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Spatial patterns of nitrogen uptake and phytoplankton in the equatorial upwelling zone (110°W–140°W) during 2004 and 2005

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ABSTRACT

The equatorial Pacific plays a central role in the global carbon cycle as the largest oceanic source of CO_2 to the atmosphere. The region has been described as a HNLC (High Nutrient, Low Chlorophyll) region with low chlorophyll being explained by either Fe limitation, $Si(OH)_4$ limitation, or a combination of the two. The autotrophic community in the equatorial upwelling zone (EUZ) is dominated numerically by small cell-sized picoplankton but also contains larger cells, including diatoms that require $Si(OH)_4$ and have been hypothesized to drive NO_3 uptake. The 1-D CoSiNE (Carbon, Silicon, Nitrogen Ecosystem) model was developed for the EUZ to evaluate the potential drivers of the HNLC condition. The model assumes two phytoplankton groups (small non $Si(OH)_4$ users and larger $Si(OH)_4$ requiring cells). Many of its predicted variables have not been measured in the field – specifically, uptake of NO_3, NH_4 and $Si(OH)_4$ by the larger cells versus the smaller picoplankton and biomass values (as particulate nitrogen, PN) of the two size classes. Two cruises to the EUZ were undertaken in December 2004 (EB04) and September 2005 (EB05) to collect these data, in part to test the conceptual basis and functioning of the CoSiNE model. These EUZ cruises were unique in having size-fractionated uptake rates and phytoplankton community composition at the same depths throughout the euphotic zone and at many stations representing a range of environmental conditions and community composition. Here, we report results pertaining to NO_3 and NH_4 uptake, PN, and *f*-ratio by different size fractions of the phytoplankton community collected during zonal (0°Eq and 0.5°N) and meridional surveys at 110°W and 140°W. Larger sized ($>5\ \mu m$) phytoplankton contributed more to NO_3 uptake (up to 85%) than cells $<5\ \mu m$ and so had higher *f*-ratios. Several autotrophic functional groups were likely responsible for NO_3 uptake in the >5-μm size class, including both diatoms and dinoflagellates. The importance of diatoms in NO_3 uptake appears to be variable, with biological "hotspots" around regions of locally enhanced upwelling associated with tropical instability waves (TIWs). In some cases, TIW activity favored diatoms, and $Si(OH)_4$ and NO_3 uptake were elevated strongly during TIW activity. Largely as a result of increased diatom productivity, integrated NO_3 uptake rates during the passage of these waves reached 6.74 mmol $m^{-2}\ d^{-1}$, exceeding the mean values previously reported for the equator by >2-fold. NH_4 concentrations and uptake were also dynamic, with lower values south of the equator and higher values to the north. The major contributors to NH_4 uptake were the smaller ($<5\ \mu m$) phytoplankton that resulted in low total community *f*-ratios of 0.26 over both years. A >2-fold increase in NH_4 uptake rates in 2005 was consistent with the observed roughly 2-fold increase in *Prochlorococcus* biomass. Our results highlight a potential area for improvement to the CoSiNE model, to include the role of autotrophic dinoflagellates.

1. Introduction

The equatorial Pacific plays a central role in the global carbon cycle as the largest oceanic source of CO_2 to the atmosphere (Takahashi et al., 2002; Tans et al., 1990). The new production budget for the region was first calculated by Chavez and Barber (1987) and subsequently demonstrated by a number of investigators using direct measurements by the stable isotopic tracer ^{15}N (e.g. Pena et al., 1990; Wilkerson et al., 1992; McCarthy et al., 1996, Raimbault et al., 1999, 2000; Le Bouteiller et al., 2003). Based on results from the US Joint Global Ocean Flux Studies (JGOFS) Program, Chavez and Toggweiler (1995) estimated that

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the region could account for ~18% of global new production due to its large areal extent. A series of subsequent cruises (e.g., those listed by Feely et al. (2002) and Le Borgne et al. (2002), Le Borgne and Landry (2003)) have further examined the details of biological contributions to the CO_2 balance between the ocean and atmosphere.

The eastern equatorial Pacific has been described as a HNLC (High Nutrient, Low Chlorophyll) region (Minas and Minas, 1992; Barber, 1992) due to the presence of primary nutrients, notably nitrate (NO_3) at the surface and low chlorophyll concentrations (e.g. Dupouy et al., 1993). The low chlorophyll biomass has been partially explained as limitation by Fe (e.g. Frost and Franzen, 1992; Martin et al., 1994; Landry et al., 1997, 2000), $Si(OH)_4$ (Dugdale and Wilkerson, 1998) or a combination of the two (Leynaert et al., 2001; Franck et al., 2003). Dugdale and Wilkerson (1998) and Dugdale et al. (1995) suggested that low concentrations of $Si(OH)_4$ compared to NO_3 is a common characteristic of HNLC areas, such that these areas might be better described as HNLSiLC (High-Nitrate, Low-Silicate, Low-Chlorophyll). Low $Si(OH)_4$ is a feature of the equatorial upwelling zone (EUZ). Using ^{228}Ra as a tracer, Ku et al. (1995) reported a low flux of $Si(OH)_4$ compared to NO_3 in the EUZ and suggested that the region would be $Si(OH)_4$-limited for diatoms. The phytoplankton community in the EUZ is dominated numerically by small cell-sized picoplankton (Mackey et al., 2002). The larger cells include autotrophic dinoflagellates and prymnesiophytes (Chavez et al., 1996; Mackey et al., 2002; Brown et al., 2003) and diatoms (Chavez et al., 1996; Iriarte and Fryxell, 1995; Bidigare and Ondrusek, 1996; Brown et al., 2003), particularly small pennate forms (Franck et al., 2003). Although diatoms are relatively rare cells in the community, Le Bouteiller et al. (2003) speculated, based on optimal Si:N ratios for growth and assuming that all of their N came from NO_3 uptake, that they could account for as much as 69% of new production at the equator.

