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The importance of *Prochlorococcus* to community structure in the central North Pacific Ocean

Abstract—Assessments of plankton community structure in the oligotrophic oceans based solely on microscopy may overstate the importance of heterotrophic bacterial biomass. Using flow cytometry to distinguish heterotrophic bacteria from the photosynthetic procaryotes *Prochlorococcus* spp., we found that *Prochlorococcus* contributed 31% of total bacterial counts in the upper 100 m at station ALOHA (22°45′N, 158°W). In terms of carbon, procaryotic biomass was the largest component (≥80%) of the microbial community, but almost half of this was photosynthetic biomass contributed by *Prochlorococcus*. Overall, the total 200-m integrated photosynthetic biomass exceeded heterotrophic bacterial biomass (55 vs. 45%). We suggest that the relative proportion of photosynthetic to heterotrophic bacterial biomass varies among oligotrophic regions of the ocean and that dominance by heterotrophic bacteria is not typical.

Flow cytometric analysis has provided significant new methodological capabilities in oceanography. The newly discovered group of photosynthetic procaryotes, *Prochlorococcus* spp., is an example (Chisholm et al. 1988). Not only are they very small, but typically they have very dim chlorophyll fluorescence making accurate enumeration by epifluorescence microscopy (blue-light excitation) almost impossible. Consequently, these cells have been overlooked in studies limited to microscopy counts (e.g. Fuhrman et al. 1989). Furthermore, when samples are labeled with DNA stains, such as DAPI or Hoescht 33342, and examined by epifluorescence microscopy (UV excitation), it is not possible to discriminate *Prochlorococcus* from heterotrophic bacteria because the chlorophyll fluorescence of the former is too dim. Epifluorescence bacteria counts, therefore, provide an estimate of total bacteria that overstates the importance of heterotrophic bacteria. In contrast, flow cytometric analysis of samples stained with Hoechst 33342 (e.g. Monger and Landry 1993) can be used to distinguish *Prochlorococcus* from nonphotosynthetic bacteria and to enumerate the bacterial component of the plankton accurately.

The biomass structure of oligotrophic ocean ecosystems has been the subject of several recent investigations. Heterotrophic bacteria were reported to be the dominant component in some instances (e.g. Fuhrman et al. 1989; Cho and Azam 1990), but at other locations they were found to equal phytoplankton (Li et al. 1992) or contribute a relatively smaller component, as in the case of the North Atlantic bloom study (Ducklow et al. 1993). Using dual-beam flow cytometry, we have examined the microbial community at the Hawaii Ocean Time series (HOT) station ALOHA in the central subtropical North Pacific to determine community structure and the relative importance of heterotrophic vs. photosynthetic components.

Samples were collected at station ALOHA (22°45′N, 158°W) during six cruises: HOT31 (October 1991) and HOT32–36 (December 1991–April 1992). Depth profiles were sampled (12 depths from 0 to 200 m) with a CTD Niskin rosette sampler. For enumeration of picoplankton, 1-ml samples were preserved with paraformaldehyde (0.2% final concn, PFA) and frozen quickly in liquid N_2, as previously described (Campbell and Vaulot 1993). For the larger phytoplankton (>3 to ~20 μm), a 200-ml volume from each depth was also preserved with PFA and stored refrigerated for immediate analysis on return to the laboratory (within 48 h).

Bacteria were enumerated with the Hoechst 33342 (0.5 μg ml^{-1}) staining protocol of Monger and Landry (1993) and dual-beam flow cytometry (200-mW UV and 1-W 488 nm) operating in colinear mode to distinguish *Prochlorococcus* from heterotrophic bacteria (Fig. 1). After staining for 2 h, samples were stored on ice until analysis to retain maximum chlorophyll fluorescence. Hoechst staining has been shown to be superior to DAPI because it

