Biomass, size structure and depth distributions of the microbial community in the eastern equatorial Pacific

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Abstract
We investigated the biomass, size structure and composition of microbial communities over a broad area of the eastern equatorial Pacific (4°N-4°S, 110-140°W) during cruises in December 2004 (EB04) and September 2005 (EB05). Vertical-profile samples were collected at 30 stations at depths extending from the surface to the 0.1% light level, and each sample was analyzed quantitatively by flow cytometry and epifluorescence microscopy. Autotrophic biomass averaged 14.8 ± 4.2 (1 s.d.) µg C L⁻¹ for the euphotic zone, with dinoflagellates comprising 39%, Prochlorococcus 28%, other flagellates 18%, Synechococcus 7.5%, and diatoms 6.3%. Nanoplankton accounted for 46% of autotroph biomass, while pico- and microphytoplankton comprised 39% and 16%, respectively. C:Chl averaged 64 ± 7% for the euphotic zone, with a mean mixed-layer value of 76 ± 20 and a minimum of 36 ± 15 at the 1% light level. Heterotrophic biomass averaged 7.0 ± 2 µg C L⁻¹ for prokaryotes, 1.6 ± 0.9 µg C L⁻¹ for dinoflagellates, 1.5 ± 1.1 µg C L⁻¹ for other flagellates, and 2.1 ± 0.4 µg C L⁻¹ for ciliates. Euphotic zone integrated biomass varied 2-fold, 1.2 to 2.5 g C m⁻², among stations, decreasing west to east with the gradient in euphotic zone concentrations of dissolved iron. Overall, community biomass and the contributions of functional groups displayed remarkable constancy over our study area, but some patterns were evident, such as the enhancement of picophytoplankton in the leading (upwelling) edges of tropical instability waves and larger diatoms in the trailing (downwelling) edges. Prochlorococcus, in particular, exhibited more variability than expected, given its generally assumed role as a stable background species in the tropical oceans, and was positively associated with the areas of enhanced autotrophic carbon and Chl a. With corrections for different methodological assumptions taken into account, our EB05 estimates of mixed-layer community biomass are 22-25% higher than values for JGOFS studies in 1992.

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1. Introduction

The eastern equatorial Pacific (EEP) is an open-ocean upwelling region that is well known for its high-nitrate, low-chlorophyll (HNLC) characteristics, iron (Fe) fertilization response, and global significance as a source of CO₂ to the atmosphere (Murray et al., 1994; Coale et al., 1996; Feely et al., 2002, 2006). The EEP is a region of zonal and meridional gradients of dissolved iron (Fe), strong currents, propagating waves, and El Niño-Southern Oscillation (ENSO) perturbations (Flament et al., 1996; Kaupp et al., 2011; Strutton et al., 2011). Yet it is also paradoxically viewed as a tightly regulated chemostat-like system that exhibits a very modest level of biological variability (Frost and Franzen, 1992; Dugdale and Wilkerson, 1998). What we know about the variability of biological communities in the EEP is however very limited. Intensive process studies along the 140°W transect in 1992 by the US Joint Global Ocean Flux Study (JGOFS), for example, provided only sparse information about community composition at a few depths and a few stations (Stoecker et al., 1996; Verity et al., 1996), while the spatial survey by Chavez et al. (1996) was restricted to surface waters and provided no physical context to assess spatial relationships. A number of investigations have dealt with microbial communities in the equatorial Pacific (Price et al., 1994; Iriarte and Fryxell, 1995; Kirchman et al., 1995; Vers et al., 1995; Stoecker et al., 1996; Verity et al., 1996; Mackey et al., 2002; Brown et al., 2003; Yang et al., 2004), though most have focused on taxonomic subsets or size classes of the total community. Of the studies that have taken a more comprehensive approach (Chavez et al., 1996; Ishizaka et al., 1997; Brown et al., 2003), Chavez et al. (1991, 1996) are the most spatially extensive within the EEP region, but sampling was only from the upper mixed-layer and abundances of Prochlorococcus were indirectly estimated. Brown et al. (2003) was the first to analyze community structure on a full transect of depth profiles.
across the equator (8°N–8°S, 180°), but was located well west of the JGOFS study area (110°–140°W) in the EEP. Similarly, Ishizaka et al.’s (1997) analysis of community size structure from bacteria to mesozooplankton was located out of the JGOFS region, did not include direct assessment of Prochlorococcus and made no distinction between autotrophic and heterotrophic dinoflagellates. Lastly, a few studies are notable in having integrated analyses of microbial community biomass and composition with growth and grazing process experiments in the equatorial Pacific (Chavez et al., 1991, 1996; Verity et al., 1996; Landry et al., 2000, 2003), but the data set is small (~40 experiments) and the approaches quite different.

The present study is part of a larger experimental investigation of the controls on phytoplankton biomass and production in the EEP, for which we revisited the JGOFS region between 110° and 140°W on cruises in December 2004 and September 2005. We sampled the microplankton community through the euphotic zone to the 0.1% light level at 30 stations, which represents for this region a unique depth-resolved data set on autotrophic and heterotrophic biomass, size structure and composition. In addition, each of the present analyses from 8 depths/station and 30 stations is associated with experimental taxon-specific assessments of growth and grazing rates (Selph et al., 2011). Consequently, the present community biomass analysis is part of the most comprehensive and spatially extensive study of plankton community structure, depth relationships, and process rates in EEP to date. Here we assess for the first time the magnitudes and variabilities of depth-integrated standing stocks over the broad domain of our study region, and relate them to environmental gradients and disturbance features. Where data can be compared in the surface mixed layer, we ask whether the stock levels show evidence of a change since JGOFS studies in 1992, as might be expected from the strengthening of trade winds since the late 1990s (McPhaden and Zhang, 2004; Feely et al., 2006). Lastly, these data also provide a community biomass context for companion studies of growth, grazing and production processes (Décima et al., 2011; Landry et al., 2011; Selph et al., 2011).

2. Materials and methods

2.1. Sampling

We investigated the spatial variability of plankton community structure and biomass in the eastern equatorial Pacific during two cruises of the R/V Roger Revelle. Samples were collected from 9–24 December 2004 (EB04) on a meridional transect along 110°W from 4°N to 4°S and on a zonal transect along the equator from 110° to 140°W (Fig. 1). Samples were collected from 8–24 September 2005 (EB05) on a meridional transect along 140°W from 4°N to 2.5°S and on a zonal transect along 0.5°N from 140° to 123.5°W. At each of the 30 stations sampled, seawater was collected at eight depths during pre-dawn (typically 0300, local time) CTD casts. For each station, we sampled the surface water (1-2 m) and depths corresponding to the penetration of 53, 31, 13, 7.6, 5.0, 0.8, and 0.1% of surface irradiance. Sampling depths were determined from the relationship between beam c light transmission and PAR, calibrated with mid-day CTD profiles (Balch et al., 2011). At all stations and depths, a similar suite of samples was collected for chlorophyll a and for microbial community analyses by flow cytometry and epifluorescence microscopy.

