large scales, smaller and smaller scales develop during the transformation of nutrients into phytoplankton, and ultimately into zooplankton. Thus the spatial variability of the successive biological populations reflect the different phases of the cascade process.

Abraham (1998) also shows that the spectral slopes for zooplankton and phytoplankton vary as a function of model parameters (from -0.7 to -2.5 for zooplankton and from -1.5 to -2.5 for phytoplankton). Basically, when the parameter range favors faster zooplankton growth, lesser small scales appear in phytoplankton because the residence time of phytoplankton is reduced. Moreover, there is only a small range of parameter values where zooplankton exhibit a steeper spectral slope than phytoplankton. This atypical situation corresponds to that of rapid zooplankton growth (preventing the generation of small phytoplankton scales) combined with rapid zooplankton mortality (preventing the generation of small zooplankton scales).

Regarding the spectral slopes of phytoplankton and zooplankton, Levy and Klein (2004) illustrate a different situation, where they vary with time (between -1 and -2), over periods of a couple months (Fig. 5.4). These changes of slope are obtained for a unique set of parameters, and are such that the steepest slope is either that for zooplankton or for phytoplankton depending on the time in the simulation. Lévy an Klein (2004) relate these changes of slope to the low frequency variability of the eddy field (the equivalent of the atmospheric weather regimes).
One important difference between the experiment of Abraham (1998) and that of Lévy and Klein (2004) is that in the latter nutrients are injected at small scale by the vertical velocity field. These two contrasting experiments suggest that it is difficult to derive general conclusions on the processes that lead to the formation of small scales by comparing the relative spectra of phytoplankton and of zooplankton.

5.2.2 Impact of stirring on the rate of vertical advection

An underlying question is how much the horizontal stirring affects the vertical transport. This has been addressed by Martin et al. (2002) and Pasquero et al. (2005) in a model of two-dimensional turbulence in which vertical nutrient advection is externally imposed as a restoring flux. Pasquero et al. (2005) show that PP is increased if upwelling is fragmented into many episodes of short duration and/or small size. The mechanism relies on the removal of nutrients from the active (i.e. upwelling) regions by horizontal advection on time scales shorter than the phytoplankton doubling time. This removal causes an increase of PP because it enables to maintain the strength of the restoring nitrate flux. The magnitude of the increase is shown to be diminished by the sheltering action of the eddies, which prevents horizontal dispersion in their core.

These two studies impose small-scale vertical advection in a somehow arbitrary manner, whereas submesoscale vertical advection is actually in phase with horizontal stirring (Klein et al, 1998; Lévy et al, 2001a). This arbitrary dimension highlights a double effect: increasing the model resolution increases the amplitude of w, but also causes w to be more fragmented. Both effects contribute to increase the vertical nutrient flux, and ultimately to increase PP.
Transport by submesoscale dynamics
Chapitre 6

Bio-physical interactions through stratification changes

The impact of mesoscale eddies on primary production has also been reported when nutrients are plentiful in the euphotic layer: during the spring bloom (Antoine et al., 1995) and in the HNLC (High Nutrient Low Chlorophyl) Antarctic Circumpolar Current (Strass et al., 2002). In such a situation, light is the main limiting factor: PP is highly sensitive to the ML depth. ML shoaling can locally increase the mean exposure time of photosynthetic organisms and promote production. In this situation, the restratificaying action of mesoscale eddies leads to beginning of bloom prior to seasonal stratification (as it has been reported in the North Atlantic by Townsend et al., 1994). Two illustrations of this mechanism, one at mesoscale, the other at submesoscale, are now presented.