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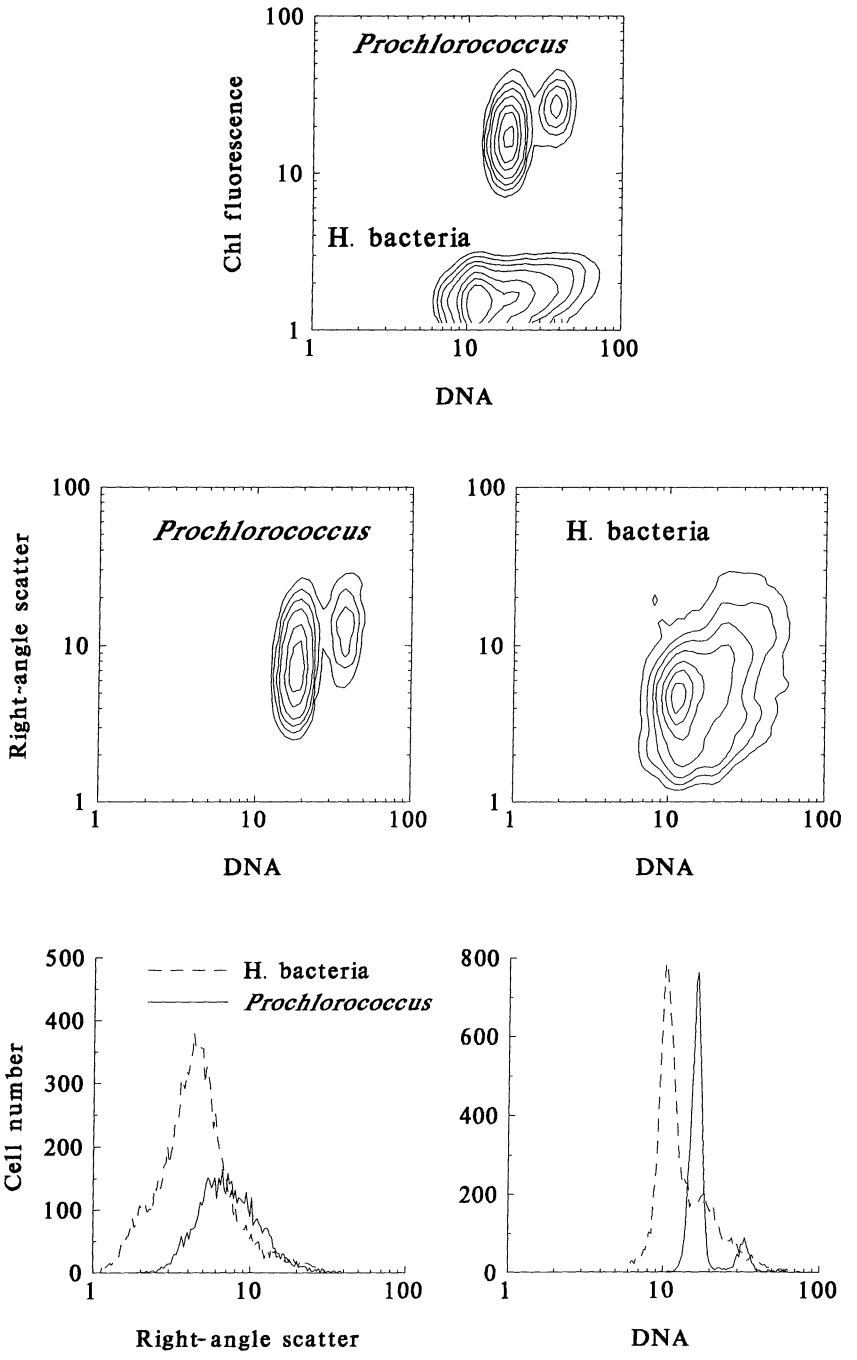

Fig. 1. February 1992 (HOT34) cruise; 78-m depth. Cytograms of chlorophyll fluorescence vs. DNA (stained with Hoechst 33342) (top) and DNA vs. right-angle light scatter (middle panels) for dual-beam (200-mW UV/1-W 488 nm) analysis. All parameters are expressed on log scales in arbitrary units. Increasing contour levels correspond to 2, 5, 10, 20, 50, 100, and 200 cells. The two bottom panels correspond to the one-parameter distributions for right-angle light scatter (left) and DNA (right).