2.2. Chlorophyll a analyses

Samples (280 ml) for Chl a analyses were filtered onto 25-mm Gelman GF/F filters and extracted in 10 ml of 90% acetone for 24 h at −20 °C. Fluorometric analyses of chlorophyll a were made with a Turner Designs AU-10 fluorometer using equations calibrated against a pure chlorophyll a standard (Holm-Hansen et al., 1963).

2.3. Picoplankton analyses by flow cytometry

Picoplankton abundances of Prochlorococcus (PRO), Synechococcus (SYN) and non-pigmented prokaryotes (H-Bact) were determined

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Fig. 1. Station locations for cruises during December 2004 (EB04, triangles) and September 2005 (EB05, circles). Station order along meridional transects was north to south in both years, while zonal transects were sampled westward in 2004 and eastward in 2005.
using a shore-based flow cytometer. These samples (2 ml) were preserved with 0.5% paraformaldehyde (v/v, final concentration) frozen in liquid nitrogen, and subsequently stored at −80 °C. Prior to analysis, batches of thawed samples were stained with Hoechst 33342 (1 μg ml⁻¹, v/v, final concentration) at room temperature in the dark for 1 h (Campbell and Vaulot, 1993; Monger and Landry, 1993). Aliquots (100 μl) were analyzed using a Beckman-Coulter EPICS Altra flow cytometer with a Harvard Apparatus syringe pump for volumetric sample delivery. Simultaneous (co-)linear excitation of the plankton was provided by two argon ion lasers, tuned to 488 nm (1 W) and the UV range (200 mW). The optical filter configuration distinguished populations on the basis of chlorophyll a (red fluorescence, 680 nm), phycocerythrin (orange fluorescence, 575 nm), DNA (blue fluorescence, 450 nm), and forward and 90° side scatter signatures. Calibration beads (0.5- and 1.0-μm yellow-green beads and 0.5-μm UV beads) were used in each sample to standardize fluorescence and scatter parameters. Raw data (listmode files) were processed using the software FlowJo (Treestar Inc., www.flowjo.com). PRO and SYN abundances from flow cytometry (FCM) analyses were converted to biomass estimates using mixed-layer estimates of parameters. Raw data (listmode files) were processed using (500 ml) Nuclepore filters overlaying 20-millimeter areas of the filters required to split connected cells, delete artifacts, and add cell outlines. The outline created after pre-processing was then applied back to the original 24-bit RGB image to collect measurements from all channels. Manual interaction was then required to split connected cells, delete artifacts, and add cells that were too dim to be segmented from the background automatically.

For the EB04 cruise, cells were identified and grouped manually into six plankton functional groups (heterotrophic flagellates, autotrophic flagellates, diatoms, heterotrophic dinoflagellates, autotrophic dinoflagellates and pynemesiophytes). Autotrophs were distinguished from heterotrophic cells by the presence of chlorophyll, seen as red autofluorescence under blue light excitation. For EB05, pynemesiophytes were included in counts of autotrophic flagellates (A-Flag), and dinoflagellates (A-Dino) and A-Flag were distinguished by a multi-layer perceptron neural network model using NeuroSolutions software (NeuroDimensions, www.nd.com) after diatoms were identified manually. The MLP neural network model was trained with a back propagation algorithm using a data set of >22,000 manually identified cells from EB05 stations 5, 9, 15 and 23. In addition to functional groupings, all cells were binned into five size categories (<5, 5–10, 10–20, 20–40 and >40 μm) based on measurement of the longest cell axis. Length (L) and width (W) measurements were converted to biovolumes (BV; μm³) by applying the geometric formula of a prolate sphere (BV=0.524 LWH). For the unmeasured dimension of cell height (H), we used H=W for diatoms (95% penate types) and H=0.5W for flagellates (94% of dinoflagellates were athecate). The rationale for this difference is described below. Carbon (C; pg cell⁻¹) biomass was computed from BV from the equations of Menden-Deuer and Lessard (2000): C=0.216×BV₀.939 for non-diatoms, and C=0.288×BV₀.811 for diatoms.

The issue of cell height arose because previous assessments of microbial community biomass in the equatorial Pacific by Chavez et al. (1991, 1996) have utilized H:W assumptions ranging from 0.5–1.0 for different categories of flagellates. We used two types of size inferences from subsets of our samples to determine how the H:W ratio should be applied in our case. For very small flagellates, the Menden-Deuer and Lessard (2000) equations give estimates of cellular carbon density (0.22-0.23 pg C μm⁻³) that are approximately the same as those used for autotrophic prokaryotes. To quantify relative carbon densities on our slides, we compared the normalized cell-integrated green fluorescence (proflavin protein binding) of our smallest size category of autotrophic flagellates (<1.8 μm ESD) to Synechococcus cells in the same samples. Carbon densities were found to be the same on average when the height H of the flagellate cells was 0.51W. For larger flagellates on the 8-μm filters, we used the capabilities of our microscope to optically section individual cells and create 3D
representations of biovolume (Z-stacked topographic images), from which we derived H:W relationships of 0.57 ± 0.19 (1 s.d.; unless otherwise stated, all ± terms represent one standard deviation) (n = 120) using digital analysis and 0.45 ± 0.11 (n = 43) using a more subjective manual assessment of depth of focus. We conclude from these analyses that the flagellates in our samples (i.e., cells with flexible membranes) generally flattened on the filters during the slide preparation process, and that a H:W ratio of 0.5 could be reasonably applied in BV estimates for both small and large cells. A more quantitative analysis of this issue and its implications for microbial carbon biomass assessments in the oceans is needed, but is beyond the scope of the present study.

On EB04, additional samples were collected for analysis of ciliates, which were sub-optimally preserved and rarely observed in the fields counted on slides. Aliquots of 250 ml were preserved with acid Lugol's solution (final concentration 5%) and stored at room temperature in the dark. Sub-samples of 100 ml were settled in Utermöhl sedimentation chambers for at least 24 h and counted and measured with a Zeiss inverted microscope. BV calculations were based on measured dimensions and the closest geometric shapes for individual cells. To convert cell biovolume estimates to carbon, we used 0.19 µg C µm⁻³ for naked ciliates (Putt and Stoecker, 1989) and the equation, C (pg) = 44.5 ± 0.053 lorica volume (µm³), for loricate ciliates (Verity and Langdon, 1984).

2.5. Contour plots

Contour plots were generated using Ocean Data View (Schlitzer, 2006). A VG gridding algorithm was used for variable resolution in a rectangular grid where grid spacing varies accordingly to data density.

