trapped aerosol from distant sources. Where aerosols of local origin are derived in part from the vegetation, they will also contain a significant proportion of material that was not ultimately derived from the local bedrock. These observations have implications for prospecting techniques based on vegetation or aerosol samples (*11*). The local nutrient reservoir is recycled from the forest floor to the standing crop of vegetation much more rapidly than nutrients are added to or lost from the reservoir. If that nutrient reservoir is lost, it is reestablished by both bedrock weathering and aerosol trapping, time-dependent processes with different rate controls. The time-integrated input of aerosols to forest nutrient reservoirs cannot be measured reliably without the use of an isotopic tracer.

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Autotrophic Picoplankton in the Tropical Ocean

Abstract. *In phytoplankton of the eastern tropical Pacific Ocean from 25 to 90 percent of the biomass (measured as chlorophyll* a*) and 20 to 80 percent of the inorganic carbon fixation were attributable to particles that could pass a screen with a 1-micrometer pore diameter. Evidence is presented that these are indeed autotrophic cells and not cell fragments.*

Members of the diverse ocean plankton community vary in size over seven orders of magnitude: their taxonomy and even trophic status, is often uncertain (*1*). Because of the complexity, a complete analysis of structure and function along taxonomic lines is usually not possible. However, analysis based on size as the single, critical characteristic of organisms has some advantages in that it is observable (*2*), has value as a physiological scale (*3*), and has been used as the basis of a theory of pelagic ecosystem structure (*4*).

Physiological experimentation on plankton of less than 10 μm depends heavily on the separation of various size fractions by differential filtration through membrane filters of varying nominal pore sizes (*5*). Organisms ("particles") from 0.2 to 2.0 μm, the picoplankton (*2*), have been implicated in heterotrophic processes (*6*) and in autotrophic production (*5*, *7*). Chroococcacean cyanobacteria have been identified as an important fraction of the picoplankton (*8*), suggesting that this fraction is photoautotrophic, but their rate of fixation of inorganic carbon in the light in the open ocean is not known. Sorokin (*9*) measured the fixation of inorganic carbon in the dark and considers that in this size range autotrophy is negligible in comparison to heterotrophy (*10*), but his results have been challenged (*11*). Finally, some investigators claim (*12*) that particles in the picoplankton size range that contain photosynthetic pigments do not represent intact viable cells but are fragments or degradation products of larger cells.

We studied two sites in contrasting oceanographic regimes (*13*): the Costa Rica Dome (9°25′N 89°30′W), an offshore site where upwelling is important to the physical and ecological dynamics (*14*), and a site called Biostat (9°45′N 93°45′W), which was selected to represent a regime typical of large tracts of the tropical ocean. Biostat is characterized by a vertical structure that is stable in time and highly uniform in horizontal extent. Samples were taken daily for 6 days at each station in March 1981.

Many of our results refer to measurements made on size-fractionated samples. We assume (*15*) that perforated polycarbonate membrane filters (Nuclepore) effect a quantitative separation of size fractions of seston. Our operational definition of picoplankton is particles that pass a 1-μm Nuclepore filter at 18-kPa vacuum but are retained on either Whatman GF/F glass fiber filters or 0.2-μm Nuclepore filters. At Biostat, 94 percent of the $^{14}CO_2$ fixation measured on 0.2-μm Nuclepore filters is retained on GF/F filters (*16*). The two sites were similar in that a substantial proportion of the total chlorophyll *a* (as determined fluorometrically on acetone extracts) was found in particles passing 1-μm Nuclepore filters (Fig. 1). At the Costa Rica Dome, where day-to-day variability in unfractionated chlorophyll was appreciable (Fig. 1C), most samples had between 25 and 70 percent of particulate chlorophyll *a* in the picoplankton size fraction (Fig. 1A). At Biostat, where the absolute concentration of chlorophyll was lower (Fig. 1D), 55 to 90 percent of the total chlorophyll *a* was commonly found in this fraction (Fig. 1B). Measurements of fluorescence in vivo on whole and size-fractionated samples, with and without the addition of the photosynthetic inhibitor DCMU (*17*), indicated the same relationship between size fractions and between sites as did measurements of extracted chlorophyll.

