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Abstract :

This paper shows with a simple analytical model, that phytoplankton concentration decreases in response to sub-mesoscale vertical circulation only in regions of strong permanent upwelling.

It is now well established that marine ecosystems are sensitive to oceanic mesoscale turbulence (Lévy, 2008). Mesoscale turbulence is characterized by interactive mesoscale eddies and submesoscale filaments, which are associated with alternate up and down vertical velocities (Klein and Lapeyre, 2009). The upward branch of this vertical circulation enhances the nutrient flux into the well-lit euphotic layer and stimulates phytoplankton growth (McGillicuddy et al., 1998; Mahadevan and Archer, 2000; McGillicuddy et al., 2007; Johnson et al., 2010). The downward branch also alters phytoplankton concentration by subducting phytoplankton or more generally organic matter (Kadko et al., 1991; Lévy et al., 2001; Niewiadomska et al., 2008; Thomas and Joyce, 2010). The strength of this vertical circulation varies in space and time depending on the intensity of the eddy activity (Lévy et al., 2010).

In oligotrophic gyres of the open ocean, model studies suggest that the intensification of mesoscale turbulence results in a net increase in phytoplankton abundance in the euphotic layer (Oschlies, 2002; Lévy, 2008). However, in coastal upwelling regions, several studies suggest that the opposite effect prevails, i.e. that phytoplankton concentration decreases in response to enhanced eddy activity (Lathuilière et al., 2010). These model studies suggest that there is a tight competition between the effects of nutrient input and of phytoplankton export driven by mesoscale turbulence. They indicate that, in oligotrophic gyres, nutrient input plays the lead role, whereas phytoplankton export dominates in upwelling regions. There are also a few observational studies that support these model results, although they are limited. Indeed, the balance between the effect of nitrate inputs and of phytoplankton export, and how this balance varies with varying mesoscale turbulence, is inherently difficult to assess from observations alone. Variation of mesoscale turbulence can be evaluated by estimating mean properties such as the eddy kinetic energy or the Lyapunov exponent (LE). This approach was applied by Rossi et al. (2008) in the coastal ocean and by Calil and Richards (2010) in the oligotrophic open ocean. These two studies respectively report a negative and positive correlation between Satellite estimated chlorophyll a and LE derived from altimetry in the coastal/open ocean.

The objective here is to rationalize the balance between these two opposing effects with a simple analytical model, and to use the model to identify the key parameters that come into play in this

balance. We first present the model and underlying hypothesis. Then the model is solved analytically and the stationary solution is examined with regards to typical values of the model parameters in the ocean. Finally our results and hypothesis are discussed.

The model describes the evolution of limiting nutrients (N) and of phytoplankton (P) in a productive surface layer the euphotic layer, whose thickness is H (Fig. 1a). Both surface and deep phytoplankton maximum are comprised within this layer. Moreover this layer is assumed to be deeper than the surface mixed layer. The model resolves the vertical exchanges of P and N between this layer and a subsurface layer, where the concentrations of phytoplankton and nutrient are fixed (P_{sub} and N_{sub}). The vertical fluxes between the two layers are assumed to result from physical processes occurring at two different scales: a large scale wind-driven upwelling and up and down-wellings associated with mesoscale turbulence. The permanent upwelling is represented by a constant positive vertical velocity w that drives a vertical input of nutrient $+w N_{\text{sub}}$. The effects of mesoscale turbulence are incorporated in the form of a large-scale flux which represents the cumulated action of small scale filaments over several months and several hundreds of kilometers. This mesoscale vertical flux is applied at the base of the euphotic layer and takes the form $-\alpha(C - C_{\text{sub}})$, where C can be either N or P and where α represents the strength of the vertical turbulence. In this study, we examine the model solutions when α varies. To facilitate the analytical calculations, we make the assumptions that $P_{\text{sub}} \ll P$ and $N_{\text{sub}} \gg N$. The assumption $P_{\text{sub}} \ll P$ is reasonable and not restrictive since phytoplankton does not survive for very long below the euphotic layer. The second assumption $N_{\text{sub}} \gg N$ requires that the surface nutrients are efficiently consumed by photosynthesis. This assumption can be violated in situations where primary production is limited by other factors such as light (which is often the case in winter), or, in specific regions, by iron (Behrenfeld et al., 1996). Note that this assumption also requires that w and α are not too large ($\alpha/H \ll 1 \text{ d}^{-1}$, $w/H \ll 1 \text{ d}^{-1}$), and thus the solutions will not be valid when α or w tends to infinity. The order of magnitude of w and α in the ocean is discussed further. With these assumptions, the vertical eddy fluxes of N and P become $+\alpha N_{\text{sub}}$ and $-\alpha P$, respectively. A vertical flux F at the bottom boundary results in a trend term of F/H in the whole euphotic layer. The biological model includes phytoplankton production (μNP) and loss (mP). A fraction of the loss term is remineralized within the euphotic layer (γmP). The rest ($(1-\gamma)mP$) is exported out of the euphotic layer and remineralized in the deep ocean. Given these choices, the two equations governing the system in the euphotic layer are the following:

$$\frac{dN}{dt} = -\mu NP + \gamma mP + \frac{\alpha + w}{H} N_{\text{sub}} \quad (1)$$

$$\frac{dP}{dt} = \mu NP - mP - \frac{\alpha}{H} P \quad (2)$$

The equilibrium solution (N_e , P_e) satisfies:

$$-\mu N_e P_e + \gamma m P_e - \frac{\alpha + w}{H} N_{sub} = 0 \quad (3)$$

$$\mu N_e P_e - m P_e - \frac{\alpha}{H} P_e = 0 \quad (4)$$

which leads to :

$$N_e = \frac{\alpha + mH}{H\mu} \quad (5)$$

$$P_e = \frac{\alpha + w}{\alpha + w_c} N_{sub} \quad (6) \text{ with } w_c = \frac{1}{\gamma} - mH \quad (7)$$

In the following, we assume that the model parameters (H , w , m , μ , γ) do not depend on the strength of the mesoscale turbulence α . The relevance of this assumption is discussed later. The sensitivity of phytoplankton concentration to α is given by:

$$\frac{dP_e}{d\alpha} = \frac{w_c - w}{(\alpha + w_c)^2} N_{sub} \quad (8)$$

Hence, the sign of $dP_e/d\alpha$ is that of $w_c - w$.

Two regimes emerge depending on the value of w (Fig. 1b):

- A regime of weak upwelling: ($w < w_c$): $dP_e/d\alpha$ is positive, which means that phytoplankton concentration is increased by mesoscale activity. Eddy-induced nutrient inputs are more efficient than eddy-induced export of phytoplankton.
- A regime of strong upwelling ($w > w_c$): $dP_e/d\alpha$ is negative. The result is a reduction of the phytoplankton content in the euphotic layer when eddy activity intensifies. The export of phytoplankton prevails.

The typical values of the model parameters are summarized in Table 1. The euphotic layer depth is close to 100m under oligotrophic conditions, and to 20m in coastal upwelling regions. The recycling parameter γ is equivalent to $(1 - f\text{-ratio})$ and typically varies between 0.9 in oligotrophic conditions to 0.5 in more eutrophic conditions (Eppley and Peterson, 1979). Typical values for phytoplankton loss rates are 0.1 to 0.3 d^{-1} (Fasham et al., 1990; Mitchell et al., 1991). This gives for w_c values ranging from 1-3 $m \cdot d^{-1}$ in both the open ocean oligotrophic gyres and in coastal upwelling