6.1 Mesoscale stratification

As demonstrated by Klein and Hua (1988), mesoscale eddies generate heterogeneity of the mixed-layer. It is now recognize that eddies have an important role in the restratification of the surface (Katsman et al., 2004; Henning and Vallis, 2005). When these eddies result from the baroclinic instability associated with the process of winter deep convection (Madec et al., 1991; Madec et al., 1996; Hermann and Owens, 1992), they act against convection and tend to restratify the convective area, gradually cutting down its edges (Nurser and Zang, 2000; Strass et al., 2002). This has been numerically evidenced in a regional model study of the spring bloom in a region of deep convection (northwestern Mediterranean, Lévy et al., 1998; 1999a; 2000). Fig. 6.1b shows the surface density signature of eddies that are formed through baroclinic instability around a deep-mixing area in an idealized model of a convective patch. The formation of the eddies enable to release the available potential energy contained...
Bio-physical interactions through stratification changes

Fig. 6.1 – a) Schematic of eddy-induced stratification and eddy induced subduction at the rim of a convective zone. Production is enhanced in the zone of eddy restratification. Model results (from Lévy et al., 1998) showing b) the density, c) the mixed-layer depth, and d) the Chl concentration (in mgChl/m³) in an area of deep mixing (sea-surface view). e) Satellite sea-color observations from Santolleri et al. (2002) in the Adriatic, showing phytoplankton developing preferentially at the rim of the Adriatic convective area.
within the dense water patch. Basically, the eddies serve as vehicles for the transfer of water masses, by sinking the denser waters out of the convective zone and at the same time upwelling lighter peripheral waters toward the center. Consequently, these mesoscale instabilities are responsible for the collapse of the dense water patch. The axial symmetry of the problem allows to schematize the action of the eddies as a function of depth and distance from the center of the convective patch (Fig. 6.1a). The transport of warmer waters from the stratified area toward the convective site across the frontal zone is responsible for the sloping of the isopycnals and hence for the shoaling of the mixed layer at the rim of the convective area (Fig. 6.1c). In winter, nutrients are plentiful within the euphotic layer and there is no obvious relationship between PP and nutrients, whereas PP increases when the mixed-layer depth decreases. Indeed, the mean exposure time of the phytoplankton cells to sunlight is inversely correlated with the mixed-layer depth. Consequently, the majority of phytoplankton production is obtained at the rim of the convective area, where the mixed layer is the shallowest (Fig. 6.1d). This ”dynamical” stratification leads to a bloom which starts earlier that induced by the more classical ”seasonal” stratification. Satellite observations from Santoleri et al. (2002) above the convective area of the Adriatic sea provide observational evidence of this eddy-fertilization process (Fig. 6.1e). Another process evidenced with the experiment of Lévy et al. (1999a) is the decorrelation in space between new and exported production. This decorrelation is induced by the eddies, which subduct phytoplankton rich waters (Fig. 6.1a). Hence, while NP is maximum at around 30 km from the center of the convective region (in the mediterranean case), EP (through the subduction of phytoplankton) is maximum at 80 km from the center.

6.2 Submesoscale stratification

In order to better assess the impact of submesoscale dynamics during the spring bloom in the north-east Atlantic, high-resolution numerical experiments were conducted in the frame of POMME (Programme d’Océanographie Multidisciplinaire Meso Échelle)(Paci et al., 2005; Lévy et al., 2005b). The domain of the experiment (16-22W, 38-45N) is covered by several eddies (Fig. 6.2a). Data collected during the first POMME survey were used for model initialization, and data from three other cruises for model validation. The model revealed much stronger space and time variability than could be seen with the resolution of the data (CTD stations were 50 km apart). Space variability during the onset of the bloom is illustrated by Fig. 6.2 which shows a snapshot of model outputs in March.