Samples were preserved with glutaraldehyde plus paraformaldehyde and concentrated on 0.4-μm Nuclepore filters. The filters were examined by epifluorescence microscopy (excitation, 365 nm; emission, > 450 nm) which revealed red and orange autofluorescing particles similar to the coccoid cyanobacteria (*8*). The particles were concentrated more in the euphotic zone (0 to 50 m) than below it, and they were much more abundant at the Costa Rica Dome (Fig. 1E) than at Biostat (Fig. 1F).

The high counts from the euphotic zone at the Costa Rica Dome (0.5×10^6 to 1.5×10^6 cells per milliliter) are about three times the maximum reported by Waterbury *et al.* (*8*) and 15 times the maximum reported by Johnson and Sieburth (*8*). The concentrations of cyanobacteria at Biostat were two orders of magnitude lower than at the Costa Rica Dome and were at the low end of the range reported by Waterbury *et al.* but similar to the direct counts reported by Johnson and Sieburth for the open

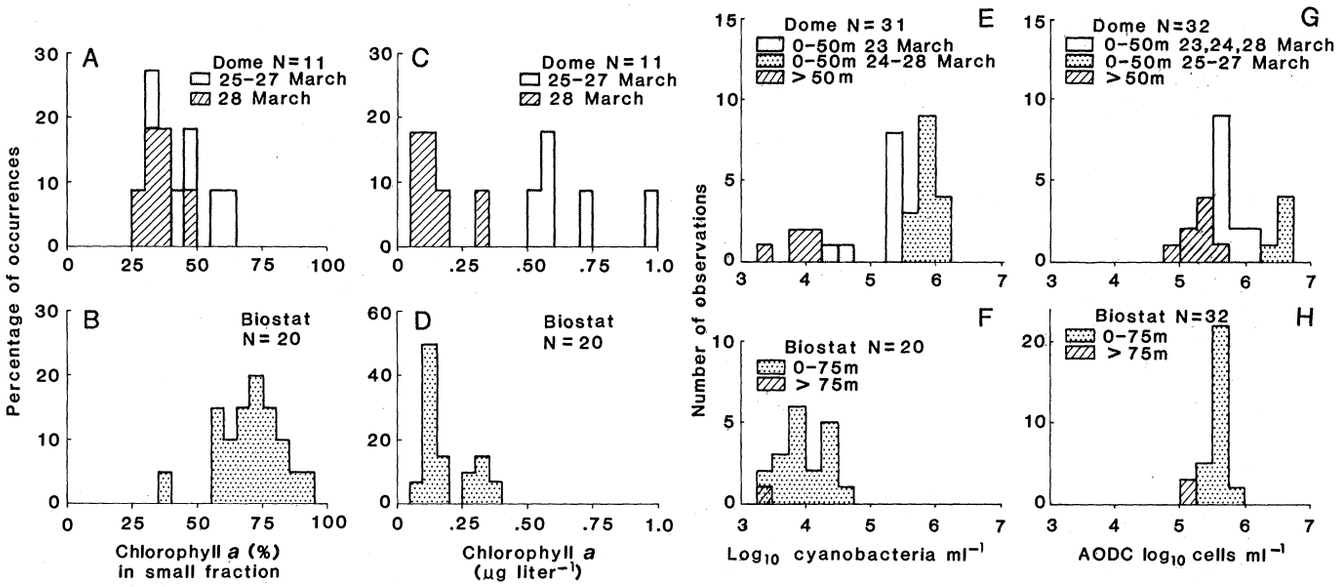

Fig. 1. Chlorophyll *a* in the small size fraction; percentage of chlorophyll *a* retained on a GF/F filter at (A) the Costa Rica Dome and (B) Biostat; micrograms of chlorophyll *a* (per liter) at (C) the Costa Rica Dome and (D) Biostat. Direct counts of micororganisms: cyanobacterial abundance from direct counts by epifluorescence microscopy on preserved samples at (E) the Costa Rica Dome and (F) Biostat. Total bacterial abundance from acridine orange direct counts at (G) the Costa Rica Dome and (H) Biostat. The euphotic depth at the Costa Rica Dome was 50 m and at Biostat, 75 m.

ocean. The relatively low counts at Biostat were apparently not an artifact of preservation or microscopic technique (*18*). We also observed aggregates of cyanobacteria comprising up to 96 cells.