1 zones. Given the typical values of w , which are slightly negative in the center of oligotrophic gyres
 2 (-0.01 to -0.2 m d⁻¹, Marshall et al., 1993) and of the order of 5 to 20 m.d⁻¹ in upwelling regions
 3 (Marchesiello and Estrade, 2010). The condition $w < w_c$ is satisfied in the center of oligotrophic
 4 gyres, while the condition $w > w_c$ is satisfied in regions of permanent large-scale upwellings.
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10 The parameter α is highly variable in space and time, as is the intensity of mesoscale activity in the
 11 ocean (Stammer, 1997). Typical values of α were estimated in a high-resolution model by Levy et
 12 al. (2010), as the annual-mean root-mean-square of the vertical velocity at the depth of the euphotic
 13 layer. In Levy et al. (2010), α ranged from 5-10 m/d in very energetic regions such as close to
 14 western boundary currents, to 1-2 m/d in more quiescent regions and in upwelling regions. This
 15 value of α in upwelling regions is also consistent with an independent estimate based on the ratio of
 16 phytoplankton concentration to the phytoplankton vertical eddy flux in a model of a coastal
 17 upwelling region (Lathuilière et al., 2010). Considering an averaged euphotic layer depth H of
 18 100m and a shallow mixed-layer, the conditions $\alpha/H \ll 1$ d⁻¹ and $w/H \ll 1$ d⁻¹ are thus generally
 19 satisfied in the ocean at the euphotic depth.
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30 The scaling obtained with this simple analytical model thus enables us to rationalize the results
 31 obtained in previous studies with 3D ocean circulation models, that phytoplankton concentration is
 32 enhanced by mesoscale turbulence in oligotrophic gyres and is decreased in coastal upwelling
 33 regions.
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39 Note that w is supposed to be positive in the formulation of Eqs (1) and (2). In the case of negative
 40 w (oligotrophic gyres), another equation system can be written and leads to the same conclusion as
 41 in the positive- w set of equations (where we assumed $w=0$ in the case of oligotrophic gyres). Indeed
 42 for negative- w s, the large-scale nutrient input ($w/H.N_{sub}$) in the nutrient equation (eq. 1) is replaced
 43 by a large-scale phytoplankton export ($w/H.P$) in the phytoplankton equation (eq. 2), which simply
 44 acts as an additional mortality term. The equilibrium concentrations for negative w thus become :
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$$51 \quad N_e = \frac{\alpha - w + mH}{H\mu} \quad (9)$$

$$52 \quad P_e = \frac{\alpha}{w_c + \alpha - w} N_{sub} \quad (10)$$

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 55 With this system of equations, valid only in the case of the center of oligotrophic gyres, $dP_e/d\alpha$ is
 56 always positive.
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4 There are however caveats to this simple model. The strongest underlying hypothesis is that the
5 model parameters do not depend on the strength of mesoscale activity. Large scale upwellings are
6 primarily driven by wind and by thermohaline processes. In particular, the location and intensity of
7 coastal upwellings are driven by wind stress. However, the large-scale circulation is also affected
8 by the cumulated effects of oceanic turbulence (Lévy et al., 2010) and this feedback on the mean
9 dynamical fields is not accounted for here. In particular, the vertical velocity at the base of the
10 euphotic layer, w , may be modified by the change in mean thermocline depth and shape near the
11 shore due to the effect of turbulence (Gruber et al., 2006). Moreover, since phytoplankton
12 distribution shows strong variability at the mesoscale, so does the depth of the euphotic layer H .
13 Finally, the physiological parameters (m , μ and γ) are also expected to vary, as the phytoplankton
14 community may evolve in response to varying levels of nutrient inputs and vertical velocity.
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25 Another over-simplification is the disregard of horizontal dynamics. Our model is thus not strictly
26 valid in areas where the lateral supply in nutrient is important. This is in particular the case in the
27 inter-gyre regions of the open ocean where a significant nutrient flux from the polar gyre fertilizes
28 the boundary of the subtropical gyre (Oschlies, 2002). In the case of coastal upwelling, our model
29 applies to a domain that has to be large enough to encompass the coastal zone, where upwelling
30 occurs, and its offshore extension, which is fed by lateral exchanges originating from the coast. In
31 such extended coastal areas, lateral fluxes become negligible (Lathuilière et al., 2010).
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39 The critical value of upwelling found in this study depends on the physiological parameters of
40 ecosystem m and γ . Clearly, the ecosystem model used here is extremely simple. It includes only
41 one inorganic nutrient and one form of organic matter export and does not account for the diversity
42 of the possible sources of nutrients and of export. Moreover, the export and loss terms are assumed
43 to be constant rates, while in reality they are strongly modulated by the presence and physiology of
44 zooplankton which is only implicitly accounted for in our model through these constant rates.
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51 The critical value of upwelling was obtained by examining the model solution at equilibrium. With
52 this approach, we examined the response of the ecosystem to a given level of mesoscale turbulence,
53 over a period of time long enough for the ecosystem to equilibrate, i. e. at the seasonal time scale or
54 above. The method does not apply to examine the response of the ecosystem to an episodic event,
55 such as the passage of one eddy.
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This approach can nevertheless be applied to other situations. It provides insights into the sensitivity