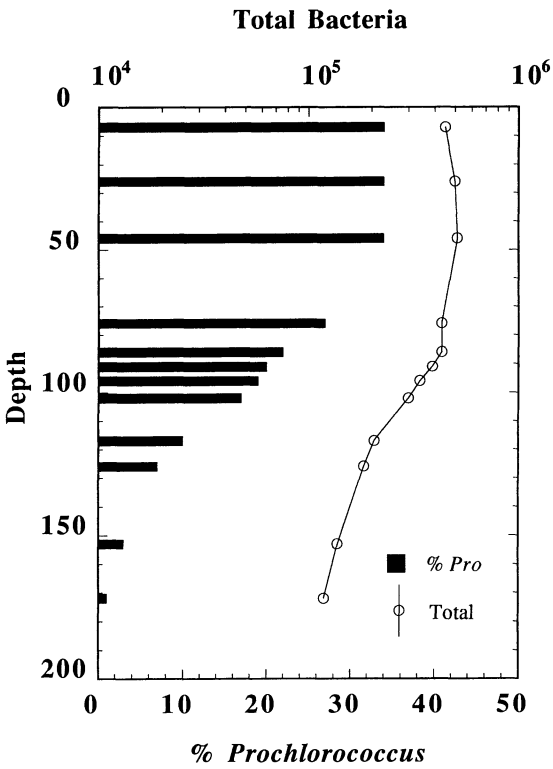

Fig. 2. January 1992 (HOT33). A typical depth profile of total bacteria abundance overlaid with the percentage of the total contributed by *Prochlorococcus* spp. (bar graph).

provides a higher signal-to-noise ratio and a lower C.V. for DNA fluorescence (Monger and Landry 1993). *Synechococcus* and the picoeucaryotes were analyzed with the standard 1-W 488-nm protocol described previously by Campbell and Vaulot (1993). For the larger phytoplankton, the laser and optical filter setups were the same, but we modified the sample delivery system (larger bore tubing and sample tube) so that samples were processed at ~10 ml min^{-1}. We found no significant difference between counts of phytoplankton samples fixed with PFA and glutaraldehyde (0.6% final concn) (Wilcoxon rank-sum test; $P > 0.05$).

To convert cell abundances to carbon biomass we used conversion factors from the recent literature so that our data would be comparable with similar studies. For heterotrophic bacteria (0.4–0.5-μm diam), we used 20 fg C $cell^{-1}$ reported by Lee and Fuhrman (1987) for cells ranging in volume from 0.036 to 0.073 μm^3. This value has been adopted by the JGOFS program (Ducklow et al. 1993). For *Prochlorococcus,* 53 fg C $cell^{-1}$ was determined assuming a 0.6-μm diameter (Morel et al. 1993) and 470 fg C μm^{-3} conversion factor for *Synechococcus* from Verity et al. (1992). Our size estimate for *Prochlorococcus* is lower than that of Chisholm et al. (1988) who reported 0.7-μm diameter. The smaller carbon content for heterotrophic bacteria is supported by light scatter data (an index of cell size): below the surface mixed layer (SML) the mean right-angle light scatter $cell^{-1}$ is smaller for heterotrophic bacteria than for *Prochlorococcus* cells (Fig. 1). The *Synechococcus* conversion factor 250 fg C $cell^{-1}$ (Kana and Glibert 1987) is similar to our calculated value assuming 1.0-μm diameter and 470 fg C μm^{-3}. For the eucaryotic algae, the relationship pg $C = 0.433 \times (\text{biovolume})^{0.866}$ was used to calculate carbon biomass (Verity et al. 1992). Cell volumes were calculated from dimensions measured by microscopic examination of cells from each of the 12 depths. Average cell volume for picoeucaryotes was 6.22 μm^3 and for larger algae 370 μm^3. Heterotrophic nanoplankton were not enumerated, so for "total living carbon" estimates the contribution of this fraction was assumed to be equivalent to picoeucaryotes for the same depth. Although possibly an overestimate, the assumed value for heterotrophic nanoplankton is a close approximation based on results of Landry et al. (1984) and Fuhrman et al. (1989) who enumerated both components.

Chlorophyll *a* and particulate organic C data (POC) were obtained from the HOT program (Winn et al. 1993; Tupas et al. 1993). POC data were corrected for a 60% (range 50–74%) loss of heterotrophic bacteria and a 15% (range 1–30%) loss of *Prochlorococcus* through the filter. These percentages were determined from flow cytometry counts of Whatman GF/F filtrates after processing 4–10 liters—the volumes routinely filtered for POC analysis. Although this is a small (<10%) correction to individual POC concentrations, as Li et al. (1992) also found, this correction becomes more significant (~20%) when comparing integrated POC values for a 200-m layer.