A very striking feature is the strong variability of the MLD on filamen-
Fig. 6.2 – Simulation of the spring bloom onset in the northeast Atlantic (adapted from Lévy et al., 2005b). a) Sea surface hight (in cm), with cyclones identified in blue and anticyclones in red, b) Buoyancy (in $w/m^2$), c) Mixed-layer Depth (in m), d) Phytoplankton integrated over the euphotic layer (in mmoleN/m²).
tary scales (Fig. 6.2b). The maximum MLD gradients are reached at the border of eddies (Fig. 6.2c); MLD changes from 200m to 50m over 10km. These fine scale structures in the MLD seem to result from the interplay between the mesoscale atmospheric forcing and the stirring induced by the eddies. The medium scale picture is that MLD is shallower over the regions previously subjected to warming (in the southeast and northeast, Fig. 6.2b) and that it is deeper over the regions subjected to cooling (in the northwest, in the center, and in the southwest). This medium scale picture is perturbed by the small scale advection, which induces a direct cascade of the MLD towards smaller scales. Incidentally, the stratification of the upper ocean is also very sensitive to the ageostrophic submesoscale dynamics induced by baroclinic eddies in the absence of atmospheric forcing (Laypere et al., 2006). At medium scale, phytoplankton variability during the bloom is driven by the variability of the buoyancy flux and of the solar radiation. At small scale, phytoplankton patterns follow the MLD distribution (Fig. 6.2d). NP is maximum over the filamentary structures of MLD minima, and conversely NP is minimum over the filaments of maximum MLD. The mesoscale dynamics therefore contribute to structuring the initial conditions for the onset of the spring bloom in specific submesoscale features. There is no nutrient limitation yet. The structuring is mainly the consequence of photosynthesis limitation by (lack of) light, which is greater when the MLD is deeper. It is worth-noting that the phytoplankton distribution is not directly correlated with the eddies; rather, the deformation field associated with the presence of eddy induced submesoscale stirring (around and inbetween eddies) which structure the ML and the growth of phytoplankton.
Bio-physical interactions through stratification changes
Chapitre 7

Conclusion

This paper attempts to review our current knowledge on the role of physical phenomena on primary production and export, on the horizontal scales of oceanic turbulence, i.e. from a few kilometers to a few hundred kilometers. It is focussed on the modeling aspect of this problem and on the processes that control PP in the open ocean.

In section 2, we gave an overview of the problem. More precisely, we have shown how biotic rates are modulated by transport and we have presented some features of the vertical and horizontal transport associated with oceanic turbulence. Some of the increasing observations that has lead the research community to pay a particular attention at the (sub)-mesoscales were also presented. Section 3 presented how biogeochemistry is introduced in OGCMs. More precisely, we argue that the impact of (sub)-mesoscale dynamics on biogeochemistry appears in the form of advective Reynolds terms when the transport equation is solved on a grid coarser than the (sub)-mesoscale. In sections 4, 5 and 6, the processes have been described in terms of how they perturb the system on the short term. Section 4 summarized the mesoscale transport process that provide nutrients to the euphotic layer. In it we distinguish the vertical transport from the horizontal transport because the ocean is strongly anisotropic in the scale range in consideration. In particular we suggest that it is difficult to recognize eddy pumping from horizontal displacement on the basis of synoptic observations, and that knowledge on the time evolution of the eddy is required. Section 5 reviewed the impact of submesoscale transport. The submesoscale dynamics is associated with intense vertical velocities, in phase with the vorticity gradients. The consequence is the development of phytoplankton localized in filaments of negative vorticity, balanced by an export of phytoplankton in filaments of positive vorticity. Our results suggest that the net balance is toward a significant increase of PP when sub-mesoscale vertical velocities are energetic, and a much more moderate increase associated with the QG mesoscale vertical velocities. Section 6 presented how (sub)-
Conclusion

Mesoscale features can result in a shoaling of the ML depth, and therefore provoke the bloom to begin prior to seasonal stratification.

This review is restricted to mid-latitude open ocean turbulence, where the mean productivity is driven by the cycling of the mixed-layer. In particular, the equatorial and coastal regions, where productivity is driven by large-scale upwelling, have their own small-scale dynamics, and possibly different impacts on productivity (Menkes et al., 2002, Gruber et al., 2005). Also, the processes were described qualitatively. Dedicated studies combining observations and models can help to estimate more quantitatively the relative contribution of the small-scale physical processes and are more and more numerous (McGillicuddy et al., 1995; Anderson et al., 2000; Anderson and Robinson, 2001; Popova et al., 2002; Strass et al., 2002b; Levy et al., 2005b). Finally, the modulation of air-sea CO2 fluxes by oceanic submesoscale turbulence is not straightforward. As discussed by Mahadevan et al. (2004), it results from a balance between the impact of mesoscale turbulence on biology, temperature and dissolved organic carbon.