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2 of an ecosystem to a process of variable intensity in competition with a constant process. The
3 variable parameter may be the stratification between the surface layer and the interior of the ocean.
4 In that case, the eddy-induced vertical exchanges $-\alpha(C-C_{\text{sub}})$ would be replaced by a stratification-
5 dependent vertical diffusion $-K/N^2(C-C_{\text{sub}})$ (with N^2 the Brunt-Väisala frequency), such that vertical
6 exchanges are inhibited by enhanced stratification. An estimate of $K/N^2/H$ can be deduced from the
7 vertical nitrate flux (0.002-0.9 mmolN/m²/d, Lewis et al., 1986) assuming that $N_{\text{sub}}-N$ ranges
8 between 5 and 20 molNm⁻³ : 10^{-4} - $2 \cdot 10^{-1}$ d⁻¹. This range is similar to the one of α/H . An increase in
9 stratification is expected to occur in response to climate warming. The simple model presented here
10 suggests that this increase is likely to reduce phytoplankton abundance, as indicated by the decadal
11 changes in phytoplankton monitored from space (Berhenfield et al., 2006), except in regions of
12 strong upwelling. The constant process could be river discharges. In that case, our model predicts
13 that phytoplankton abundance should decrease in presence of mesoscale dynamics in cases of large
14 river discharges.
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27 In conclusion, this study presents a simple model of phytoplankton sensitivity to mesoscale and
28 sub-mesoscale vertical dynamics in the presence of a constant large-scale nutrient upwelling. Two
29 regimes are distinguished depending on the strength of the large-scale upwelling. In weak upwelling
30 conditions, such as generally in the open ocean, phytoplankton abundance increases in phase with
31 the intensity of mesoscale turbulence. In contrast, when the upwelling is stronger than a critical
32 value w_c , phytoplankton abundance decreased due to the intensification of mesoscale turbulence. In
33 this case, the governing process is the downward export of phytoplankton below the euphotic layer.
34 The critical value w_c depends on physiological parameters of the ecosystem model and on the
35 thickness of the euphotic layer. In high-resolution ocean circulation models, a common way to vary
36 the intensity of vertical mesoscale dynamics is to change the horizontal grid resolution: higher
37 resolution permits the emergence of higher frequency processes, which are often associated with
38 higher vertical velocities. In the coming decade, global bio-physical simulations will have sufficient
39 resolution to enable the emergence of mesoscale dynamics. The comparison of these simulations
40 with lower resolution simulations will provide a complementary view of the sensitivity of
41 phytoplankton abundance to mesoscale intensity, which will enable modifications of the mean state
42 of the dynamics and of the ecosystem by mesoscale turbulence to be explored.
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Fig. 1a) Scheme of the analytical box model
Fig. 1b) Schematic synthesis of the two regimes

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Tab. 1) model parameters and rough estimates

parameter			Rough estimate	References
Symb.	name	unit		
μ	Phytoplankton growth rate	$\text{d}^{-1} \cdot \text{mmolN}^{-1}$	0.1-1	Aumont and Bopp (2006)
m	Phytoplankton loss rate	d^{-1}	0.1-0.3	Fasham et al. (1990) Mitchell et al. (1991)
γ	Recycling parameter	-	0.5 – 0.9	Eppley and Peterson (1979)
H	Euphotic depth	m	20-100	Morel (1988)
w	Upwelling velocity	$\text{m} \cdot \text{d}^{-1}$	0-20	Marchesiello and Estrade (2010)
α	Mesoscale-induced vertical fluxes strength	$\text{m} \cdot \text{d}^{-1}$	0-5	Lévy et al. (2010)
w_c	Critical upwelling velocity	$\text{m} \cdot \text{d}^{-1}$	1-2	-