3. Results

3.1. Hydrographic and nutrient environments

Detailed descriptions of the physical and nutrient environments during our two cruises are given by Strutton et al. (2011), Dugdale et al. (2011), Kaupp et al. (2011) and Selph et al. (2011). The basic features of the system are summarized briefly below as context for our euphotic zone sampling of the microplankton community. Euphotic zone depth, defined as the depth of penetration of 0.1% surface irradiance, varied from 96 to 112 m on the equatorial transect during EB04 and from 94 to 101 m along 0.5°N on EB05. Euphotic depths were shallowest on the equatorial transect area from 4 to 110°W transect (EB05) (Dugdale et al., 2011). The principal feature of the growth environment for phytoplankton during our study was the developed subsurface Chl a maximum (0.25 mg Chl a L⁻¹), especially at the equator and at 3-4°N (Fig. 2D).

Depth-averaged euphotic-zone concentrations of Chl a varied by a factor of 2.8 (0.14–0.39 µg Chl a L⁻¹) in our study region (Table 1), with a value of 0.24 ± 0.06 µg Chl a L⁻¹. On the EB04 equatorial transect, mixed-layer Chl a was highest in the west, from 135–140 W, and concentrations decreased toward the east (Fig. 2A). However, a strong subsurface Chl a maximum was evident at 110 W between 50 and 75 m (Fig. 2A, D). On the 0.5 N transect for EB05, the area of elevated Chl a concentration (> 0.3 mg Chl a L⁻¹) from 123.5 to 130.5 W (Fig. 2B) coincided with the occurrence of a Tropical Instability Wave (TIW) (Selph et al., 2011; Strutton et al., 2011). The enhanced Chl a between the equator and 1°S on the 140°W transect (Fig. 2C) was the location of active upwelling and high Fe concentration. Consistent with the E-W gradient in iron, Chl a values were generally lower along the 110°W transect than at comparable latitudes along the 140°W transect. The 110°W transect was further distinguished by well-developed subsurface Chl a maxima (> 0.25 mg Chl a L⁻¹), especially at the equator and at 3-4°N (Fig. 2D).

Depth-averaged euphotic-zone estimates of autotrophic biomass ranged 2.5-fold, from 10 to 25 µg C L⁻¹, with a mean concentration of 14.9 ± 4.1 µg C L⁻¹ for the study region (Table 1). The EB05 transect along 140°W had the highest autotrophic carbon values (AC) (18.3 µg C L⁻¹), while mean concentrations were lowest (12.6 µg C L⁻¹) in the east at 110°W (Fig. 2C and D). Along the 140°W transect, the highest mixed-layer values of AC (> 30 µg C L⁻¹) were located in the area of active upwelling around 1°S (Fig. 2C). Although distributions of autotrophic carbon have some features in common with Chl a, the carbon profiles are somewhat more uniform in appearance. Specifically, they do not show a corresponding significant response to the TIW during EB05 (Fig. 2B), nor are carbon values enhanced in the deep Chl a maxima seen along the 110°W transect during EB04 (e.g., Fig. 2D).
due to a calculation artifact if cells in the lower euphotic zone are degrading and therefore have substantially lower C:BV than our assumed conversion factors. The highest station estimates of C:Chl (492; 2 standard deviations above the mean) were found at 41 S, 110° on EB04 and at the equator, 140°W on EB05. The four lowest station ratios of C:Chl (43-45; 2 standard deviation below the mean) occurred along the 0.5°N transect during EB05, with the TIW-influence area between 125 and 131°W accounting for three of them (Table 1, Fig. 2B).

### 3.3. Biomass estimates of phototrophic and heterotrophic prokaryotes

Biomass estimates of the phototrophic bacteria, Prochlorococcus (PRO) and Synechococcus (SYN), averaged 5.6 μg C L⁻¹ over the full euphotic zone (station range = 1.6 to 10.5 μg C L⁻¹) (Table 1), accounting for 37% (range 16 to 65%) of total autotrophic biomass. The mean biomass and abundance ratios, respectively, of PRO to SYN were 4:1 and 12:1. Biomass of SYN, averaging 1.5 μg C L⁻¹...
(range = 0.4 to 2.9 μg L⁻¹; Table 1), was relatively evenly distributed on all four transects and largely confined to the upper 50 m of the water column. The highest areas of SYN biomass were between 125.7 and 127.8 W on the 0.5 N transect (> 3.5 μg C L⁻¹ in the upper 25 m), and between the equator and 1° S on the 140 W transect (> 2.5 μg C L⁻¹ in the upper 45 m). The lowest SYN concentrations were on the 110°W transect (average = 0.7 μg C L⁻¹). Similar high and low biomass features appear prominently in transect contour plots for PRO (Fig. 4). The area of high mixed-layer (< 8 μg C L⁻¹, upper 30 m) biomass at 127.8 W on the 0.5 N transect (EB05) is the region of TIW influence (Fig. 4B), and the active upwelling area just south of the equator at 140 W (Fig. 4C) had the highest PRO biomass levels (11.5 μg C L⁻¹) sampled during our study. PRO concentrations in the mixed layer were generally lower (3-5 μg C L⁻¹) along the equator during EB04 (Fig. 4A), with the 110 W transect showing a local minimum (~ 2 μg C L⁻¹) at the equator, increasing symmetrically to the north and south (Fig. 4D).

Heterotrophic bacteria (H-Bact) averaged 7 μg C L⁻¹ over the euphotic zone, almost double the mean biomass of total heterotrophic flagellates (including heterotrophic dinoflagellates) and 58% of total heterotrophic biomass at the stations where ciliates were included in the analyses (Table 2). Biomass distributions of H-Bact were similar to the trends for total autotrophs, giving a strong positive relationship between the two measurements (R² = 0.63, p < 0.0001; logarithmic regression) (Fig. 5).

3.4. Size-class distributions of autotrophic biomass

On average, nano-sized phytoplankton (A-Nano; 2–20 μm) comprised the highest proportion (mean = 46%) of total autotrophic biomass, with A-Pico (< 2 μm) and A-Micro (20-200 μm) cells comprising 39 and 16%, respectively (Table 1). A-Pico biomass was strongly dominated by phototrophic bacteria (Table 1); thus, A-Pico contours in Fig. 6 show similar distributions and features to those in Fig. 4. All size classes were elevated in the upwelling area on the 140 W transect between the equator and 1° S (Fig. 6C). On the EB04 equatorial transect (Fig. 6A), A-Micro differed from smaller phytoplankton in displaying a pronounced eastward decreasing gradient, a consequence of not having elevated concentrations between 110 and 120 W like smaller cells. A-Micro also differed in having a local biomass minimum in the TIW-influenced area of the 0.5 N transect on EB05 (Fig. 6B). A-Nano distributions were intermediate between pico- and micro-size classes, displaying most of the local high and low features seen for the smaller cells, but with more uniform distributions along each transect. However, A-Nano biomass levels along the 0.5 N transect of EB05 was notably about a factor of two lower than on other transects.