At the Costa Rica Dome, cyanobacterial counts and chlorophyll concentrations for the small size fraction were compatible measures of photoautotrophic biomass: we assumed that cyanobacteria are spheres 1.0 μm in diameter and our estimate of 0.5×10^{-15} g of chlorophyll *a* per cell corresponds roughly to what we measured. However, at Biostat, chlorophyll concentrations in the small size fraction were substantially higher than expected from cyanobacterial counts (*19*) even though the autofluorescing particles had similar dimensions at both sites and despite the fact that chlorophyll per cell would be expected to be higher, if different at all, at the upwelling site (*20*). Counts of total bacteria (autotrophic and heterotrophic) (Fig. 1, G and H) made by the acridine orange epifluorescence microscopic technique (*21*) showed that cyanobacteria comprised a much smaller proportion of the total bacteria at Biostat than at the Costa Rica Dome.

More than 70 percent of the total measurable activity of the enzyme ribulosebisphosphate carboxylase (RuBPC) was found in the picoplankton fraction at both sites, providing additional evidence of the association of small particles with primary production. The relative difference of absolute RuBPC activity in the small size fraction between sites was about five- to tenfold, more consistent with chlorophyll concentration than with cyanobacterial counts.

The photosynthetic activity of the particles in the picoplankton fraction can be inferred from the uptake of ^{14}C-labeled bicarbonate during simulated in situ experiments. The percentage contribution of picoplankton to the total uptake of $H^{14}CO_3^-$ (Fig. 2A) increased with depth. At the Costa Rica Dome, the uptake in

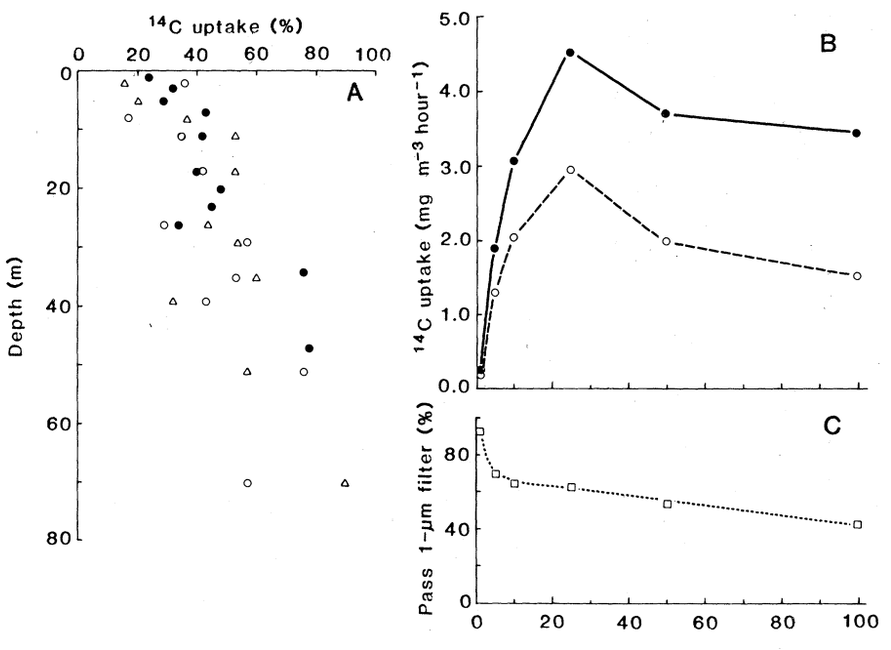

Fig. 2. (A) Depth profiles of photosynthesis associated with particles passing 1-μm Nuclepore filters. Closed circles represent Costa Rica Dome station (28 March 1981). Open circles and triangles represent Biostat stations, 31 March and 3 April 1981, respectively. Results from 8-hour incubations in light-attenuated deck incubators. (B) Effects of light intensity on photosynthetic rate of size-fractionated plankton from the Costa Rica Dome, 27 March 1981. Closed circles denote total production; open circles represent production passing a 1-μm filter. Sample taken from 10 m and incubated under a range of light intensities. (C) Results of experiment in (B): picoplankton ^{14}C activity as a percentage of total activity.

