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Zonal and meridional patterns of phytoplankton biomass and carbon fixation in the Equatorial Pacific Ocean, between 110°W and 140°W

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ABSTRACT

Primary production (P_{prim}) and calcification (C_{calc}) were measured in the eastern and central Equatorial Pacific during December 2004 and September 2005, between 110°W and 140°W. The design of the field sampling allowed partitioning of P_{prim} and total chlorophyll *a* (B) between large (> 3 μm) and small (0.45-3 μm) phytoplankton cells. The station locations allowed discrimination of meridional and zonal patterns. The cruises coincided with a warm El Niño Southern Oscillation (ENSO) phase and ENSO-neutral phase, respectively, which proved to be the major factors relating to the patterns of productivity. Production and biomass of large phytoplankton generally covaried with that of small cells; large cells typically accounted for 20-30% of B and 20% of P_{prim}. Elevated biomass and primary production of all size fractions were highest along the equator as well as at the convergence zone between the North Equatorial Counter Current and the South Equatorial Current. C_{calc} by > 0.4 μm cells was 2-3% of P_{prim} by the same size fraction, for both cruises. Biomass-normalized P_{prim} values were, on average, slightly higher during the warm-phase ENSO period, inconsistent with a "bottom-up" control mechanism (such as nutrient supply). Another source of variability along the equator was Tropical Instability Waves (TIWs). Zonal variance in integrated phytoplankton biomass (along the equator, between 110° and 140°) was almost the same as the meridional variance across it (between 4° N and 4° S). However, the zonal variance in integrated P_{prim} was half the variance observed meridionally. The variance in integrated C_{calc} along the equator was half that seen meridionally during the warm ENSO phase cruise whereas during the ENSO-neutral period, it was identical. No relation could be observed between the patterns of integrated carbon fixation (P_{prim} or C_{calc}) and integrated nutrients (nitrate, ammonium, silicate or dissolved iron). This suggests that the factors controlling integrated P_{prim} or C_{calc} are more complex than a simple bottom-up supply model and likely also will involve a top-down grazer-control component, as well. The carbon fixation within the Equatorial Pacific is well balanced with diatom and coccolithophore production contributing a relatively steady proportion of the total primary production. This maintains a steady balance between organic and inorganic production, relevant to the ballasting of organic matter and the export flux of carbon from this important upwelling region.

1. Introduction

High nutrient-low chlorophyll (HNLC) waters are found in several regions of the world ocean and their cause is still debated (de Baar et al., 1995). First described in the 1980's (Minas et al., 1986), surface waters in HNLC regions are characterized by persistently high concentrations of macronutrients (principally nitrate, phosphate and silicate) but unexpectedly low phytoplankton biomass (as chlorophyll concentration, B), lower than one would expect if all the nutrients were consumed (Cullen, 1991). HNLC conditions can result from a variety of oceanographic situations including where the phytoplankton community has not had sufficient time to consume recently-upwelled nutrients; here we use HNLC to refer to those areas in which there has been sufficient time to consume the nutrients but some other factor is rate limiting to phytoplankton growth. HNLC waters are found in a wide variety of areas: Southern Ocean, Northeast Subarctic Pacific, and the Equatorial Pacific. In HNLC waters, new production (Dugdale and Goering, 1967; Eppley and Peterson, 1979) (or "net community production"=growth minus mortality (Banse, 1991)) may be limited by top-down control such as grazing (Cullen, 1991), and/or low specific growth rates associated with some rate-limiting trace nutrient such as iron (Martin et al., 1991).

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The Equatorial Pacific Ocean is the largest oceanic CO_2 source on earth (Tans et al., 1990) as CO_2-rich water is upwelled to the surface and degasses. It extends around 44% of the earth's equator. The HNLC condition of these waters also keeps CO_2 concentrations high since primary production (P_{prim}) is limited and phytoplankton CO_2 drawdown is minimal. Further, the P_{prim} of the region is strongly regulated by the El Niño-Southern Oscillation (ENSO) (Feely et al., 1987; Feely et al., 1995) which changes ocean circulation and effectively regulates nutrient upwelling and the associated P_{prim} of the region (Barber et al., 1996). Tropical instability waves (TIWs) along the equator have also been suggested as being important for upwelling of nutrients and regulating phytoplankton biomass (Evans et al., 2009; Strutton et al., 2005).

Despite the fact that the Equatorial Pacific is a HNLC region, it is responsible for a significant export flux of particulate organic matter (Honjo et al., 2008). While not as high a flux-rate as coastal or other upwelling regions, the sheer area of the Equatorial Pacific makes it a significant part of the global ocean biological carbon pump (Honjo et al., 2008). One factor which regulates the vertical export of particulate organic carbon (POC) from the euphotic zone is its association with biogenic minerals, as a form of ballast (Klaas and Archer, 2002). The inorganic:organic ratio of particles is strongly related to the sinking rate of particulate matter in the sea since greater biomineral content increases the particle density from a value close to that of seawater to high values approaching the mineral density (Takahashi and Be, 1985). The carbonate portion of the carbon cycle has come under increasing scrutiny due to the fact that $CaCO_3$ (particulate inorganic carbon, PIC) is one of the densest biominerals in the sea and has a first-order effect on sinking particulate organic carbon from surface waters to the deep sea (Armstrong et al., 2002; Francois et al., 2002; Klaas and Archer, 2002).

