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Submesoscale hotspots of productivity and respiration: Insights from high-resolution oxygen and fluorescence sections

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ABSTRACT

Modeling studies have shown that mesoscale and submesoscale processes can stimulate phytoplankton productivity and export production. Here, we present observations from an undulating, towed Video Plankton Recorder (VPR-II) in the tropical Atlantic. The VPR-II collected profiles of oxygen, fluorescence, temperature and salinity in the upper 140 m of the water column at a spatial resolution of 1 m in the vertical and < 2 km in the horizontal. The data reveal remarkable "hotspots", i.e. locations 5–10 km wide which have elevated fluorescence and decreased oxygen, both of which are likely the result of intense submesoscale upwelling. Based on estimates of source water, estimated from identical temperature and salinity surfaces, hotspots are more often areas of net respiration than areas of net production — although the inferred changes in oxygen are subject to uncertainty in the determination of the source of the upwelled waters since the true source water may not have been sampled. We discuss the spatial distribution of these hotspots and present a conceptual model outlining their possible generation and decline. Simultaneous measurements of O₂/Ar in the mixed layer from a shipboard mass spectrometer provide estimates of rates of surface net community production. We find that the subsurface biological hotspots are often expressed as an increase in mixed layer rates of net community production. Overall, the large number of these hotspots support the growing evidence that submesoscale processes are important drivers in upper ocean biological production.

1. Introduction

The mechanisms responsible for seasonal accumulation of oxygen within the euphotic zone in the oligotrophic waters of the open ocean (Jenkins and Goldman, 1985; Shulenberg and Reid, 1981) remain enigmatic. Both observations and models have suggested that episodic processes such as eddies and fronts play a role in providing nutrients to fuel upper ocean productivity (Falkowski et al., 1991; Klein and Lapeyre, 2009; Lévy et al., 2001; Mahadevan and Archer, 2000; McGillicuddy, 2016; McGillicuddy et al., 2007; Oschlies, 2002) and to increase carbon export (Omand et al., 2015). In particular, numerical studies have shown that episodic upwelling, associated with submesoscale fronts (Klein and Lapeyre, 2009; Lévy et al., 2001), may be able to provide nutrients required for phytoplankton growth (Lévy et al., 2012a, 2012b) and consequently may result in patches of biological production (Brody et al., 2016; Mahadevan, 2016; Resplandy et al., 2012).

Observational work has illustrated submesoscale variations in many of the parameters associated with biological production (i.e.

fluorescence, community structure, etc.), though studies of direct variations in rates of production are much fewer. In particular, filamentous patterns in chlorophyll encircling an eddy have been observed from remote sensing that mimic patterns in sea surface temp and align with sea surface altimetry (Calil and Richards, 2010). Spectral analysis of high resolution chlorophyll data has usually shown more variability in chlorophyll than in temperature (Hodges and Rudnick, 2006; Mahadevan and Campbell, 2002). While chlorophyll is one of the best studied parameters, perhaps because of its detectability with remote sensing, high resolution sampling of other biologically relevant variables has occurred. For example, a high resolution spatial survey based on fast rate repetition fluorometry showed intensified phytoplankton activity near fronts (Guidi et al., 2012). Patchiness has also been shown in community structure through high resolution flow cytometry studies (Martin et al., 2005, 2008, 2010). Additionally, rates of net community production and export production have been measured on the submesoscale through O₂/Ar ratios and high resolution ²³⁴Th (Estapa et al., 2015).

New observational approaches using autonomous profiling floats

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and gliders have provided insight into the biogeochemical dynamics of episodic processes (Johnson et al., 2010; Mahadevan et al., 2012; Nicholson et al., 2008), but thus far the space-time coverage of such deployments has not been sufficient to fully characterize these phenomena. Here we utilize towed undulating instrumentation to obtain synoptic cross-sections of physical and biogeochemical properties in the upper ocean. These data provide a detailed view into the structure of mesoscale and submesoscale fluctuations in fluorescence and oxygen, from which inferences can be made about net community production (NCP).

Both towed vehicles and gliders are extremely useful for gaining information on the mesoscale and submesoscale (Rudnick, 2016). It is important to note, however, that towed vehicles can resolve much shorter temporal and smaller spatial scales than gliders, owing to the greater speed at which they move through the water (Rudnick and Cole, 2011). In particular, instrumentation can be towed an order of magnitude faster than gliders and thus offer a “snapshot” of the ocean state which allows them to be used to assess submesoscale spatial variability. For example, in the data presented here, one transect consisting of 438 profiles to 140 m depth and covering 300 km was completed in 19 h. In contrast, in a study by Nicholson et al. (2015), the gliders sampled in a bowtie pattern over a 50 km × 50 km square for 3.5 months and completed 14 profiles to 700 m every 24 h. The slower speed of gliders makes it difficult to separate spatial and temporal variability, with gliders more often being used to assess temporal variability (Damerell et al., 2016; Nicholson et al., 2015) than spatial. Other differences include that gliders can persist in the water for much longer than towed vehicles which allows them to give very useful pictures of temporal evolution. Gliders typically sample deeper in the water column (to 700 or 1000 m) than towed vehicles (140 m in the case of the Video Plankton Recorder II and 500 m in the case of SeaSoar II). Both gliders and towed vehicles can be outfitted with biogeochemical sensors such as those for fluorescence, oxygen, and nitrate, yielding detailed views of variations in net community production (Biddle et al., 2015; Damerell et al., 2016; Nicholson et al., 2015; Pidcock et al., 2010).