the small size fraction was about five times higher in absolute terms than that at Biostat and was equal (on a per cell count) to the maximum rate reported by Morris and Glover (*22*) for cultures of *Synechococcus* sp. (strain DC-2).

The relative enhancement of inorganic carbon uptake in the small size fraction at depth is apparently attributable to the ability of the small phytoplankton to use relatively dim light efficiently: a sample from 10 m incubated under a range of light intensities, showed a photosynthetic response (Fig. 2B) similar to that observed for vertical profiles of simulated in situ photosynthesis (Fig. 2, A and C).

Investigation of the dynamic role of the < 1-μm size fraction with radioisotope tracers is not straightforward since there are several possible routes for the transfer of radiolabeled carbon from dissolved $H^{14}CO_3^-$ to the picoplankton. These include direct uptake by both picophototrophs (photosynthetic and nonphotosynthetic) and picoheterotrophs (nonphotosynthetic), as well as indirect uptake by picoheterotrophs of radiolabeled excreted photosynthates. To determine the relative importance of the various routes, we monitored time courses of ^{14}C accumulation in different size fractions.

The light-dependent nature of ^{14}C accumulation was evident from an experiment in which radiolabeling of picoplankton was monitored 22 hours (Fig. 3A): the rate of accumulation was substantially less during the dark period than the rates in the light periods preceding and succeeding it. These results alone, however, do not force us to reject the hypothesis that picoplankton are nonphotosynthetic. It is possible that the light dependence of ^{14}C accumulation in picoplankton reflected a tight coupling in the sequence of tracer movement from bicarbonate to net- and nanophytoplankton to excreted dissolved organic material to picoplankton. However, in a parallel incubation of the same water sample from which net- and nanoplankton were initially excluded by screening (1-μm Nuclepore), the same light dependence was observed in the rate of radiolabeling in the picoplankton (Fig. 3B). We therefore conclude that the picoplankton were photosynthetic.

Since the picoplankton included phototrophic members, we investigated the possibility that this photoautotrophic fraction excreted radiolabeled photosynthates which were then taken up by heterotrophic members of the same size class. An illuminated water sample was labeled with radiocarbon for 5 hours and then screened (1-μm Nuclepore). The picoplankton that passed through the screen were incubated for five more hours. Since the sequence from inorganic carbon to phototrophs to soluble organic carbon to heterotrophs is probably a simple catenary sequence, a time lag would be expected in the appearance of label in components in the sequence farthest from the source of inorganic carbon (*23*). During the 5 hours of incubation before filtering, we assume the pool of soluble photosynthates, whether derived from net- and nanophytoplankton or from picophototrophs, to be uniformly available for assimilation by the picoheterotrophs. When the net- and nanophytoplankton were removed by filtering, we might expect some time to pass before the picoheterotrophs diminished the photosynthate pool and shifted down to a rate of ^{14}C accumulation commensurate with photosynthate excretion only by the picophototrophs.

If this were the case, the rate of ^{14}C accumulation by picoplankton after removal of the larger organisms should gradually diminish. In fact, the rate of ^{14}C accumulation by picoplankton after removal of net- and nanoplankton was constant (Fig. 3D) and the same as that of a parallel picoplankton sample that was labeled in the absence of larger organisms (Fig. 3C). This suggests that the rate of ^{14}C accumulation by picoplankton was independent of the rate of ^{14}C excretion by phototrophs. Since the size and specific activity of the various pools are not known, these results do not constitute definitive evidence of the relative unimportance of exudates in accounting for ^{14}C in picoplankton. However, the results are corroborated by a distinctly different kinetic pattern for the accumulation of a mixture of tritiated amino acids (Fig. 3E) formulated to resemble a typical algal protein hydrolysate (*24*). The simplest hypothesis that we find to be consistent with all the observations in Fig. 3 is that most of the ^{14}C that appears in the picoplankton during the light period is due to photosynthetic assimilation.