The above arguments on ballasting suggest that the PIC export ratio (PIC:POC) is of fundamental importance to sinking carbon and ultimately is a determinant of whether an ocean region is characterized by high new production, high f ratio, high export ratio, and a strong net carbon sink (Eppley and Peterson, 1979; Honjo et al., 2008). The export ratio (PIC flux:POC flux from the base of the euphotic zone) has been estimated indirectly in the Equatorial Pacific (using alkalinity and nitrate data), to be $\sim 8.7\% \pm 0.5\%$ (Sarmiento et al., 2002), a relatively high value. Previous direct measurements in the Equatorial Pacific (Balch and Kilpatrick, 1996) demonstrated elevated concentrations of PIC, plated coccolithophores and detached coccoliths in the South Equatorial Current, along with elevated ratios of calcification (C_{calc}) to P_{prim} (of up to 11%). This elevated C_{calc} would imply that the new production of the Equatorial Pacific could be driven, in part, by PIC. Certainly, the presence of carbonate sediments underlying the equatorial Pacific attests to high export of this mineral-rich ballast (Archer, 1996; Arrhenius, 1952). For a one month cruise during August-September, 1992, the average integrated C_{calc} rate was 2.75 mmol m^{-2} d^{-1} between 5°N and 5°S which is of the same magnitude as the export POC flux calculated using Thorium-234 during the Fall '92 ($\sim$2.6 mmol m^{-2} d^{-1}) (Buesseler et al., 1995). To date, the C_{calc} measurements made in 1992 remain the only direct ^{14}C C_{calc} measurements that exist from this biogeochemically-important region. Moreover, no measurements were ever made to examine the zonal variability along the equator in order to assess the relative importance of tropical instability waves (TIWs) on C_{calc}.

The NSF-sponsored Biocomplexity program focused on the central question of the importance of iron versus silicate in regulating P_{prim} and export production in the Equatorial Pacific. The work consisted of a combination of field surveys as well as carboy experiments in which surface waters of the Equatorial Pacific were incubated with various nutrient enrichment treatments (Brzezinski et al., 2011). We performed measurements of P_{prim} and C_{calc} as well as the standing stock of chlorophyll, PIC and phytoplankton species abundance. Here we present the results of the two field surveys of carbon fixation into POC and PIC, as well as results on standing stocks of chlorophyll and PIC that were sampled along meridional transects at 110° and 140°W plus zonal transects along the Equator.

2. Methods

2.1. Study region

The work described herein was performed during two cruises of the R/V *Roger Revelle*. The first (Zhng01RR; hereafter called EB04) left from San Diego, CA, USA on 3 December 2004 and ended in Papeete, Tahiti on 2 January 2005. A line of stations was sampled along 110°W (4°N to 4°S) and then along the equator from 110°W to 140°W. The second cruise (Cruise Zhng10RR hereafter called EB05) departed from Honolulu, HI, USA on 2 September 2005 and ended in San Diego, CA, USA on 1 October 2005. Stations were sampled along the 140°W meridian between 4°N and 3.25°S then along the 0.5°N parallel from 134°W to 123.4°W. For all standing stock measurements, eight light depths were sampled within the euphotic zone (100%, 52%, 31%, 13%, 8%, 5%, 0.8% and 0.1%). The method used to calculate the light depths was based on in situ, scalar irradiance measurements (photosynthetic available radiation, PAR) compared to shipboard downwelling irradiance PAR measurements during daytime casts. During nighttime casts (e.g. all productivity casts), the predicted light depths were determined using in situ beam attenuation data, combined with an empirical relation between beam transmisson (630 nm) and PAR diffuse attenuation taken from preceding CTD casts (Appendix A).

2.2. Sampling and analytical methods

2.2.1. Size fractionated chlorophyll

Extractions for chlorophyll were done in 90% acetone at −20 °C in darkness for at least 12 h (JGOFS, 1996). We size fractionated pigment samples in parallel using 0.45 and 3 μm nitrocellulose filters (Millipore Corporation) in order to better discriminate the production of the entire community from that of the larger cells (including diatoms). During EB05, replicate samples were filtered on both 0.4 and 3 μm pore-size polycarbonate filters and nitrocellulose filters in order to check filter efficiencies (see Appendix B). Note, nitrocellulose filters dissolve in acetone while polycarbonate filters do not, particularly convenient for minimizing filter particulates in the extract during fluorescence analyses. All extractions were centrifuged for 5 minutes prior to analysis. Readings were made with a Turner Designs fluorometer, calibrated with purified chlorophyll *a* standards.

2.2.2. Calcification/photosynthesis measurements

Water samples for rate measurements were taken pre-dawn with a trace-metal clean rosette sampler in 30 L GOFLO bottles (with Silicone O-rings). Water was sampled from 6 light depths: 52%, 31%, 13%, 5%, 0.8% and 0.1% calculated as described in Appendix A. Water samples for incubation were transferred from GOFLO bottles to incubation bottles inside a positive-pressure, trace-metal clean van, under subdued light conditions. Incubations were performed in 250 mL polycarbonate tissue culture bottles that were previously acid-cleaned, rinsed with reverse-osmosis water, then rinsed 5× with each sea water sample prior to filling. C_{calc} and P_{prim} were measured using the microdiffusion technique (Paasche and Brubak, 1994) with modifications by Balch et al. (2000). ^{14}C bicarbonate