Two major issues still need further investigations. The first issue is the role of the oceanic turbulence in the competition between different species. This aspect is crucial to the biogeochemical cycles since the efficiency of the biological pump is very closely related with the phytoplankton species (Boyd and Newton, 1999; Bury et al., 2001): large cells are more likely grazed by large grazers who produce fast sinking fecal pellets and an efficient carbon export, while small cells are involved in the regeneration network. A number of observation now provide evidence that the phytoplankton community is structured by (sub-)mesoscale turbulence (Vaillancourt et al., 2003; Sweeney et al., 2003; Claustre et al., 2005, Batten and Crawford, 2005). Modeling studies by Bracco and Provenzale (2000), Martin et al. (2001), Lima et al. (2002) and Pasquero et al. (2004) also suggest that (sub-)mesoscale turbulence plays a role in the structuration of the ecosystem. The responses of those models depend very much on the choice of the parameters. A complete understanding of how (sub-)mesoscale turbulence structures the ecosystem now requires more systematic studies covering a large range of the parameter space. These studies should bring some new insight on the importance and variability of the biological Reynolds term.

The second issue is the role of the oceanic turbulence in the long term and large scale equilibrium of the nutrient distribution, i.e. in the subsurface nutrient reservoir. This far field effect of eddies has been shown to be important in idealized studies (Lee et al., 1997; Lee and Williams, 2000). The 1D view, appealing in simplicity, is that the upward flux of nutrients in the euphotic layer is balanced locally by a downward flux of organic material. This view relies on the premise that the remineralization of organic matter at depth occurs faster than the physical processes that advect the nutrients upward. This view neglects the lateral processes that deliver
nutrient to the subsurface. These lateral processes can be due to the large scale Ekman transport (Williams and Follows, 1998a) or associated with the formation and advection of mode waters (Palter et al., 2005; Lévy et al., 2005c). They can also be attributed to the eddy transport (Visbeck et al., 1997; Williams and Follows, 2003), and possibly to the transport by submesoscale structures. Model studies suggest that eddies could modify the subduction rates (Hazeleger and Drijfhout, 2000; Valdivieso da Costa et al., 2005); this also could have an impact on the subsurface nutrient pool.

Although our understanding of the impact of mesoscale turbulence on biological production has been progressing very rapidly in the last decade, efforts are still needed before we can get a complete picture, i.e. a precise quantification of this impact on the short-term, local impact and on the large scale maintenance of production. Today, the most powerful supercomputers (Los Alamos, Earth Simulator, Oakridge) allow the first global simulations of the ocean circulation at 1/10° (i.e. Nakamura and Kagimoto, 2006). The resolution at submesoscale, with a complete description of the biogeochemical cycles requires an increase in computer power of approximately two orders of magnitude. Idealized basin scale studies are affordable at very high resolution, and are an alternative to reconcile and quantify the various pathways through which mesoscale turbulence impacts biogeochemical cycles and ultimately to derive and to test parametrizations of these impacts for climate models.

In view of the different pathways through which mesoscale turbulence modifies marine productivity, it is very unlikely that a unique parametrization of these impacts for climate models will be able to encompass all the processes. Rather, the identification and characterization of the different processes, as has been attempted here, should be seen as a first step towards parametrization. The second step is the parametrization of the physical transport alone. For instance, regarding lateral transport at the mesoscale, Gent and McWilliams (1990) has proposed a parametrization of eddy-induced water mass exchanges in the form of an additional eddy-induced advection flux which depends on the large scale slope of the isopycnals. This parametrization improved the distribution of water masses simulated with an OGCM (Danabasoglu et al., 1994). Treguier et al. (2003) warn however that this representation does not account for the transport within individual eddies traveling over long distances. Regarding lateral transport occurring at the sub-mesoscale, Dubos (2001) proposed a spatially selective parametrization which led promising results in 2D-turbulence. This parametrization remains to be tested in OGCMs. Regarding vertical transport, I am not aware of parametrization of the strongly ageostrophic vertical transport associated with mesoscale turbulence. The third step is the imbrication of the physical parametrization for biogeo-
chemical purposes. For instance, Lévy et al. (1999b) have shown that the use of the Gent and McWilliam (1990) scheme could very nicely represent the eddy-induced restratification around a convective area and greatly improve the prediction of the pre-bloom phytoplankton growth in the NW Mediterranean Sea. Pasquero (2005) experiments suggest that when eddy diffusion is used to mimic lateral turbulent transport, a smaller diffusion coefficient has to be used for non-conservative tracers such as phytoplankton or nutrient. She convincingly argues that turbulent transport can be significantly overestimated if the reaction time scale of the transported tracers is not accounted for. Finally, the importance of the biological Reynolds terms has to be assessed and eventually parametrized. Parametrization of small-scale transport and biology is a big challenge for climate studies, and to take up this challenge will require the strengthening of interdisciplinary approaches.
Perspectives