Our measurements indicate that a substantial proportion of the autotrophic

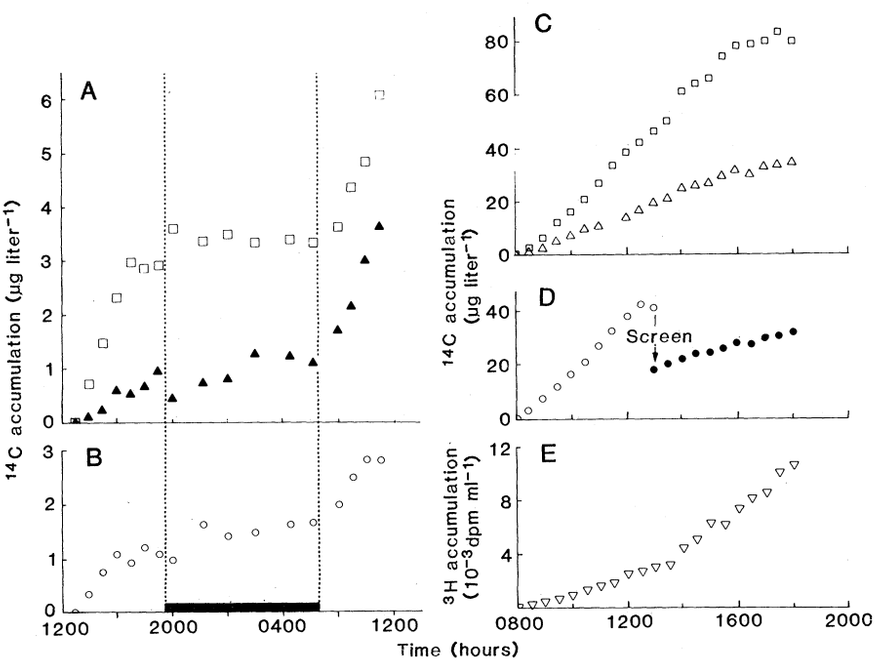

Fig. 3. (A and B) Time course of ^{14}C accumulation by plankton radiolabeled with $NaH^{14}CO_3$ (1.0 μCi ml^{-1}) from a sample collected at Biostat from a depth of 35 m and incubated on deck at 25 percent incident surface irradiance. (A) $NaH^{14}CO_3$ was introduced to the intact sample at 1300 hours and, at the times indicated, plankton were collected on 1-μm Nuclepore membranes (□); filtrates passing the 1-μm filter were collected on 0.2-μm Nuclepore membanes (▲). (B) $NaH^{14}CO_3$ was introduced at 1300 hours to the portion of the sample passing a 1-μm Nuclepore membrane and plankton collected on 0.2-μm Nuclepore membranes (○). (C to E) A sample collected at the Costa Rica Dome from the sea surface was incubated on deck at 25 percent incident surface irradiance. (C) Time course of ^{14}C accumulaton by plankton labeled with $NaH^{14}CO_3$ (1.0 μCi ml^{-1}). Parallel incubations were performed with an unscreened sample (□) and one screened through a 1-μm Nuclepore membrane before labeling (△). (D) A third parallel incubation was performed with an initially unscreened sample (○); at 1300 hours, the sample was screened through a 1-μm Nuclepore membrane and the incubation continued (●). (E) Time course of ^{3}H accumulation by plankton labeled with a mixture of ^{3}H–amino acids (0.01 μCi ml^{-1}). A fourth parallel incubation was performed with a sample screened through a 1-μm Nuclepore membrane before labeling (▽). All samples were then collected on 0.2-μm Nuclepore membranes.

production at two oceanic sites in the Pacific is associated with particles able to pass 1-μm screens. The importance of this fraction increases toward the base of the euphotic zone, a feature that is understandable in terms of the higher effective optical cross section for smaller cells (*25*), which leads to a higher efficiency of utilization of the available light at depth. We cannot exclude totally the possibility, at least at the Biostat site, that there may be a population of very small pigmented cells that did not survive normal sampling procedures, is invisible to conventional light microscopy, or did not respond to our incubation techniques (that is, did not survive the experimental procedure).

