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The influence of diurnal winds on phytoplankton dynamics in a coastal upwelling system off southwestern Africa

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ABSTRACT

At a coastal upwelling zone near 30°S latitude, diurnal wind variability forced energetic inertial current oscillations ($>0.5\ \mathrm{m\ s^{-1}}$) that materially influenced phytoplankton distribution and productivity. The diurnal–inertial band resonance found at this latitude in the Benguela upwelling system allowed rapid, efficient transfer of energy from counterclockwise rotating winds into anticyclonic currents upon the onset of the transition from relaxation to upwelling conditions. These inertial band oscillations caused regular pycnocline outcropping at the surface and the vertical advection of nutrient-rich waters in the coastal zone. Vertical pycnocline outcropping was coincident with the vertical redistribution of chlorophyll *a* fluorescence from a subsurface maximum to entrainment into the surface mixed layer, in effect turning vertical phytoplankton gradients into horizontal ones. The shear caused by the vertical structure of the inertial oscillations during (and after) the onset of wind forcing was intense enough to erode the strong stratification established during a prior relaxation period, according to Richardson number and strain analyses. This diapycnal mixing also had the consequence of mixing heat and chlorophyll downwards and nutrient-rich water upwards, such that the surface nitrate concentration became non-zero. Chlorophyll concentrations thereafter increased in what qualitatively appeared to be a phytoplankton bloom. This diurnal–inertial resonance-driven mechanism for mixing-driven nutrient flux, embedded within the low-frequency advective vertical flux forced by Ekman dynamics, enhanced the efficiency of wind forcing to produce high phytoplankton productivity, and is likely to be of first-order importance in bloom dynamics in the study area (including harmful algal blooms). Our results argue that, in general, high-frequency physical dynamics should be considered when studying the bottom-up forcing of algal blooms and red tide events.

1. Introduction

The classic upwelling-relaxation paradigm describes temporal variability in wind forcing, coastal currents, and the response in the phytoplankton community induced by the alleviation of nutrient limitation and the reduction in advective loss (Roughan et al., 2006). Phytoplankton growth rate and community response are embedded within a forcing regime that leads to reversing transport in the surface waters on the timescale of days. In this manner, nutrients are brought to the surface during upwelling, enhancing phytoplankton productivity, while the resulting high biomass phytoplankton assemblages later advect onshore during poleward winds. In some upwelling regimes, including the waters off the west coast of South Africa, these high biomass phytoplankton blooms can include toxigenic harmful algal bloom (HAB) species or contribute to local anoxia and subsequent macrofaunal mortality (Pitcher et al., 2010; Pitcher and Probyn, 2011).

Wind-driven coastal regimes are subject to forcing across a range of temporal and spatial scales. The high-frequency component of wind variability is often assumed to be of less biological significance than variability on subinertial timescales. However, diurnal (sea-breeze) variability, common in coastal upwelling zones (Gille et al., 2003, 2005; Hyder et al., 2011), can drive large temperature and chlorophyll *a* fluorescence fluctuations (Kaplan et al., 2003), and has the potential to force significant alongshore and cross-shore transport. Furthermore, the classic upwelling paradigm invokes an advective and therefore reversible process. However, it is clear that irreversible diapycnal mixing must occur during upwelling to account for the rapid response of phytoplankton communities to upwelling-mediated nutrient flux, given the very low biomass of nutrient-rich sub-thermocline waters (Kudela et al., 2006). Such diapycnal mixing acts to redistribute

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nutrient fluxes in such a way that they would remain available for phytoplankton in the euphotic zone even after the cessation of upwelling favorable winds. The diapycnal mixing pathways in upwelling systems are at present not completely understood, but likely involve physical dynamics at higher frequencies and smaller spatial scales than those invoked to describe wind-forced Ekman upwelling.

These facts suggest that the understanding of upwelling-driven phytoplankton productivity and relaxation-mediated transport pathways may be expanded by a consideration of the contribution of the high-frequency component of the physical forcing. The following manuscript describes high-resolution observations collected by wave-powered profiling vehicles during transitions from downwelling to upwelling conditions in the wind-forced regime off the west coast of South Africa, within the Benguela Current System. These observations of the physical and biological water column variability – including temperature, salinity, density, dissolved oxygen, chlorophyll *a* concentration, and currents – indicate that wind-forced current variability on diurnal frequencies plays a fundamental role in both nutrient fluxes to the euphotic zone and phytoplankton dynamics across the shelf.