Since directly measured rates by different size fractions of phytoplankton in the equatorial Pacific have been scarce, simulation models have largely been used to explore the effects of community structure on new production measurements. Dugdale and Wilkerson (1998), for instance, put forth a preliminary EUZ biological model with two functional groups of phytoplankton (diatoms and picoplankton). This simple model was based upon the suggestion of $Si(OH)_4$-limited diatoms by Ku et al. (1995) and later confirmed by Leynaert et al. (2001), rapid phytoplankton growth rates (Cullen et al. 1992; Landry et al., 1997), and a high proportion of NH_4 uptake to total nitrogen uptake (Pena et al., 1990; Wilkerson and Dugdale, 1992; McCarthy et al., 1996). These model formulations were incorporated into the nitrogen-based EUZ model of Chai et al. (1996) to produce the CoSiNE (Carbon, Silicon, Nitrogen Ecosystem) model (Chai et al., 2002), which parameterized two forms of nitrogen (NH_4 and NO_3) for use, respectively, by picoplankton and diatoms, two size classes of grazers (micro- and mesozooplankton), and included Fe effects on photosynthesis.

The 1-D CoSiNE model is based on predictions of variables and functions, for which validation data have been largely unavailable for the EUZ. Specifically, there has been no basis from direct size-fractionated measurements of NO_3, NH_4 and $Si(OH)_4$ uptake to partition rates due to larger cells (including $Si(OH)_4$ requiring diatoms) versus the smaller picoplankton (non $Si(OH)_4$ users). The relative biomass (as particulate nitrogen, PN) and composition of the two size classes have also been poorly quantified, particularly in relation to measured nutrient uptake rates of any kind. We conducted experiments on two EUZ cruises in December 2004 (EB04) and September 2005 (EB05) with the goal of producing a better integrated understanding of nutrient availability (including Fe, Kaupp et al., 2011), uptakes rates of N (this paper; Dugdale et al., 2007), $Si(OH)_4$ (Krause et al., 2011) and carbon (Balch et al., 2011), and phytoplankton biomass, composition, growth and grazing rates (Landry et al., 2011; Selph et al., 2011; Taylor et al., 2011).

Here, we report results pertaining to the NO_3 and NH_4 uptake from these two sampling efforts. This dataset differs from previous N uptake studies for the EUZ in the availability of size-fractionated N uptake rates, together with extensive phytoplankton community analysis from the same stations and depths (Taylor et al., 2011; Selph et al., 2011), allowing us to reference the patterns in NO_3 or NH_4 uptake to variations in the size and compositional structure of phytoplankton. Extensive zonal coverage along the equatorial band (0°Eq and 0.5°N) provides the opportunity to observe substantial variation in both N uptake and community structure as a result of tropical instability wave activity. This study assesses the relationship of NO_3 uptake and different phytoplankton taxa in the >5-μm fraction, which the CoSiNE model ascribes entirely to diatoms. The resulting data therefore allows us to evaluate and comment on the conceptual basis for predictions of the CoSiNE model.

2. Materials and methods

2.1. Study site and sample collection

Dissolved inorganic nitrogen (NO_3 and NH_4), particulate nitrogen (PN), and phytoplankton nitrogen uptake rates were determined along four transects in the eastern equatorial Pacific during two research cruises aboard the *R/V Roger Revelle* between 10 and 28 December 2004 and 8 and 24 September 2005. During the 2004 cruise, two transects were occupied, a meridional transect from 4°N to 4°S at 110°W, and a zonal transect from 116.7°W to 140°W at the equator. In 2005, two additional transects were completed, a meridional transect from 4°N to 2°S at 140°W, and a zonal transect at 0.5°N (132.5°W to 125°W). Detailed descriptions of station location and hydrography are presented in Strutton et al. (2011).

Due to a tight water budget, we used two separate CTD/rosette systems for water collections for ^{15}N uptake studies during 2004. For vertical profiles within the photic zone (used to calculate depth-integrated N uptake), we used a trace-metal (TM) clean rosette system operated and maintained by C. Measures (see Kaupp et al., 2011, Measures et al., 2008) which was deployed daily at 0400. The photic zone was sampled at eight depths equivalent to 100, 52, 31, 13, 8, 5, 0.8 and 0.1% of surface light penetration depth (LPD). Sampling depths were determined from the relationship between beam c light transmission and PAR, calibrated with mid-day CTD profiles (Balch et al., 2011). Nutrient concentrations and most N uptake rates for cells >0.7-μm diameter (i.e. captured onto a GF/F filter) reported for 2004 were collected using the TM rosette. A second, conventional CTD/rosette system maintained by the ship was deployed at 0700 daily with samples collected at three selected depths (52, 13, 0.8% LPD) for fractionated N uptake (in cells >5-μm diameter and all phytoplankton >0.7-μm diameter). During 2005, all nutrient analyses and ^{15}N incubations were conducted on water collected using the conventional ship CTD/rosette from eight depths (100, 52, 31, 13, 8, 5, 0.8 and 0.1% of LPD) in the photic zone.

We compared estimates of NO_3 and NH_4 uptake in cells >0.7 μm from water collected using the ship CTD/rosette and TM rosette systems at each station in EB04. Biomass-specific uptake rates, VNO_3, measured from the ship CTD/rosette were lower than those measured using the TM rosette (model II regression slope 0.64 ± 0.06, $r^2 = 0.69$, $n = 41$). VNH_4 comparisons were more variable also with lower values in water collected from the ship