The range of total bacteria counts ($2–9 \times 10^5$ cell ml^{-1}) was typical for the oligotrophic ocean using epifluorescence microscopy (Cho and Azam 1990). Heterotrophic bacteria alone

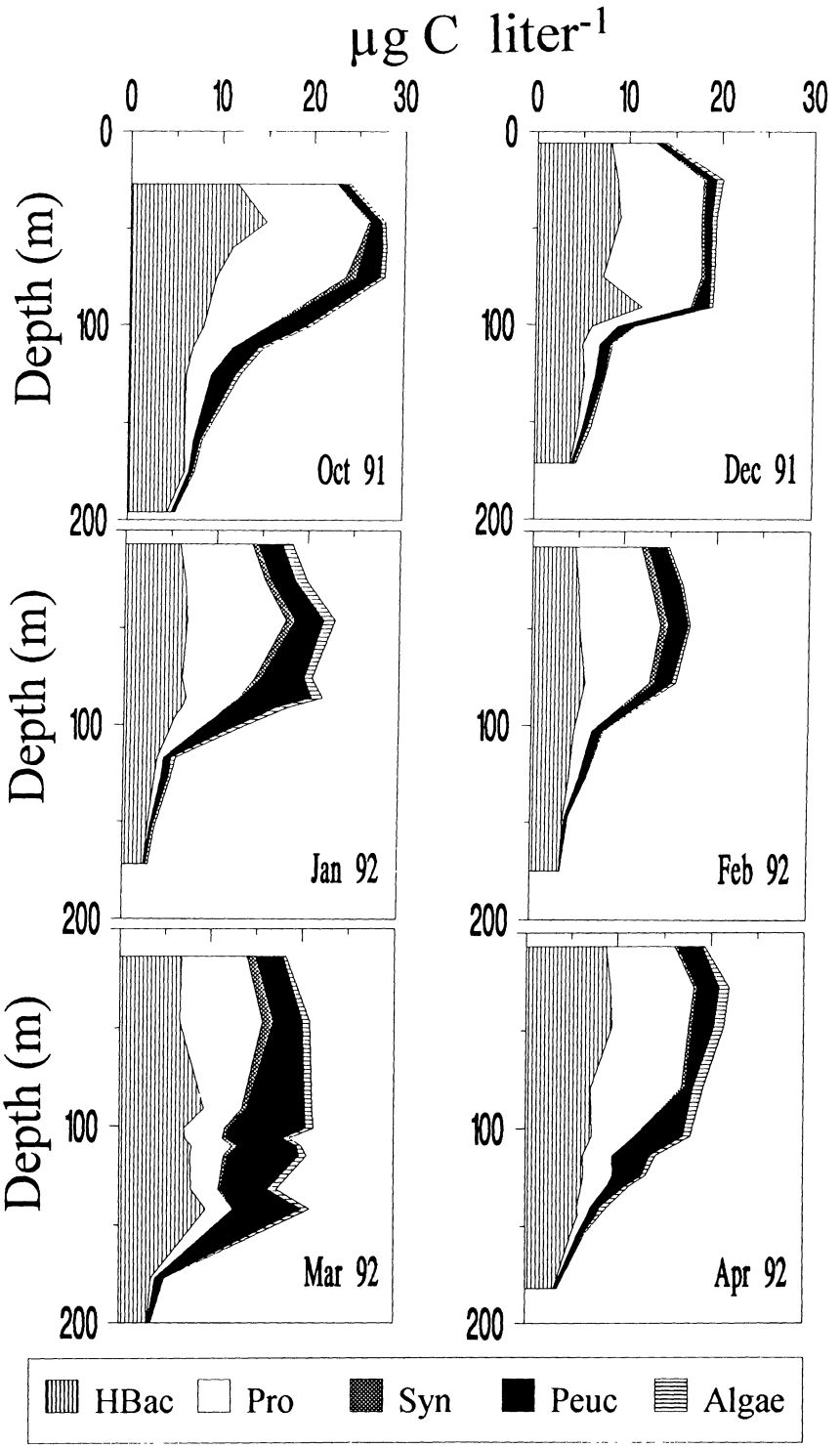

Fig. 3. Carbon biomass (μg C liter^{-1}) for heterotrophic bacteria (HBac), *Prochlorococcus* (Pro), *Synechococcus* cyanobacteria (Syn), <3-μm picoeucaryote algae (Peuc), and larger 3–20-μm algae (Algae) calculated from flow cytometry counts and conversion factors from the literature (*see text*) for station ALOHA cruises HOT31–36.