3.5. Biomass distributions of heterotrophic flagellates

Depth-averaged biomass estimates of heterotrophic flagellates (H-Flag) from epifluorescence microscopy ranged slightly more than 5-fold, from 1.5 to 8.0 μg C L⁻¹, with a mean concentration...
of 3.2 μg C L⁻¹ for the study region (Table 2). This component of the community includes heterotrophic dinoflagellates (H-Dino) and H-Flag, which contributed 1.64 versus 1.54 μg C L⁻¹, respectively, on average to total heterotrophic biomass. It does not however include the biomass contribution of ciliated protists, which is considered separately below (Section 3.6). Nano-sized heterotrophic flagellates (H-Nano, 2-20 μm) comprised the majority (mean = 72%) of the biomass, while H-Pico (< 2 μm) and H-Micro (20-200 μm) cells accounted for 4 and 24%, respectively (Table 2). Along all transects, H-Nano distributions were similar to A-Nano, although slightly less uniform. This is most apparent on both meridional transects, where H-Nano concentrations were higher and extended deeper into the water column south of the equator at 140 W and north of the equator at 110 W (Fig. 7C, D). H-Nano biomass was elevated in the upwelling region between 1 S and the equator along the 140 W transect, while H-Micro biomass did not display a pronounced maximum in this same region (Fig. 7C). Biomass distributions of H-Nano and H-Micro along the EB04 equatorial transect followed the same eastward decreasing gradients as autotrophic cells of comparable size (Fig. 7A). Both H-Nano and H-Micro had pronounced, but vertically separate, biomass maxima in the TIW-influenced area of the 0.5 N transect on EB05 (Fig. 7B). H-Micro biomass in the TIW-influenced area of the 0.5 N transect (mean = 1.6 μg C L⁻¹) was more than double the average on other transects (0.6 μg C L⁻¹) (Table 2).

### Table 2

Mean station concentrations of heterotrophic bacteria (H-Bact) and ciliate (CIL) biomass, and heterotrophic eukaryote abundance and biomass by size class. H-Pico (0.2-2 μm), H-Nano (2-20 μm) and H-Micro (20-200 μm). H-Protist biomass is w/o CIL. Total heterotrophic biomass (HC) is w/CIL. Units are cells mL⁻¹ for abundance, and μg C L⁻¹ for biomass.

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<th>Biomass (μg C L⁻¹)</th>
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#### Fig. 5

Relationship between total autotrophic carbon (Autotrophs) and heterotrophic bacteria (H-Bact) biomass for all samples collected. R² = 0.63, p < 0.0001; logarithmic regression.

#### 3.6. Integrated community composition, biomass and size structure

For the 30 stations at which flow cytometric and epifluorescence (EPI) microscopical assessments of community biomass can be combined, the euphotic zone integrated values varied by 2-fold, ranging from 1.2 to 2.5 g C m⁻², with a mean concentration of 1.8 g C m⁻² (Table 4). Adding the 8-station average for ciliate biomass (0.2 g C m⁻²) to other stations where inverted microscopy measurements were not made increases the average to 1.9 g C m⁻². The percentages of community biomass for each functional group identified were also fairly consistent across the study area; although compositional variability was greater than total integrated biomass, largely due to divergent responses of the
different community components in the TIW area on the 0.5°N transect (Table 4). Biomass contributions of each phototrophic functional group to the total phytoplankton community are shown for the EB04 110°W meridional and equatorial zonal transects in Fig. 8. Similar patterns (not shown) were also found for the EB05 140°W meridional and 0.5°N zonal transects.

Photosynthetic dinoflagellates (A-Dino) dominated the phytoplankton community, comprising 39%, on average (range 17 to 62%), of total integrated autotrophic biomass (Table 3). PRO (mean = 28%), A-Flag (18%, including prymnesiophytes), SYN (7.5%), and diatoms (6.3%) followed in order of their mean contributions to total autotrophs (Table 3).

The average integrated biomass for A-Dino was 0.54 g C m⁻² for the study region (Table 4), 77% residing in the nano size class. The highest depth-integrated values for A-Dino biomass (0.9 g C m⁻²), in the upwelling area between 1°S and the equator on the 140°W transect, reflected a large increase in >20-µm cells (Fig. 9C, Table 4). Biomass of >20-µm A-Dino was also elevated along the EB04 equatorial transect from 127 to 140°W (Fig. 9A).

Along the 140°W meridional transect, vertical distributions of A-Dinos showed biomass maxima in the upper mixed layer, decreasing gradually with depth. Along the 110°W meridional transect, however, concentrations decreased rapidly below the mixed layer (Fig. 10D). Biomass of >20-µm A-Dinos was also

![Fig. 6. Contour plots of phytoplankton biomass distributions by size class along the equatorial (A), 0.5° N (B), 140° W (C), and 110° W (D) transects. A-Pico (0.2–2 µm), A-Nano (2–20 µm), and A-Micro (20–200 µm). Units are µg C L⁻¹, and scales are the same for all plots.](image1)

![Fig. 7. Contour plots of heterotrophic biomass distributions by size class along the equatorial (A), 0.5° N (B), 140° W (C), and 110° W (D) transects. H-Nano (2–20 µm) and H-Micro (20–200 µm). Units are µg C L⁻¹, and scales are the same for all plots.](image2)
elevated in the TIW-influenced area of the 0.5°N transect around 130.5 W (Fig. 9B).

Among the groups identified, diatoms comprised, on average, the smallest percentage (6.3%) of phytoplankton community biomass in the study area, but they also exhibited more variability (an 18-fold range, from 0.9 to 16.5%; Table 4) than other groups. The variability in biomass can be attributed to changes of size-class structure of the diatom community, as opposed to changes in diatom community abundance. Diatoms <20-μm showed relatively little variation in integrated biomass. In contrast, >20-μm diatoms had distinct areas of high biomass, with the highest concentrations along the equator at 125.3 W and 140°W (0.19 g C m⁻²) and in the TIW-influenced area on the EB05 0.5°N transect at 132.5 W (0.22 g C m⁻²) (Fig. 9A, B).

At the 8 stations along the equatorial transect of EB04 where ciliates (CIL) were analyzed by inverted microscopy, they averaged 2.1 ± 0.36 μg C L⁻¹ and 220 ± 38 mg C m⁻² for the euphotic zone, accounting for 47 ± 5.6% of the total biomass of heterotrophic protists. A loricate (i.e., naked) forms consistently dominated ciliate biomass (93 ± 5%; n=64) at all stations and depths analyzed. Ciliate biomass estimates from inverted microscopy averaged 2.0 ± 0.8 times greater than estimates for H-Dino taxa by the same method. Thus, ciliates dominated the H-Micro size category, at least for this subset of EB04 stations, consistent with most H-Dino biomass residing in nano-sized cells. For the 8 stations where biomass estimates include ciliates, the depth-integrated ratio of autotrophic to heterotrophic carbon biomass (AC:HC) averaged 1.2 ± 0.16. Even without ciliates considered, comparably low ratios were found along the 0.5°N transect on EB05, averaging only 1.1 (range 1.0 to 1.2).

