



Response of biological production and air–sea CO₂ fluxes to upwelling intensification in the California and Canary Current Systems

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ABSTRACT

Upwelling-favorable winds have increased in most Eastern Boundary Upwelling Systems (EBUS) in the last decades, and it is likely that they increase further in response to global climate change. Here, we explore the response of biological production and air–sea CO₂ fluxes to upwelling intensification in two of the four major EBUS, namely the California Current System (California CS) and Canary Current System (Canary CS). To this end, we use eddy-resolving regional ocean models on the basis of the Regional Oceanic Modeling System (ROMS) to which we have coupled a NPZD-type ecosystem model and a biogeochemistry module describing the carbon cycle and subject these model configurations to an idealized increase in the wind stress. We find that a doubling of the wind-stress doubles net primary production (NPP) in the southern California CS and central and northern Canary CS, while it leads to an increase of less than 50% in the central and northern California CS as well as in the southern Canary CS. This differential response is a result of i) different nutrient limitation states with higher sensitivity to upwelling intensification in regions where nutrient limitation is stronger and ii) more efficient nutrient assimilation by biology in the Canary CS relative to the California CS because of a faster nutrient-replete growth rate and longer nearshore water residence times. In the regions where production increases commensurably with upwelling intensification, the enhanced net biological uptake of CO₂ compensates the increase in upwelling driven CO₂ outgassing, resulting in only a small change in the biological pump efficiency and hence in a small sensitivity of air–sea CO₂ fluxes to upwelling intensification. In contrast, in the central California CS as well as in the southern Canary CS around Cape Blanc, the reduced biological efficiency enhances the CO₂ outgassing and leads to a substantial sensitivity of the air–sea CO₂ fluxes to upwelling intensification.

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1. Introduction

Equatorward winds along the eastern boundaries of the Atlantic and Pacific induce offshore surface Ekman transport and the upwelling of nutrient-rich water into the euphotic zone, thereby stimulating high phytoplankton growth and leading to some of the most productive marine ecosystems in the world (Carr, 2001; Carr and Kearns, 2003; FAO, 2009; Pauly and Christensen, 1995). The high planktonic productivity in Eastern Boundary Upwelling Systems (EBUS) supports a large net fixation and subsequent export of organic carbon, which compensates the upwelling of CO₂-rich water (Muller-Karger et al., 2005). This tends to make these systems much smaller sources of CO₂ to the atmosphere than expected on the basis of their upwelling (Chavez and Takahashi, 2007). These air–sea CO₂ fluxes are highly variable in space and time, reflecting the high variability in the coastal upwelling and the strong modulation of the air–sea CO₂ exchange by biology, temperature, and the lateral carbon fluxes (Aristegui et al., 2004; Cai et al., 2006; Hales et al., 2005). Overall, upwelling systems located in the mid to high

latitudes tend to be overall small sinks with seasonally reversing air–sea CO₂ fluxes (Borges and Frankignoulle, 2002; Hales et al., 2005), whereas those in the low latitudes tend to be a net source of CO₂ to the atmosphere because of a more intense and permanent upwelling (e.g., Lefèvre et al. (2002)).

While supporting extremely rich ecosystems, EBUS are vulnerable to various anthropogenic perturbations, such as upper ocean warming (Di Lorenzo et al., 2005; Roemmich and McGowan, 1995), ocean acidification (Feely et al., 2008; Gruber et al., submitted for publication; Hauri et al., 2009), ocean deoxygenation (Bograd et al., 2008), and their possible interactive effects (Gruber, 2011). A particularly important perturbation is the increase in upwelling favorable wind (Bakun, 1990), for which there is mounting evidence that it has occurred already over the 20th century in several EBUS (Gutiérrez et al., 2011; Leduc et al., 2010; McGregor et al., 2007; Mendelssohn and Schwing, 2002; Schwing and Mendelssohn, 1997; Shannon et al., 1992). This strengthening of the wind forcing has been related to a global warming-induced increase in the land–sea thermal gradient (Bakun, 1990), and is therefore projected to increase further in the future (Diffenbaugh et al., 2004; Snyder et al., 2003). Yet, the effects of this physical perturbation on marine ecosystems in EBUS are neither well understood nor well quantified. In particular, the question of how biological production

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and air–sea CO₂ fluxes in these systems might respond to such enhanced wind forcing has not been addressed yet, but is the main subject of this paper.

While the high production in EBUS is driven to first order by the upwelling of nutrient-rich water to the surface (Allen, 1973; Brink, 1983), only about half of the variations in net primary production (NPP) across all EBUS can be explained by differences in upwelling favorable winds (Carr, 2001; Carr and Kearns, 2003; Gruber et al., 2011; Lachkar and Gruber, 2012; Thomas et al., 2001). Moreover, recent observed changes in primary production show at best a moderate correlation with changes in wind (Demarcq, 2009; Kahru et al., 2009), suggesting different sensitivities of production to upwelling changes in the different EBUS. Hence, a better understanding of what controls this sensitivity of production to upwelling favorable wind change is needed for predicting potential future productivity changes and the impacts this has on the air–sea exchange of CO₂. This will also be needed in order to better evaluate future changes in ocean acidification and ocean deoxygenation.