Table 1. Average percentages (and SE, $n = 6$) of the contribution to total carbon biomass for each component of the microbial community at station ALOHA (22°45'N, 158°W) during cruises in October 1991 and December 1991–April 1992 in the SML (0–75 m), at the DCM (~112 m), and below the 0.05% I_0 level (150–170 m), together with the overall percentage contribution for the 200-m water column and the average integrated values for biomass (mg C m^{-2}) (integrated). Data from Fig. 3.

Plankton component	SML	DCM	<0.05% I_0	Integrated	
	(%)			(%)	(mg C m^{-2})
Procaryotes					
Heterotrophic bacteria	40(2.2)	42(3.4)	70(2.0)	45	1,273(96)
Prochlorococcus prochlorophytes	44(1.1)	27(1.5)	10(0.7)	35	973(58)
Synechococcus cyanobacteria	3(0.1)	1(0.2)	0	2	58(9)
Eucaryotes					
Picoeucaryotes (<3 μm)	10(1.6)	26(3.1)	13(1.2)	14	404(67)
Large algae (3–20 μm)	3(0.6)	4(0.5)	7(0.9)	4	98(15)

ranged from 2.5 to 5.5 × 10^5 cell ml^{-1} in the SML from 0 to 75 m and decreased to <10^5 cells ml^{-1} below the euphotic zone. *Prochlorococcus* contributed an average of 31% (SE 1.3%, $n = 12$) of the total cells in the SML, 16% (SE 1.7%, $n = 6$) at the deep chlorophyll maximum (DCM; avg depth, 112 m; Letelier et al. 1993), and only 3% (SE 0.73%, $n = 6$) below the 0.05% incident light (I_0) depth (Fig. 2). Abundance profiles for other phytoplankton were similar to previous observations (Campbell and Vaulot 1993). Typically, these populations vary <2-fold over the year, and the larger phytoplankton are comparatively rare.

Vertical profiles of carbon biomass (Fig. 3) for the procaryotes show that *Prochlorococcus* and heterotrophic bacteria each contributed a large fraction of the total biomass, while *Synechococcus* was a minor contributor. These vertical profiles display the same distribution of total bacteria biomass as inferred from the lipopolysaccharide assay for the South China Sea (Maeda et al. 1983) and for station ALOHA (C. Winn pers. comm.). Maeda et al. (1983) could not explain why bacterial counts were greatest at 0–50 m depths; however, the abundance of *Prochlorococcus* in the surface layer could account for their observation. Additional biomass from photosynthetic picoeucaryotes was small, except at the DCM where the picoeucaryote contribution was maximum. Procaryotic biomass dominated (≥80%) the integrated 200-m water column (Table 1). Overall, the relative proportion of total photosynthetic biomass was greater than heterotrophic bacterial biomass [55% (SE 1.7%) vs. 45% (SE 1.8%), $n = 6$] during all cruises (Table 1).

To avoid any bias introduced by carbon conversion factors, we also calculated the contribution of each group to community structure based on biovolume alone. Using the same volumes as in the calculations above, we found no large difference from the carbon-based percentages (Table 1). Altogether, the procaryotic component contributed 2–5 times more biovolume than the eucaryotic phytoplankton. The estimated contribution by *Prochlorococcus* decreased by ~10% and the contribution by the large algae increased 2-fold when based on biovolume, so the relative percentages of integrated biovolumes for the photosynthetic and heterotrophic bacterial components remained the same. As an additional check, we assumed *Prochlorococcus* cell size increased from 0.6- to 0.7-μm diameter below the SML. We based this assumption on our observation of light scatter data (e.g. Fig. 1) which remained relatively constant throughout the upper 200 m for heterotrophic bacteria but increased below the SML for *Prochlorococcus*. Results of these calculations were again similar, and in fact much closer in agreement, to the carbon-based percentages.