### Table 3

Percentage contribution of each phytoplankton functional group to euphotic-zone integrated autotrophic community biomass along the 110°W and equatorial transects (2004), and the 0.5°N and 140°W transects (2005). Prochlorococcus (PRO), Synechococcus (SYN), prymnesiophytes (PRYM), autotrophic flagellates (A-Flag), diatoms, and autotrophic dinoflagellates (A-Dino). Data are means ± standard deviations.

<table>
<thead>
<tr>
<th>Cruise</th>
<th>TRANSECT</th>
<th>PRO</th>
<th>SYN</th>
<th>A-Dino</th>
<th>Diatom</th>
<th>A-Flag</th>
<th>Prym</th>
</tr>
</thead>
<tbody>
<tr>
<td>EB04</td>
<td>110 W</td>
<td>24.5 ± 7.9</td>
<td>4.6 ± 0.9</td>
<td>37.6 ± 4.7</td>
<td>7.3 ± 3.7</td>
<td>14.6 ± 2.8</td>
<td>11.4 ± 1.5</td>
</tr>
<tr>
<td></td>
<td>Equatorial</td>
<td>19.8 ± 6.5</td>
<td>5.3 ± 1.7</td>
<td>37.3 ± 7.3</td>
<td>8.4 ± 3.6</td>
<td>16.6 ± 4.0</td>
<td>12.6 ± 3.4</td>
</tr>
<tr>
<td>EB05</td>
<td>140 W</td>
<td>31.5 ± 6.6</td>
<td>8.4 ± 2.0</td>
<td>44.8 ± 7.7</td>
<td>2.9 ± 1.7</td>
<td>12.3 ± 3.9</td>
<td>nd</td>
</tr>
<tr>
<td></td>
<td>0.5 N</td>
<td>40.4 ± 5.1</td>
<td>13.8 ± 2.9</td>
<td>33.1 ± 4.9</td>
<td>6.9 ± 5.6</td>
<td>5.8 ± 3.7</td>
<td>nd</td>
</tr>
</tbody>
</table>

3.7. **Mean biomass profiles**

Mean profiles of carbon biomass (± 95% confidence limits) are plotted in Fig. 11 as a function of light depth for component groups of the EEP microbial community. While surface concentrations of Chl a extend relatively deep in the euphotic zone, or are often exceeded by deep maximum values (Fig. 2), autotrophic carbon falls off sharply as a rule below the 10% I₀ light depth. Diatom biomass, on average, is highest at high light levels close to the surface and declines fairly uniformly with depth below. A-Dino biomass, which dominates the depth pattern for total autotrophs, is more uniformly high or increasing with depth in the upper third of the euphotic zone, with a sharper break at 10% I₀. We did not account in our analyses for larger cell size of the deep populations of *Prochlorococcus*, which would increase their biomass at 1% light depth and below by 50 to 100% (Binder et al., 1996), and we may have also overestimated substantially (Fig. 3) the carbon biomass of degrading eukaryotic *Prochlorococcus* in our 0.1% I₀ samples. Therefore, PRO could be the dominant contributor to autotroph C at 0.1% I₀. This would be consistent with DVChl a, the signature photosynthetic pigment of PRO, only exceeding MVChl a in the 0.1% I₀ samples (Selph et al., 2011).

Relative to autotrophs, surface concentrations of heterotrophic protists extend deeper in the euphotic zone, only declining to about half of surface values at the 0.1% light depth (Fig. 11). H-Dino, H-Flag and ciliates can be all be seen as significant contributors to protistan grazer biomass, with H-Flag and H-Dino sharing co-dominance of the H-Nano size class and CIL dominating the H-Micro.
4. Discussion

4.1. Community biomass comparisons

Previous studies of microbial community biomass, size structure, composition and carbon to chlorophyll a ratios have established a baseline of estimates for the upper euphotic zone in the eastern equatorial Pacific (EEP) region. Unfortunately, these studies are not easy to compare directly among themselves and with the present results because they involve substantial differences in measured variables, technologies (analysis by eye versus digitally enhanced images), geometric biovolume (BV) calculations and BV conversions to carbon equivalents. Nevertheless, by taking these differences into account when comparing the present study to historical estimates we can make some broad observations on how they relate and assess whether differences in microbial community abundance may have occurred over time.

To establish a climatological mean estimate of autotrophic carbon for the EEP region we use data reported by Chavez et al. (1996) and Brown et al. (2003), the most spatially extensive...
and complete previous studies in the equatorial Pacific. Chavez et al. (1996) reported mean estimates of autotrophic carbon in mixed-layer samples of 23.3 \( \mu g \text{L}^{-1}/C_0 \) (n = 23 samples) during normal upwelling condition in September-December 1992, 18.6 \( \mu g \text{L}^{-1}/C_0 \) (n = 24) during El Niño conditions in March-May 1992, and 16.1 \( \mu g \text{L}^{-1}/C_0 \) (n = 20) for a suite of historical cruises between 1988 and 1990. The climatology of the area for autotrophic biomass is therefore 19.4 \( \mu g \text{L}^{-1}/C_0 \), which compares to estimates of 24.3 \( \pm \) 4.4 \( \mu g \text{L}^{-1}/C_0 \) (n = 53 samples) for the upper 50 m from Brown et al. (2003) and an average of 19.0 \( \pm \) 6.4 \( \mu g \text{L}^{-1}/C_0 \) (n = 120) for the upper 1/3rd of the euphotic zone in the present study. However, we need to take methodological differences

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Fig. 10. Biomass distributions of diatoms, autotrophic dinoflagellates (A-Dino) and autotrophic flagellates (A-Flag) along the equatorial (A), 0.5°N (B), 140°W (C), and 110°W (D) transects. Units are \( \mu g \text{L}^{-1} \), and note that a different scale is used for A-Dino.

Fig. 11. Mean depth profiles for total autotrophs and total heterotrophic protists [H-Dino+H-Flag] (A), and various components of the autotrophic and heterotrophic assemblages in the eastern equatorial Pacific: Prochlorococcus (PRO) and Synechococcus (SYN) (B), autotrophic dinoflagellates (A-Dino) and diatoms (C), and heterotrophic dinoflagellates (H-Dino) and flagellates (H-Flag) (D). Profiles a-d are the means for 30 stations. Profiles for ciliates (CIL) and total H-protists (H-Dino+H-Flag+CIL) (E) are the means of 8 stations where ciliates were analyzed by inverted microscopy of acid Lugol’s preserved samples. Error bars are 95% confidence intervals.
between the studies into account and apply appropriate conversion factors to the historical data before we can begin to compare them quantitatively.