We will show that bottom-up limitation factors such as light and temperature, as well as the water residence time in the nearshore region modulate the biological response to wind increase in EBUS. We will also demonstrate how these changes in production exert a major control on the sensitivity of the net air–sea CO₂ fluxes to upwelling changes in EBUS. Of particular relevance is the change in the efficiency of the biological pump, i.e., the relative balance between the nutrients and carbon that are transported and mixed upward into the euphotic zone and the nutrients and carbon that are fixed into organic matter and exported downward again (Sarmiento and Gruber, 2006). An efficient biological pump tends to cause uptake of CO₂ from the atmosphere, while an inefficient pump tends to lead to strong outgassing (Gruber and Sarmiento, 2002). We will show that those regions whose primary and export production increase commensurably with the upwelling maintain their biological pump efficiency and hence experience little change in their net air–sea CO₂ balance. In contrast, the regions where primary and export production increase less strongly turn into substantial sources of CO₂ for the atmosphere as a result of their decreased pump efficiency.

To arrive at these results, we undertook a comparative modeling study contrasting two of the four major EBUS, namely the California Current System (California CS) and the Canary Current System (Canary CS). The comparison of these two upwelling systems provides a framework for developing a better understanding of the underlying dynamics of EBUS ecosystems in general. Moreover, the comparative modeling approach provides a means to investigate how a single model produces a range of ecological and biogeochemical responses under slightly different external forcings. Using a series of eddy-resolving simulations of the California CS and the Canary CS under different wind forcing scenarios, this study identifies the potential response of biological production and air–sea CO₂ fluxes to upwelling intensification in EBUS and quantifies the key governing processes that determine the magnitude of this response.

2. Methods

We employ here the same model setups for the California and Canary Current Systems as described by Lachkar and Gruber (2011), but augmented with an interactive carbon cycle module. These two model setups are based on the UCLA-ETH version of the Regional Ocean Modeling System (ROMS) (Shchepetkin and McWilliams, 2005) and build on previous versions (e.g. Gruber et al., 2006; Marchesiello et al., 2003). Both model grids have a horizontal resolution of 5 km and 32 vertical levels with surface refinement.

The ecological–biogeochemical model is a nitrogen-based NPZD model (Gruber et al., 2006) with a single phytoplankton functional group, parameterized to represent a diatom-like group. Previous studies have shown that when addressing one type of ecosystems (e.g., EBUS in this study), NPZD-type models can be as successful as multiple functional group models for reproducing bulk ecosystem properties such as

chlorophyll and primary production (Friedrichs and Hofmann, 2001; Friedrichs et al., 2007). Detritus is split into two pools: a large one that sinks fast, and a small one that sinks slowly, i.e., that behaves similar to dissolved organic matter. The model considers a dynamic phytoplankton chlorophyll-to-carbon ratio (θ) which mimics photoacclimation in phytoplankton (Falkowski and Raven, 1997). The chlorophyll-to-carbon ratio depends on irradiance, nutrient availability and temperature following the model of Geider et al. (1997). It is highest under high temperature, low irradiance and nutrient replete conditions and lowest at high irradiance, low temperature and under nutrient-limiting conditions. This down regulation in θ occurs as the rate of the photosynthetic energy supply from light absorption exceeds the capacity to assimilate photosynthate for growth.

Net primary production (NPP) is limited in our model by the amount of photosynthetically available radiation (PAR), I , the concentrations of nitrate, N_n , and ammonium, N_r , temperature, T , chlorophyll-to-carbon ratio, (θ), and phytoplankton biomass, P , in the following manner:

$$\text{NPP} = \gamma(N_n, N_r) \cdot \mu_p^{\max}(T, I, \theta) \cdot P \quad (1)$$

where $\gamma(N_n, N_r)$ is a non-dimensional nutrient limitation factor and $\mu_p^{\max}(T, I, \theta)$ is the temperature-dependent, light-limited growth rate under nutrient replete conditions. The nutrient limitation factor $\gamma(N_n, N_r) \leq 1$, is parameterized using the Michaelis–Menten equation, taking into account that ammonium is taken up preferentially over nitrate, and that its presence inhibits the uptake of nitrate by phytoplankton (Wroblewski, 1977). The maximum nutrient limitation corresponds to $\gamma(N_n, N_r) = 0$ while nutrient-unlimited growth is indicated by $\gamma(N_n, N_r) = 1$. We use an additive function weighted toward ammonium:

$$\gamma(N_n, N_r) = \frac{\gamma(N_n) + \gamma(N_r)}{\frac{N_n}{K_{N_n} + N_n} + \frac{N_r}{K_{N_r} + N_r}} \quad (2)$$

where K_{N_n} and K_{N_r} are the half-saturation constants for phytoplankton uptake of nitrate and ammonium, respectively. The temperature-dependent, light-limited growth rate is given by:

$$\mu_p^{\max}(T, I) = \frac{\mu_p^T(T) \cdot \alpha_p \cdot I \cdot \theta}{\sqrt{(\mu_p^T(T))^2 + (\alpha_p \cdot I \cdot \theta)^2}} \quad (3)$$

Table 1

Rates of phytoplankton biological sources and sinks (in day⁻¹) under modern and increased winds in the California CS. Data are averaged vertically over the euphotic zone and horizontally over the 300 km wide nearshore area.

Wind forcing	Growth rate	Grazing loss	Mortality	Coagulation	Net growth
Modern wind (control)	0.21	0.1	0.024	0.01	0.08
Wind stress × 1.5	0.25	0.13	0.024	0.01	0.1
Wind stress × 2	0.28	0.14	0.024	0.01	0.11

Table 2

Rates of phytoplankton biological sources and sinks (in day⁻¹) under modern and increased winds in the Canary CS. Data are averaged vertically over the euphotic zone and horizontally over the 300 km wide nearshore area.

Wind forcing	Growth rate	Grazing loss	Mortality	Coagulation	Net growth
Modern wind (control)	0.21	0.11	0.024	0.01	0.07
Wind stress × 1.5	0.24	0.12	0.024	0.01	0.09
Wind stress × 2	0.3	0.15	0.024	0.01	0.13

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