For a more realistic characterization of the community composition based on carbon biomass, we examined samples from three strata within the upper 200 m: SML, DCM, and <0.05% I_0 (generally 150–170 m). Obvious differences in the composition were apparent at each depth (Table 1). Procaryotic organisms

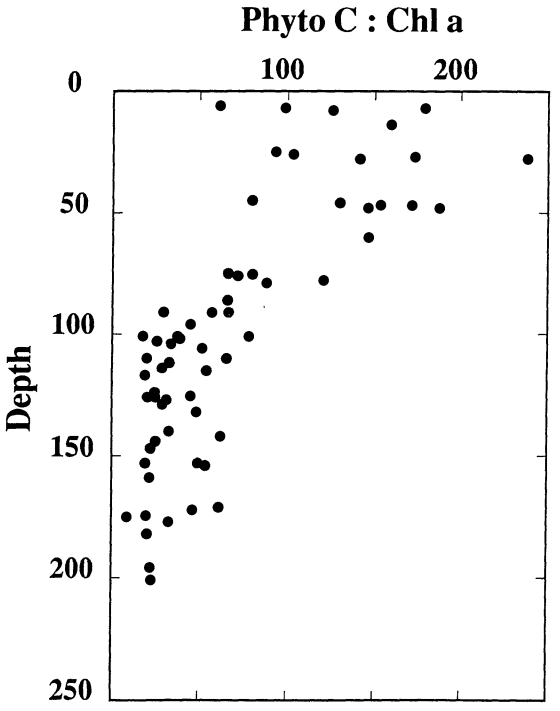

Fig. 4. The ratio of phytoplankton C to Chl *a* (Phyto C:Chl *a*) vs. depth for station ALOHA cruises HOT31–36. The average Phyto C:Chl *a* are 128 (SE 9.9, $n = 23$) for the SML, 40 (SE 0.5, $n = 23$) for the DCM, and 33 (SE 3.6, $n = 19$) below the 0.5% I_0. The overall average calculated from integrated 200-m water-column Chl *a* and Phyto C (Table 1) is 71 (SE 4.5, $n = 6$).

were the majority at all depths, but were ≥80% in both the SML and at 0.05% I_0. The contribution by heterotrophic bacteria alone increased with depth (Table 1). The picoeucaryotes biomass peak occurred at the DCM, but it was still a minor component in comparison to the procaryotes. The large eucaryotic algae contributed a small percentage throughout, although the very large and rare algae are probably underestimated due to sampling and analysis constraints. The calculated phytoplankton C:Chl *a* ratio decreased with depth from 128 (SE 9.9, $n = 23$) in the SML to 40 (SE 0.5, $n = 23$) at the DCM and to 33 (SE 3.6, $n = 19$) below the 0.05% I_0 (Fig. 4). These values are in close agreement with previous reports for the central Pacific (Furuya 1990), which further substantiates the conversion factors used for photosynthetic biomass calculations. Together, heterotrophic bacteria and *Prochlorococcus* were ~50% of the total POC (Table 2). Again, the *Prochlorococcus* contribution was greatest in the SML where it was 30% of the POC. Previously, estimates of total living POC (=heterotrophic bacteria + *Prochlorococcus* + cyanobacteria + phytoplankton + heterotrophic nanoplankton) were reported to be 50% of the total POC (e.g. Eppley et al. 1988). Our estimate of living POC for the SML at station ALOHA is considerably higher at 76% (Table 2).

Table 2. Contribution of plankton components to total particulate carbon. Average percentages (and SE, $n = 6$) of heterotrophic bacteria alone (HBac), heterotrophic bacteria + *Prochlorococcus* (HBac + Pro), phytoplankton (Phyto C = *Prochlorococcus* + *Synechococcus* + picoeucaryotes + large algae), and total living carbon (Live = HBac + Phyto C + heterotrophic nanoplankton) at station ALOHA at the SML, the DCM, and below the 0.05% I_0 level (as in Table 1). Heterotrophic nanoplankton biomass is assumed to be equal to picoeucaryote biomass (cf. Landry et al. 1984; Fuhrman et al. 1989).

Component of POC	SML	DCM	<0.05% I_0	Integrated
HBac	25(1.6)	30(2.8)	34(3.3)	30(2.0)
HBac + Pro	56(2.7)	44(4.7)	38(3.7)	46(3.7)
Phyto C	42(2.1)	31(5.6)	10(2.8)	30(3.0)
Live	76(3.4)	76(10.5)	49(6.0)	68(4.0)

Studies of community structure, in particular for the oligotrophic open ocean where *Prochlorococcus* is a considerable percentage of the total bacteria, can be inaccurate for a variety of reasons. If only epifluorescence microscopy is used, obviously *Prochlorococcus* will be overlooked in the phytoplankton total but counted as heterotrophic bacteria (e.g. Fuhrman et al. 1989). When flow cytometry is used to enumerate only *Prochlorococcus,* it is counted twice: first as *Prochlorococcus* (flow cytometry) and second as heterotrophic bacteria (epifluorescence microscopy) (e.g. Li et al. 1992). Similarly, in studies where Chl *a* is compared with epifluorescence microscopic counts, *Prochlorococcus* is included twice (e.g. Cho and Azam 1990). Thus, dual-beam flow cytometry provides one of the best ways to overcome these artifacts and provide accurate and statistically significant enumeration of the picoplankton, which is critical to biomass calculations.