Chavez et al. (1996), for example, converted their indirect estimates of PRO cell abundance to carbon using a factor (24 fg C cell\(^{-1}\)) that is substantially lower than presently accepted values. Given the mean upper eutrophic estimate of \(5.5 \pm 2.9 \mu g \text{C L}^{-1}\) for PRO in our samples, correcting for the lower cellular C estimates of Chavez et al (1996) should increase their autotroph biomass estimates by \(\sim 1.4 \mu g \text{C L}^{-1}\) on average. By the same token, their estimates of carbon values were elevated relative to ours by using H:W assumptions of 0.75 for athecate dinoflagellates and 1.0 for other autotrophic flagellates. We accounted for these systematic differences by applying appropriate factors to their Table 4 biomass estimates by taxonomic group, and also by reducing eukaryote biomass by an additional 10% to represent the mean offset in moving BV-corrected carbon estimates from Eppley et al. (1970) equations to the Menden-Deuer and Lessard (2000) calculations. With all of these changes, the mean mixed-layer estimates (5 N to 5 S) of autotrophic C for the EqPac Survey 1 and Survey II cruises from Chavez et al. (1996) are lowered to 15.6 and 17.5 \(\mu g \text{C L}^{-1}\), respectively. Applying similar corrections to the tabulated estimates in Brown et al. (2003) give a mean value of 16.2 \(\mu g \text{C L}^{-1}\) for 0-50 m autotrophs collected from 4 N to 4 S at 180° under cold-tongue conditions. The grand weighted average from these previous studies is 16.4 \(\mu g \text{C L}^{-1}\). Our estimates for the upper eutrophic zone during the mild El Niño condition of EB04, 16.2 \(\pm 3.5 \mu g \text{C L}^{-1}\), is right on this historical average. The average for ENSO-neutral conditions on EB05, 22.2 \(\pm 7.6 \mu g \text{C L}^{-1}\), is about 35% higher. A similar reanalysis of heterotrophic protist biomass from Chavez et al. (1996), to conform to the present methodological assumptions, yields biomass estimates 4.6 and 4.7 \(\mu g \text{C L}^{-1}\) for the 1992 Survey I and II cruises, respectively. Again, our EB04 estimate for heterotrophic protists (4.8 \(\mu g \text{C L}^{-1}\)) is very close to the historical values, while the EB05 values with ciliates added (nominally 7.5 \(\mu g \text{C L}^{-1}\)) are substantially higher.

Our upper-layer biomass estimate for heterotrophic protists from EPI microscopy is 4.2 \(\pm 2.1 \mu g \text{C L}^{-1}\). The average for EB05 (5.0 \(\pm 2.5 \mu g \text{C L}^{-1}\)) is more than double that for EB04 (2.3 \(\pm 0.8 \mu g \text{C L}^{-1}\)). The ciliate analysis for EB04 adds 2.5 \(\pm 0.7 \mu g \text{C L}^{-1}\) to total mixed-layer estimates of heterotrophic protists for this cruise (i.e., mean \(=4.8 \mu g \text{C L}^{-1}\)). If we assume comparable ciliate abundance during EB05, the average for that cruise increases by 50% to 7.5 \(\mu g \text{C L}^{-1}\). Chavez et al. (1996) reported values of 6.5, 5.6 and 4.0 \(\mu g \text{C L}^{-1}\) for 1992 normal upwelling, 1992 El Niño and 1988-1990 cruises, respectively. Their EPI analyses explicitly included ciliates, which averaged 1.3-1.5 \(\mu g \text{C L}^{-1}\) for the two survey cruises in 1992, with mean abundance estimates of 2.1-3.0 ciliates ml\(^{-1}\). These ciliate biomass values are somewhat lower than ours, but, given the very different approaches used, the Chavez et al (1996) abundances are reassuringly similar to our estimate of 2.6 \(\pm 1.0 \text{cells ml}^{-1}\). In contrast, Verity et al. (1996) reported extremely low densities (0.07 \(\pm 0.04 \text{ciliates ml}^{-1}\) and biomass estimates (0.2 \(\pm 0.1 \mu g \text{C ml}^{-1}\) from inverted microscopical analyses of formalin-preserved samples from 1992. This large discrepancy from Verity et al (1996) and the present study would seem to suggest that most of their ciliates were lost during collection or preservation. We conclude from these comparisons that ciliates make substantially larger contributions to the consortium of protistan grazers in the equatorial Pacific than suggested by the Verity et al. (1996) study.

In a companion study, Décima et al. (2011) found that mesozooplankton biomass was 26% higher during EB05 relative to EB04, and that standing stocks compared on a comparable basis averaged 80-90% higher than collections made on the correspondingly EqPac El Niño and upwelling cruises in 1992. This led Décima et al. (2011) to suggest that conditions had changed to support higher standing stocks of zooplankton since the early 1990’s, similar and proportional to the documented decadal increase in mesozooplankton in the North Pacific Subtropical Gyre (NPSG) observed in monthly net sampling at Stn. ALOHA (Sheridan and Landry, 2004). The present study provides some evidence for, but falls short of fully supporting, the notion that the growth environments for mesozooplankton have been enhanced, both in the EEP and NPSG, by their linked response to increasing trade wind strength since the late 1990’s (Feely et al., 2006). At the stations sampled, our community biomass assessments for EB05 are 29% higher than previous estimates for the region compared on the same basis. However, the EB04 results show no enhancement relative to historical values, which may or may not be because the stations sampled on this cruise were mostly on the low side (110°W) of the W-E biomass gradient. Regardless, whatever mechanism supported higher standing stocks of mesozooplankton during our study, it clearly did not involve proportionally higher biomass levels of the lower trophic levels, as compared here to historical estimates for the equatorial region.

4.2. Carbon:chlorophyll ratios

For the area from 4 N to 4 S, Chavez et al. (1996) provide mixed-layer values of C:Chl, taken from plotted points in their Figure 15, of 97 \(\pm 30\) for the 1992 El Nino conditions (Survey I cruise) and 154 \(\pm 56\) for 1992 normal upwelling (Survey II). For the same latitudinal range at 180° in 1996, the C:Chl ratios of Brown et al. (2003) average 99 \(\pm 18\) for the upper 50 m of the water column. These ratio estimates decrease in proportion to the calculated changes in autotrophic carbon above, giving new estimates of 81 for Survey I, 116 for Survey II (Chavez et al., 1996), and 67 for Brown et al. (2003). Our mean mixed-layer C:Chl of 78 \(\pm 20\) is lower than all previous estimates based on microscopical analyses of the plankton community in the equatorial Pacific, but is intermediate among historical values where the calculation of autotrophic biomass derives from the same assumptions.