In the above conclusions, I have drawn the general perspectives that I see for mesoscale bio-physical interactions. Among these, I will now briefly focus on my own perspectives. In the next few years, the questions I intend to address are:

– How realistic are ecosystem models embedded in a mesoscale field?
– Can the processes evidenced from sub-mesoscale model studies be validated with satellite data?
– How do eddies affect the subsurface nutrient reservoir?
– What are the particularities of bio-physical submesoscale interactions in coastal regions?
– What is the global impact of eddies on biogeochemical budgets?
– Can (sub)-mesoscale bio-physical interactions be parameterized?

A question that has always puzzled me is the realism of the ecosystem models that we use, particularly when they are incorporated in highly variable conditions, which is the case in eddy-resolving models. Analysing the sensitivity of an ecosystem model and validating it with a limited in situ data set has been the rule so far. My feeling is that we seriously lack laboratory experiments to validate the cogency of the mathematical formulations used in these models. This is the reason why I am reluctant to use complicated models, although I believe that they are interesting questions regarding the structuring of the ecosystem in a turbulent environment. This is also the reason why I am involved in the APPLE (Adaptation of Photosynthesis : Parametrisation from Laboratory Experiments) project coordinated by Antoine Sciandra which aims at studying the growth of phytoplankton in a variable environment. Indeed, the formulation of primary production in most ecosystem models relies on experiments at equilibrium, which is far from being the case in a turbulent field. Do we have the right to extrapolate this formulation to study bio-physical interactions at the mesoscale? What error result from this approximation? This program, which involves a collaboration between experimentalists and modellers, should provide answers to these questions.
The tremendous amount of high-resolution data available thanks to the success of the ongoing SeaWiFS and MODIS missions enable to quantitatively analyze the sub-mesoscale variability of sea-surface chlorophyll. Moreover, dynamical information derived either from operational model outputs, from altimetry data or from sea-surface temperature data should enable to identify the physical processes responsible for the observed variability, at sub-mesoscale, at mesoscale, and at larger scales. This is what we are trying to do in the frame of the project MULTICOLOR (Variabilité multi-échelle - de la sub-mésoéchelle à l'interannuel- de la couleur de l'eau dans l'Atlantique Nord) sponsored by CNES and MERCATOR that I am coordinating. Yoav Lehahn and Cyril Lathuilliere are both doing their thesis in the frame of this project, Francesco d'Ovidio (post-doc at LMD/IPSL) and Laurent Dubroca (post-doc in Italy) are important contributors. With this multi-sensor approach, we try to validate the theoretical model results regarding the impact of sub-mesoscale physics on the distribution of plankton, in particular the horizontal stirring by the flow into small-scale filaments, the upwelling of nutrients in specific small-scale regions in phase with the stirring, and the low-frequency variability of the spectral slope of phytoplankton.

The far field effect of the eddies has received little attention so far. More particularly, the question is how do eddies modify the large scale nutrient distribution, and in particular how is the sub-surface nutrient reservoir affected by mesoscale and sub-mesoscale ocean dynamics? To answer these questions, I pursue two complementary approaches.