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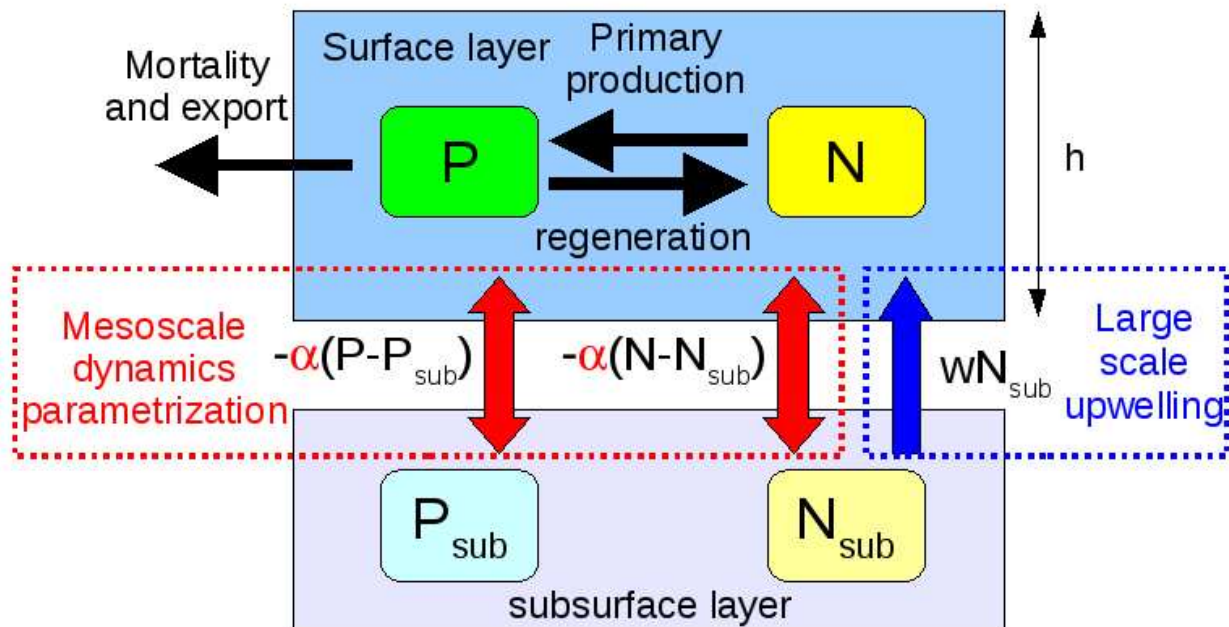


Fig. 1a) Scheme of the analytical box model

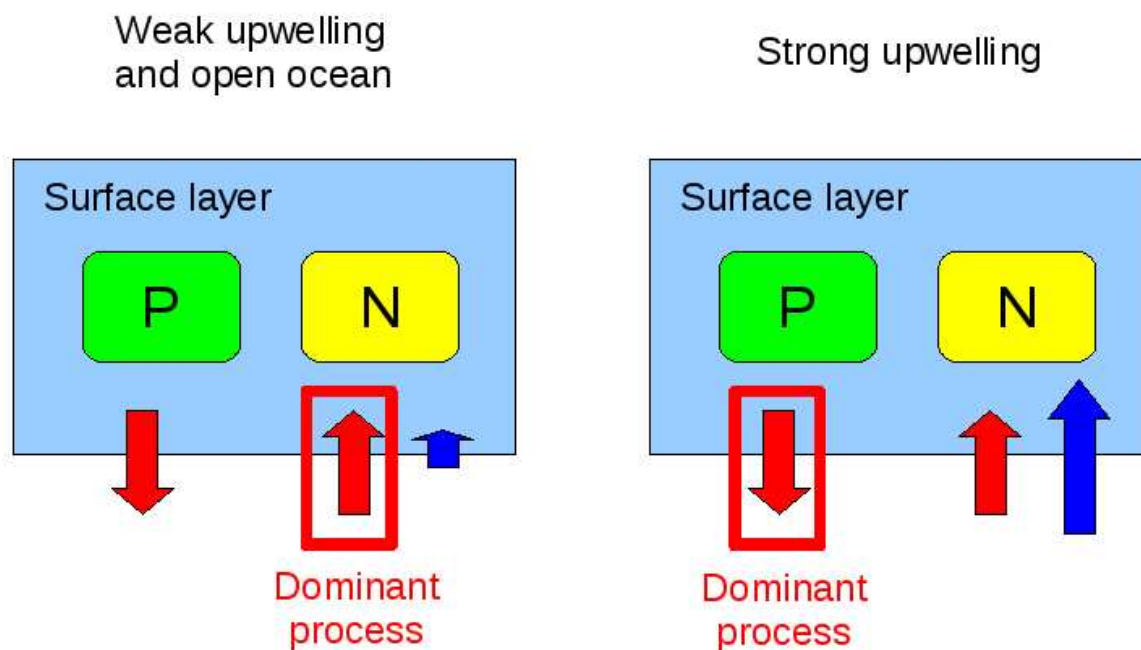


Fig. 1b) schematic synthesis of the two regimes