Our euphotic-zone integrated estimate of C:Chl (64 \(\pm 14\)) is substantially lower than those from previous microscopy-based studies in the equatorial Pacific. However, it is relatively close to the commonly used value of 58 from Eppley et al. (1992), which comes from the slope of the regression of POC versus Chl a. On face value, Eppley’s (1992) method would seem to provide an upper limit for the C:Chl a ratio of autotrophs, since Chl a is specific to phytoplankton while C comes from many sources. However, POC measurements individually provide weak constraints to the C:Chl a estimate, leaving the regression analysis subject to bias by variability in the other contributors to C. In the present study, for example, autotroph carbon accounts for substantially less than half of the typical POC values of 50-100 \(\mu g \text{C L}^{-1}\) (Eppley et al., 1992; B. Balch, pers com.).

While the convergence of microscopical and regression-based estimates of C:Chl for the equatorial Pacific is encouraging, the application of this variable to interpreting the dynamics of the region demands some caution. There is a clear depth-dependency to this ratio (Fig. 3), reflecting physiological and community adaptations in the opposing gradients of light and nutrients (Fe). Mixed-layer values of 78 \(\pm 20\) would therefore be the most appropriate ratio to use for assessing mean carbon equivalents of ocean color images from satellites. The ratio also displays substantial variability, even within the mixed layer where the measurement precision is relatively good and 3 independent
samples are analyzed per station. High values exceed 100 in the vicinity of the equator. For example, the 3 high-Chl α stations associated with equatorial upwelling (0° to 1 S) at 140° W on EB05 averaged a C:Chl ratio of 96. In contrast, three stations with similarly high Chl α values associated with the tropical instability wave on the same cruise (0.5° N, 125°-131° W) had mean mixed-layer ratios ranging narrowly from 57 to 59. Rapid physiological responses of cellular Chl α content to light and nutrient conditions often give exaggerated impressions of the carbon biomass response of phytoplankton. From the above comparison, however, it should also be noted that substantial differences in phytoplankton carbon response to differing growth environments can be masked by the appearance of chlorophyll uniformity in satellite images or shipboard measurements.

Our calculated C:Chl ratios increased between the 1.0 and 0.1% light levels at all stations. We attribute this effect to the degradation of carbon content of cells, relative to biovolume, in the deep euphotic zone. The cells contained enough DNA (DAPI fluorescence) to appear viable and were counted by microscopy. However, process studies in this portion of the euphotic zone suggest that it is a stratum of negative growth and mineral regeneration (Krause et al., 2011; Landry et al., in press). Therefore, it seems unlikely that C:BV conversion factors derived for healthy and actively growing cells would be applicable in this portion of the euphotic zone.

4.3. Microplankton composition and size structure

Given the broad area covered in the sampling on two cruises, the most striking result of our study is the relative constancy of integrated community biomass, and to a slightly lesser extent, the biomass contributions of each functional group (Fig. 8). As a consequence, and despite some environmental variability evident in gradients of Fe concentration, TIW effects, proximity to upwelling and ENSO conditions (EB04 occurred during mild El Niño conditions; EB05 was ENSO neutral), the mean biomass profiles for different components of the microplankton community in Fig. 11 suggest relatively robust regional patterns of light-depth relationships. Since most previous analyses of microplankton community biomass structure in the equatorial Pacific have been based on samples from surface waters, these light-depth patterns may be useful in extrapolating surface stocks to the rest of the euphotic zone. One important point, for example, is the substantially slower decrease in biomass of heterotrophic protists with depth in the euphotic zone compared to autotrophs. This is consistent with the observation that the grazing impact of microzooplankton may still be quite high at depths where phytoplankton growth rate is severely diminished by low light (Landry et al., in press). Thus, inferences based on the coupling of growth and loss processes in the upper layers of high light may not reflect the balance of processes for the full euphotic zone (Landry et al., in press).

Previous studies of picophytoplankton populations in the tropical Pacific, which have involved the analysis of many hundreds of samples since high-precision flow cytometry was first applied to oceanographic research in the early 1990s, have shown them to be ubiquitous and important components of the microplankton assemblage (Landry and Kirchman, 2002). Prochlorococcus, in particular, has appeared broadly distributed at comparable densities in subtropical gyres, the western warm pool and the HNLC eastern sector of the Pacific, suggesting that it provides to the food web a stable base of small cells upon which the more dynamic populations of larger cells are overlain (Landry and Kirchman, 2002). Consistent with this view, we found nanophytoplankton cells to dominate autotroph biomass in our mesotrophic study region, while Prochlorococcus alone often comprises half or more of phototrophic biomass in adjacent oligotrophic waters of the subtropical gyres (Karl, 1999; Kraay and Veldhuis, 2004). Interestingly, however, we found that PRO and SYN also varied appreciably (factors of 4 and 3, respectively) along physiochemical gradients in the region. Selph et al. (2011) also observed a significant relationship between phytoplankton Chl α and Fe concentration along the equator that was almost entirely explained by the response of the DVChl α specific to Prochlorococcus rather than the MVChl α. PRO therefore seems to have greater relative variability within the phytoplankton than previously assumed. Rather than providing a constant base to the phytoplankton assemblage, both PRO and SYN varied with total eukaryotic photosynthetic biomass in our samples, showing similar to higher biomass responses in the hot spots of biological activity associated with TIW and upwelling just south of the equator at 140° W (Fig. 4). On a depth-integrated basis, PRO biomass was more variable as a percent of its mean value than A-Dino biomass, but less so than diatoms or SYN. We should keep in mind, however, that the variabilities observed for PRO and SYN are at the species level, or for a small number of eco-types that dominate different depth strata. Within the broader groups of our analysis, individual species may vary much more dynamically in their abundances at different stations.

Dinoflagellates were the dominant functional group in our samples, accounting on average for 27% of total microbial community biomass (including H-Bact), and 39% of the photo-autotrophs. Consistent with previous studies, dinoflagellates in the nano-size class were the major contributors to both autotrophic and heterotrophic biomass (Vors et al., 1995; Chavez et al., 1996; Stoecker et al., 1996; Verity et al., 1996; Mackey et al., 2002; Landry et al., 2003; Yang et al., 2004).

Diatoms, in contrast, comprised a small portion of autotrophic community biomass (~6%). Nano-size pennate forms dominated numerically and were a relatively consistent component of the community. Larger (~20 μm) diatoms were rare in general, but strongly enhanced in the areas of active upwelling and near the TIW-influenced area along the equatorial and 0.5° N zonal transects (Fig. 9). Even larger forms (~40 μm) dominated the community response when Fe or Fe + Si were added in microcosm grow-out experiments conducted on shipboard during the cruises (Brzezinski et al., 2011). Diatoms thus display a greater pronounced size dependency in terms of their ability to respond to natural variability or deliberate manipulations of growth conditions (Fe and Si concentrations) in the HNLC equatorial Pacific.