1.1. Wind-forced upwelling

In the classic, two-dimensional view of coastal upwelling, equatorward alongshore wind stress drives offshore surface transport due to the influence of the rotation of the earth. The coastal boundary and continuity require that this offshore transport be balanced by onshore transport at depth and vertical transport at the boundary. More recently it has been demonstrated that the three-dimensional upwelling and relaxation process leads to significant departures from the assumption of classic Ekman dynamics, including significant along- and cross-shore transport (e.g. Washburn et al., 2011). Other studies have shown the importance of the cross-shore component of the wind stress on cross-shore currents (Dorman et al., 2006; Fewings et al., 2008; Wang et al., 2011), and the existence of dynamically important ageostrophic submesoscale frontal processes (Capet et al., 2008a, 2008b; Ryan et al., 2010).

1.2. Phytoplankton response

Phytoplankton community structure is strongly influenced by temporal variability in nutrient fluxes, transport, and light availability. In a broad sense, phytoplankton communities during active upwelling are typically dominated by large phytoplankters such as diatoms with high affinities for nitrate and silicate (Kudela and Dugdale, 2000; Wilkerson et al., 2006). At some lag after upwelling-driven nutrient injection, particularly in the case of relaxing or reversing winds that favor stratification, the phytoplankton community may be dominated by motile organisms such as dinoflagellates that specialize in recycled nutrients (Seeyave et al., 2009; Kudela et al., 2010). Less is known about the horizontal gradients in phytoplankton communities during upwelling and transitional events. It is clear that strong horizontal gradients in physical variables are common in upwelling systems, and that those gradients are often reflected in surface chlorophyll concentrations as seen synoptically from satellite ocean color sensors (Kudela et al., 2006). These chlorophyll and biomass gradients are often coincident with community composition changes (Pitcher et al., 1991).

1.3. High-frequency variability in wind-forced upwelling systems

Inertial currents, which are energetic throughout the world's oceans, are circular, oscillatory motions resulting from a balance between radial and geostrophic accelerations (Simpson et al., 2002). Such motions are strongest in the presence of periodic forcing that is resonant with the local inertial frequency (Craig, 1989; Simpson et al., 2002; Orlić and Pasarić, 2011; Hyder et al., 2011). In the case of horizontally uniform forcing, inertial currents are slab-like oscillations with no horizontal variability. In the vicinity of the coast, however, the behavior of inertial currents changes significantly. Simpson et al. (2002), following Craig (1989), showed that the presence of a coastal boundary drives a cross-shore sea surface height gradient, even in the case of a simple, two layer, frictionless, one-dimensional model. This cross-shore sea surface slope is driven both by the cross-shore wind directly and by a geostrophic adjustment to the alongshore winds. The resulting pressure gradient force acts at all depths across both layers, while the wind forcing only acts on the surface layer. The result is cross-shore flow with a 180° phase shift at the interface between the layers.

More recent theoretical studies have explored the detailed contribution inertial and higher frequency components of wind variability to coastal systems (e.g. Sherman, 2005; Orlić and Pasarić, 2011; Hyder et al., 2011). In a simple analytical model, Orlić and Pasarić (2011) showed that analytical solutions to simplified equations of motion in a two-layer system bounded by the coast and subject to periodic, rotating winds describe strong pycnocline oscillations for both subinertial and super-inertial wind forcing. In the subinertial case, the alongshore wind drives most of the pycnocline variability, as is the case in classic Ekman dynamics. In the super-inertial case, the cross-shore component of the wind contributes most to pycnocline oscillations. Pycnocline variability is strongest where the diurnal and inertial frequencies are resonant, but only if the rotation of the wind variability is in the same sense (counterclockwise-rotating winds and counterclockwise rotating inertial currents, in the case of the Southern Hemisphere). These analytical solutions suggest that pycnocline oscillations, which may drive biologically relevant vertical fluxes of nutrients and impact the light climate of phytoplankton, should be energetic in areas close to the critical latitude subject to diurnally variable wind forcing.

1.4. Study area

The waters off the west coast of Southern Africa are dominated by a large and intense upwelling regime (the Benguela upwelling system). Stretching from ~34°S to ~20°S, this relatively low-latitude upwelling system drives extremely high biological productivity across the entire range of oceanic trophic levels. In the southern Benguela three upwelling centers are distinguished all of which coincide with a narrowing of the shelf: the Cape Peninsula (34°S), Cape Columbine (33°S) and the Namaqua (30°S) upwelling cells. This study was located in the St. Helena Bay region in the lee of Cape Columbine (Fig. 1). Here seasonal stratification is maintained by the advection of cold upwelled water onto the shelf and by sun-warming of the surface layer, and functions together with the retentive properties of the Bay to enhance productivity (Weeks et al., 2006; Pitcher and Weeks, 2006). These conditions are conducive to the development of high biomass events and red tides that typically impact the coastline of St. Helena Bay during periods of wind relaxation or reversal, and cause major fisheries impact through anoxia and related mortality events in the coastal rock lobster population and through toxin accumulation in shellfish (Pitcher and Weeks 2006; Pitcher and Nelson, 2006; Pitcher et al., 2008).