Changes in oxygen concentration can be used to quantify rates of photosynthesis and respiration. Photosynthesis produces oxygen and respiration consumes it and thus the net change in oxygen reflects the net amount of photosynthesis and respiration, i.e. NCP. However, oxygen is also affected by physical processes such as mixing and gas exchange, with the saturation state of oxygen being dependent on temperature and to a lesser degree, salinity. In the mixed layer, argon (Ar) is often used as an abiotic analogue for oxygen since it has similar physicochemical characteristics. Thus, the ratio of O₂/Ar (Emerson et al., 1991) or the difference between the saturation states of O₂ and Ar (Craig and Hayward, 1987; Spitzer and Jenkins, 1989), can be used in a steady state model and combined with estimates of diffusive gas exchange to calculate mixed layer NCP (e.g. Hendricks et al., 2004; Juranek and Quay, 2005; Reuer et al., 2007). At depths between the base of the mixed layer and the euphotic zone, a time series of O₂/Ar measurements can be used to calculate NCP. Below the euphotic zone, Ar is not as useful as an analogue for O₂, since Ar profiles with depth are often different than those of O₂; O₂ declines sharply below the euphotic zone due to remineralization, but Ar changes much less. Additionally, Ar is less useful since gas exchange does not directly affect the water below the mixed layer. O₂ concentration alone can be used to quantify rates of net community production if there is some independent “clock” – either a water mass being followed for a certain amount of time (Riser and Johnson, 2008) or a tracer age calculated (Stanley et al., 2012). If there is no clock, as in the case of the data presented here, then exact rates cannot be calculated but the sign of NCP can be inferred by the difference of the O₂ concentration compared to the apparent source waters, i.e. net photosynthesis or net respiration.

In this work, we used the Video Plankton Recorder II (VPR-II), a towed undulating instrument (Davis et al., 2005), to collect profiles of oxygen, fluorescence, temperature and salinity in the upper 140 m of

the subtropical and tropical Atlantic Ocean at roughly 2 km horizontal resolution. In Section 2, we describe the data collection and analysis. In Section 3, we present results showing that hotspots can be seen in the O₂ and fluorescence records. These are regions, usually a few km in width and ten meters or so in depth, that have elevated fluorescence and usually decreased oxygen concentrations compared to the water at the same depth. The decrease in oxygen could be a signature of the source water for these events (i.e. upwelled oxygen debt) or could be a result of increased respiration over photosynthetic production and thus could be reflecting negative NCP. We also present a statistical analysis of the hotspot distribution, including the decorrelation length scales in the vertical and horizontal directions, and a conceptual model of hotspot evolution. We furthermore link the subsurface hotspots to surface expressions of rates of net community production, which tend to be positive in the overlying waters within the mixed layer.

2. Methods

2.1. Cruise description

Data for this research were collected on the R/V *Oceanus* (Voyage #471) in the subtropical and tropical Atlantic (12°N and 32°N and 53°W to 66.5°W, see Fig. 1 for cruise-track) between April 25, 2011 and May 13, 2011. Eddy features were targeted through the use of real-time altimetric data (Leben et al., 2002), supplemented by data from shipboard acoustic Doppler current profiler (ADCP), expendable bathythermographs (XBT) and the VPR-II. Retrospective analysis of the shipboard observations was carried out in the context of Absolute Dynamic Topography (ADT) from AVISO (<http://www.aviso.oceanobs.com>), which is the sum of sea level anomaly (SLA) and mean dynamic topography (Rio et al., 2011). ADT is more appropriate than SLA for defining the eddy field in areas of significant mean currents, insofar as fluctuations in the mean flow can be expressed as mesoscale variations in SLA.

Fifteen VPR-II tows (Fig. 1), most of which were 300–400 km in length, were completed throughout the cruise. The initial and final latitude and longitude of each tow are listed in Supplementary Table S1. Before each VPR-II tow, a conductivity, temperature, depth (CTD) rosette was lowered to allow for collection of water for chemical and biological analysis. Data from the cruise, including all the VPR data, are archived at the biological-chemical oceanography data-management office (BCO-DMO) under project 2104:

<http://www.bco-dmo.org/project/2104>.

2.2. Profiles from the VPR-II

The VPR-II (Davis et al., 2005) undulated between the surface and typically 140 m depth and collected 6–7 profiles of a suite of physical and biogeochemical parameters every 10 km. The average ship speed was 10 knots and the average VPR vertical velocity was 1 m s⁻¹. The horizontal resolution of the VPR-II along the cruise-track was 1.5 km, as measured between the shallowest depth (~5 m) of two adjacent profiles (or 0.75 km if comparing up-cast and down-cast profiles instead of two up-cast profiles). The resolution along the towtrack was centimeters to meters, depending on the response time of the sensors. Data were collected in 1 s averages and then were averaged into 1 m bins to facilitate analysis of the suite of variables on a common grid. Between 30 m and the surface, the VPR-II flew off to the side of the ship in order to avoid the ship's wake (Davis et al., 2005). The VPR-II contained numerous sensors. The Video Plankton Recorder (VPR) itself is an underwater video system that yields a continuous record of plankton and seston abundance and community structure (Davis et al., 2004, 2005; Hu and Davis, 2005). However, the VPR does not yield estimates of phytoplankton biomass because only the larger size classes (e.g. diatoms) are detected in the optical imagery. A CTD gave detailed characterization of the physical properties of temperature, salinity, and thus by extension

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