The first approach is the analysis of the subsurface nutrient data acquired during the POMME (Programme Océan Multidisciplinaire MésoÉchelle) program in the North East Atlantic. A particular point of interest concerns the distribution of nitrate along a given isopycnal. The eddy-pumping mechanism relies on the hypothesis that this distribution is homogeneous. This implies that isopycnal diffusion is fast enough to counter-balance the effects of remineralization and of formation of new water masses. In collaboration with Gilles Reverdin, we will test this hypothesis and focus on the evolution along the year of the nutrient content of the sub-polar mode waters. The resolution of the POMME data set should enable to partially capture the mesoscale variability of the nutrient reservoir associated with these mode waters. Also, given that the role of the eddies in the formation of the mode-waters is understood, we should gain some insight on their role in the sub-surface nutrient distribution. If the data do not support the assumption of sub-surface nitrate being aligned with density, than the mesoscale variability of the sub-surface nutrient reservoir will have to be accounted for in our representation of processes.
The second approach is an idealized model study, a double-gyre representative of the North Atlantic. In order to fully evaluate the contribution of mesoscales and submesoscales on biogeochemical budgets at basin and seasonal scales, i.e. to evaluate both the local and the far field contributions, we will compare the equilibration of the model at different resolutions. Up to now, similar attempts at basin scale have focused on the spin-up phase (5 first years). The far field effect cannot be fully evaluated during this phase. Indeed, properties of sub-surface waters must be at equilibrium for this effect to be properly assessed. This requires long integrations. The size of the double-gyre domain is small enough to enable these long integrations (100 years) at high horizontal resolution (up to 2km) (Fig. 7.1). The dynamical runs have been performed on the Earth Simulator, in the framework of a Memorandum Of Understanding with Japan and of an ANR (Agence National de la Recherche) project (INLOES : Etudes des interactions non-linéaires des échelles océaniques grâce au Earth Simulator). The coupling with biology is the heart of the thesis of Anne-Sophie Kremeur, who I supervise with Gilles Reverdin.

The double-gyre configuration provides a perfect framework for developing and testing parametrizations. Those parametrizations will have to take into account the mean biogeochemical gradients and the mean state of the ocean (baroclinicity, turbulent kinetic energy). Appropriate representations of vertical and lateral mixing will have to take into account the sub-grid scale transport of nutrient and export of organic material.

![Fig. 7.1 – Snapshot of Sea surface salinity, surface relative vorticity and vertical velocity at 50m in a double-gyre configuration with a horizontal resolution of 4 km](image-url)
To complete the picture of the impact of the eddies, a second track that I want to pursue is their impact in the coastal ocean, in particular regarding the exchange of material between the coast and the open ocean. I am doing this work in collaboration with Vincent Echevin and Gurvan Madec, in the frame of the thesis of Cyril Lathuillière. We are currently setting up an idealized model configuration for the African upwelling (off Mauritania) in order to identify the different control parameters. In this region, the seasonal cycle is very contrasted to the south of 18°N, but not to the north. A particular question that we want to address is how the sub-mesoscale processes involved in the exchanges between the shelf and the open ocean are modulated by the strength of the upwelling seasonal cycle.

The last logical step is to fully achieve a high-resolution regional study. For this, I want to focus on the Indian Ocean, in the frame of the collaboration that I have started with the NIO (National Institute of Oceanography in India). This region is particularly interesting in terms of eddy activity since eddies result from a variety of different processes. Primary productivity is one of the highest of the world’s ocean, partly because of a strong coastal upwelling during the summer monsoon. It is worth to test how the mesoscale and sub-mesoscale processes contribute to this budget at the coast and in the open ocean, and how it competes with the strong seasonal cycle associated with the two monsoons.
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Curriculum vitae

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Education

April 1998 Summer school ”Transport in geophysical flows”, Aosta, Italy
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1993-1996 Ph. D in Oceanography, Meteorology and Environment, University ParisVI : Modelisation des processus biogeo-
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onnier et Variabilité mesoéchelle. Advisors : L. Memery, G. Madec and J.-M. André
Aug 1993 Summer school ”Primary production in the ocean”, Sophia-Antipolis, France
1992-1993 Master in Oceanography, Meteorology and Environment, University ParisVI
1989-1992 Ecole Polytechnique, Palaiseau, France
Mobility

Sep-Dec 2005 Visiting scientist at the National Institute of Oceanography (NIO), Goa, India
1998-present Chargé de recherche at Centre National de Recherche Scientifique (CNRS), working at LOCEAN
1997-1998 Postdoctoral fellow at Lamont-Doherty Earth Observatory (LDEO) of Columbia University, USA

Awards

2005 CNRS bronze medal
1999 ACI for young scientists sponsored by the French Ministry of Research
1997 Postdoctoral fellowship sponsored by LDEO