Our results indicate an autotrophic to heterotrophic biomass ratio of ~1.2 in the EEP. Prokaryotes (PRO, SYN and H-Bact) comprise 60% of the living biomass and are major contributors to both the autotrophic and heterotrophic components of the A:H ratio. Including ciliates, protistan grazers average about 39% of autotrophic carbon and 20.5% of the combined biomass of phytoplankton and H-Bact, which comprise the bulk of living food resources. Landry and Calbet (2004) have noted that 2 to 3:1 biomass ratios for autotrophs and protistan grazers are typical of open-ocean ecosystems with high grazing turnover and similar growth rates of grazers and prey. These factors suggest a relatively tight coupling between primary production and grazer utilization within the microbial community, as found previously in the EEP as well as in companion experimental studies (e.g., Landry et al., 1997, 2011; Selph et al., 2011).

H-Dino <20-μm were major contributors to heterotrophic biomass, and their distributions consistently followed Chl α and autotrophic biomass. H-Dinos >20 μm were more variable in distribution and most conspicuous at locations where autotrophic biomass was enhanced. Given the dinoflagellate propensity for
mixotrophic nutritional strategy, predatory feeding on more efficient competitors for Fe uptake may well explain how A-Dinos dominate autotroph carbon to such an extent. In addition, widespread phagotrophy among the A-Dinos would more than double the biomass of potential protistan grazers. Using fluorescently labeled bacteria (FLB) to track the uptake of bacterial-sized prey by pigmented and non-pigmented flagellates, Stukel et al. (this issue) have estimated that about half of the grazing could be due to cells that we have characterized here as autotrophs.

4.4. Physical controls on phytoplankton communities

Despite the appearance of relative constancy in many biological properties, the eastern equatorial Pacific is a dynamic region with strong currents, upwelling and propagating waves. System perturbations occur on varying time scales with changes in the strength of the trade winds, TIWs, and El Niño/La Nina events affecting nutrient delivery to the euphotic zone, and therefore biomass and production. To the west of our study region, the nutrient-rich EUC generally resides too deep to influence the euphotic zone, but it shoals as it enters the eastern equatorial Pacific, where normal upwelling conditions bring the upper EUC to photic depths. In the present study, the Fe content from upwelled EUC waters was sharply depleted between 140° and 110°W (Kaupp et al., 2011). That gradient is reflected in our findings of a W-E zonal decrease of Chl a and phytoplankton biomass along the equator (Fig. 2A). As noted above, Selph et al. (2011) determined that the Chl a response was largely explained by DVChl a, specific to Prochlorococcus. In contrast, the E-W carbon gradient is most apparent for larger phytoplankton, with A-Micro showing 3-fold higher biomass levels on the western portion of the equatorial transect (Table 1, Fig. 6). While cell abundances of PRO, SYN and A-Nano phytoplankton were also higher on the western side of the transect (135-140°W, Fig. 4), the interpretation of their biomass variations on the eastern side of our transect were more confounded by passing TIWs than those for larger autotrophs.

TIWs are anticyclonic vortices of about 500-km diameter which propagate from east-to-west along the equator, creating localized areas of upwelling and downwelling, respectively, on their leading and trailing edges (Flament et al., 1996). During the equatorial transect on EB04, the broad band of relatively low biomass between our sampling stations at 120° and 127°W was an area of strong southern flow (ADCP currents), and therefore in the trailing edge of a TIW (Selph et al., 2011). Since we traveled in the direction of TIW propagation on this cruise, we likely sampled the same feature at different locations over several days. At 116 W, samples from the leading edge (northward flow) of an adjacent vortex showed strong enhancement of PRO (A-Pico) and A-Nano, but no effect on larger phytoplankton (Fig. 6A). Similarly, stations sampled in the leading edge of a TIW (northward currents of >50 cm s⁻¹) between 125° and 130°W on the 0.5°N transect during EB05 showed pronounced increases in Chl a, PRO, A-Pico, H-Nano and A-Nano, but A-Micro biomass was anomalously low (Figs. 2, 4 and 6). Larger diatoms (>20 μm) were highest at two locations of southerly flow (125 W on the EB04 equatorial line, and 132.5 W on the EB05 0.5°N line), presumably catching TIW trailing edges. These few observations suggest that smaller and larger size classes of phytoplankton have different areas of enhancement in the TIW flow field and may vary out-of-phase spatially. Dynamically, it is not clear how in situ growth versus advective processes determine these observed effects. This is an area where Lagrangian-based experimental process studies tracking the movement of water parcels would be very helpful in elucidating the temporal and spatial scales of variability in TIWs and their relationships to ocean ecology and biogeochemistry.

Advective processes clearly have important influences on distributional patterns off the equator. The expected symmetry in biomass distributions as upwelled waters diverge to either side of the equator is best illustrated for the EB04 transect along 110°W (Figs. 2, 4, 6, 10). Symmetry was not evident, however, in sampling along the 140°W transect, where strong southward flow at the time of sampling pushed the center of the upwelling divergence to about 1°S. It is interesting to note that biomass levels for most plankton groups showed local minima in the zone of active equatorial upwelling at 110°W, while the area of upwelling centered south of 140° on EB05 was the site of biological enhancement for the same groups (Figs. 2, 4, 6, 10). Small and large plankton size classes co-vary at these two sites, presumably in response to the E-W gradient of bioavailable Fe, but different from the spatial separation of small and large cells in TIW flows. Selph et al. (2011) have suggested that variations in modes and rates of Fe delivery to the euphotic zone can impact the community structure of equatorial plankton in ways that are not expected from direct Fe fertilization of surface waters or shipboard microcosms (e.g., Coale et al., 1996). Our results further indicate that, even in a system renowned for its relative constancy, community responses to different drivers of physical variability do not necessarily follow the same pattern.

5. Conclusions

For 30 stations sampled over a broad area during two cruises in the eastern equatorial Pacific, the microplankton community displayed a remarkable constancy in integrated biomass, composition, size and depth structure, despite substantial environmental gradients and perturbations to the system from upwelling and TIWs. Nonetheless, the community was not everywhere the same, but it did respond to environmental variability following a consistent pattern. Of particular note, Prochlorococcus exhibited surprising variability given its generally assumed role as a stable background species in the tropical oceans. Higher concentrations of Prochlorococcus generally defined the areas of enhanced autotrophic carbon and Chl a, more so, in the case of the leading edges of TIWs, than the biomass of larger phytoplankton. Such complexities and departures from conventional wisdom speak to the potential difficulties of interpreting the fine-scale dynamics of phytoplankton community biomass and size structure from remotely sensed optical signals (e.g., Mouw and Yoder, 2005). Even when ambient standing stocks are directly measured, however, there are significant challenges remaining in understanding and modeling microbial community dynamics of the region. The present data, for example, do not elucidate the temporal and spatial scales of community responses to physical perturbations like upwelling and TIWs, which may have important implications for production processes, trophic coupling and biogeochemical cycling in the equatorial region. Future experimental studies need to be designed to understand community trajectories and underlying process rates in water parcels entrained in the equatorial flow field.

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