Although frequently it is assumed that the open ocean is dominated by heterotrophic bac-

terial biomass, it appears that the relative proportions of photosynthetic biomass to heterotrophic bacterial biomass can vary among oligotrophic regions of the ocean. Comparison of the Sargasso Sea near Bermuda (Bermuda Atlantic time series study station) with the central North Pacific (Sta. ALOHA) provides an example. Total bacterial abundances are very similar between stations (Knap et al. 1993), whereas *Prochlorococcus* numbers are considerably lower at Bermuda (Olson et al. 1990; Campbell and Vaulot 1993). Procaryotic biomass is clearly the major component in both ocean regions, but the relative importance of heterotrophic biomass is significantly higher than at station ALOHA. The observations of heterotrophic bacterial biomass (even after correcting for double counting) in July 1989 near Bermuda (Fuhrman et al. 1989) may have been an extreme example. The relative importance of *Prochlorococcus* also differs among oceanic regions and seems to vary inversely with *Synechococcus* abundance (Campbell and Vaulot 1993). At station ALOHA, *Synechococcus* is a relatively small component in comparison with *Prochlorococcus,* but the northern Indian Ocean represents the opposite extreme: *Synechococcus* abundance is extremely high and exceeds *Prochlorococcus* abundance (Veldhuis and Kraay 1993).

It has been argued that heterotrophic bacterial growth rates are slower in oligotrophic than in coastal waters based on the observed high ratio of bacteria to phytoplankton biomass and the calculated bacterial consumption of primary production that would be required to maintain this ratio (Fuhrman et al. 1989). If, however, biomass is correctly allocated between heterotrophic and photosynthetic components—especially in regions such as station ALOHA where abundance of *Prochlorococcus* is very high (Campbell and Vaulot 1993)—heterotrophic bacterial growth rates may in fact be greater. Our results indicate we should reevaluate estimates of heterotrophic bacterial abundance and growth rates in oligotrophic regions of the ocean.

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Biogeochemical control of phosphorus cycling and primary production in Lake Michigan

Abstract—A 3-yr study in Lake Michigan has shown a 27 mmol P m^{-2} increase in the mass of total P (TP) in the water during spring when the lake is mixed from surface to sediment. This value is an order of magnitude greater than the annual P input from external sources. TP changed in concert with increases in chlorophyll *a* and organic N and decreases in nitrate and soluble Si. The concentration of soluble reactive PO_4^{3-} (SRP) remained relatively constant throughout the study. We hypothesize that the SRP concentration is maintained by a chemical equilibrium with calcium-phosphate species. The increased mass of TP arises from the sequestering of P by algae which displaces the chemical equilibrium and allows more P to be released to the water from the sediments. Solar irradiance and the duration of mixing determine the magnitude of the spring bloom and the demand for P that must be supplied through the flux of P from the sediments to the overlying water.

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Numerous studies have been conducted in the Laurentian Great Lakes and other freshwater bodies which indicate that phosphorus limits the growth of primary producers. There is, however, a growing body of evidence which suggests that internal supplies of P from the sediments can support new primary production (Caraco et al. 1992; Marsden 1989). Our observations in Lake Michigan suggest that the flux of P from the sediments is a significant source of P for the primary producers.

Monthly cruises were run during 1986–1988 to a 100-m-deep station in Lake Michigan, 27 km NE of Milwaukee, Wisconsin (43°11′40″N, 87°40′11″W). This station has been sampled on a regular basis for many years and is representative of the open waters of Lake Michigan during the spring mixing period. This assessment is based on previous sampling experience (Rousar 1973; Bartone and Schelske 1982) and the evaluation of satellite images showing uniform lake surface temperatures ≤4°C during spring at this and other offshore locations (Bolgrien and Brooks 1992).

Samples were collected with Niskin bottles at 10–14 depths (*see Fig. 1*). Temperature profiles were measured with a bathythermograph. Colorometric analyses were run for total P (TP), soluble reactive P (SRP), soluble Si, total or-