Current research projects

BRIO Biological Responses in the Indian Ocean (IRD, PI : J.-M. André)
INLOES Études des interactions non-linéaires des échelles océaniques grâce au Earth Simulator (ANR, PI : P. Klein)
POMME Programme Océan Multidisciplinaire MésoÉchelle (PI : L. Memery and G. reverdin)
MULTICOLOR Variabilité multi-échelle (de la sub-mésoéchelle à l’interannuel) de la couleur de l’eau dans l’Atlantique Nord (MERCATOR/CNES - PI : M. Lévy)
SUBMESO Impacts de la physique de sub-mésoéchelle sur les flux biogéochimiques aux échelles régionales et de bassin : rationalisation, quantification et paramétrisation (PROOF, PI : M. Lévy)
APPLE Adaptation of Photosynthesis : Parametrisation from Laboratory Experiments (PROOF, PI : A. Sciandra)
BIONUTS Biophilic Nutrients and Operational Oceanography (MERCATOR, PI : P. Monfray)

Supervision

Master

– Florian Léger, stage DEA (2005). Modélisation de la région POMME durant aout-septembre (Pomme 3)
– Clara Gosselin, stage 3ème (2005), stage d’observation de la recherche
Curriculum vitae

- Anne-Sophie Kremeur, stage DEA (2004). Impact des processus rapides de petite échelle sur le rôle du puits de gaz carbonique atmosphérique de l'océan Atlantique Nord
- Xavier Pfeuty, stage maîtrise (2002). Étude de la variabilité du phytoplancton dans la zone POMME a partir de données satellites de couleur de l’eau
- Louis Rostand et Karim Ait Braham, stage de licence de physique (2002). Mise au point d’une base de données haute résolution d’images satellites de couleur de l’océan
- Riadh Elloumi, stage de l’Ecole Polytechnique (2001) Modélisation de tourbillons océaniques et de leur interaction avec la biologie en présence d’un forçage atmosphérique variable
- Audrey Estublier, stage de l’école Centrale de Nantes (2000), Quel Schéma numérique pour le transport d’organismes biologiques par la circulation océanique ?

Thesis

- Cyril Lathuillière (started in 2005) : 30%, supervisor G. Madec, Echanges côtes-large dans la région des Canaries
- Anne-Sophie Kremeur (started in 2004) : 70%, supervisor G. Reverdin, Impact de la sub-mésoéchelle sur les bilans de l’Atlantique Nord (sels, eau, nitrates)
- Pierre Karleskin (started in 2004) : 30%, supervisor L. Memery, Modélisation de la production primaire et de l’export dans l’Atlantique nord-est : bilans annuels
- Sonia Roudesli (to be defended in 2006) : 30%, supervisor L. Memery, Modélisation de la production primaire et de l’export dans l’Atlantique nord-est : impact de la mésoéchelle
- Blaise Faugeras (defended in 2002) : 20%, supervisor J. Verron, Assimilation de données à Dyfamed
- Franck Olivier (defended in 2001) : 30%, supervisor L. Mémery, Modélisation de la production primaire et de l’export dans le front Almeria-Oran
Other activities

Teaching  In charge of the master 2 module NU221 "Coupling between Physics, Biology and Chemistry in the ocean" of the University Paris 6

Model  Coordination of the developpement of the TOP-model (Tracers and Ocean Plankton) included in the NEMO system

Commities  Member of the "Conseil scientifique de l’IPSL"

Technical notes


Recent meeting presentations

2006  Observation of Small-Scale Horizontal Chlorophyll Stirring : Comparaison of Finite-Size Lyapunov Exponents and Chlorophyll Structures in SeaWiFS Images, AGU-OS, Hawaii

2006  Impact of subduction on the nitrate content of North Atlantic subtropical mode waters, AGU-OS, Hawaii


2005  Primary production variability : driving mechanisms at different scales, EGU, Vienna (invited contribution)

2004  A 4D mesoscale map of the spring bloom during the POMME experiment, EGU, Nice

Published papers

Curriculum vitae


13. **M. Lévy**, L. Memery and G. Madec : Combined effects of mesoscale processes and atmospheric high-frequency variability on the spring


Papers in revision

- Lévy, M: The modulation of biological production by oceanic mesoscale turbulence, submitted to Lecture notes in Physics, Transport in Geophysical flow: Ten years after