Our results, the time-course measurements in particular, indicate that the picoplankton include photosynthetically active cells. These results are contrary to those reported by Herbland and LeBouteiller (*12*), who concluded that the size fraction of particles < 3 μm comprised mainly inactive phytoplankton. Their results, however, may not be definitive because the filters they used as terminal screens (effective pore size 2 to 3 μm) may have been too coarse (*26*).

A probable corollary to our results is that, because the autotrophic cells in the picoplankton fraction are active rather than dormant or inert, they or their aggregates must be grazed by some organism or organisms at about the same rate as they are being produced. These results support a view of the structure of the pelagic ecosystem in which most of the activity (production and metabolism) is carried by very small organisms (*27*). The significance for quantification of autotrophic biomass and primary production in the ocean is that use of filters not able to trap particles at least 0.2 μm or smaller will lead to results that are too low.

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18. Fresh samples excited at 400 nm (Zeiss BG12) and preserved samples excited at 450 to 490 nm (acridine orange combination) yielded the same counts as preserved samples excited at 365 nm.
19. The discrepancy between cell counts and chlorophyll measurements could be reconciled in terms of "excess chlorophyll" or "invisible photoautotrophs" at Biostat. The excess chlorophyll may represent detrital chlorophyll-like pigments [Gieskes *et al.* in (*12*)] or fragments of larger algae disrupted during sampling and filtration [Lasker and Holmes, in (*12*)]. Cyanobacteria that are not visible for direct counting have been reported [Johnson and Sieburth, in (*8*)]; also, fragile flagellated forms have been observed to "simply vanish" during preparation for enumeration [R. R. Parker and D. J. Tranter, *Aust. J. Mar. Freshwater Res.* **32**, 629 (1981)]. To calculate chlorophyll per cell we used the following constants: specific gravity, 1.0; ratio of dry to wet weight, 0.1; ratio of carbon to dry weight, 0.4; and ratio of carbon to chlorophyll *a*, 40.
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8 September 1982

Sulfide Binding by the Blood of the Hydrothermal Vent Tube Worm *Riftia pachyptila*

Abstract. *The blood of the deep-sea hydrothermal vent tube worm* Riftia pachyptila *Jones contains a sulfide-binding protein that appears to concentrate sulfide from the environment and may function for sulfide transport to the internal endosymbiotic bacteria contained within the coelomic organ, the trophosome.*

Clusters of the large red vestimentiferan tube worm *Riftia pachyptila* (phylum Pogonophora) occur in association with actively venting warm water at deep-sea hydrothermal vent sites, including the Rise site at 21°N on the East Pacific Rise (*1*). The worms at this site live where water temperatures average about 10°C (*2*) and hydrogen sulfide is present (*3*). *Riftia pachyptila* has internal bacterial symbionts that appear to be capable of oxidizing sulfide to obtain energy (*4*). The trophosome organ, which contains the bacterial symbionts, is highly vascularized and is linked to the apparent site of gas exchange, the obturacular plume, by dorsal and ventral blood vessels, with a heart located in the dorsal vessel (*4, 5*). We have examined the role of the hemoglobin-containing blood (*6, 7*) of this animal in the transport of sulfide from the obturacular plume to the trophosome. We show that the blood of *R. pachyptila* has a high capacity for sulfide and has the ability to transport sulfide as well as other gases to the internal bacterial symbionts.

The tube worms were collected at 2600 m by the D.S.R.V. *Alvin* from the collapsed pit site (20°50′N, 109°06′W) on the East Pacific Rise at 21°N (*1*) and were brought to the surface in thermally insulating polyethylene boxes. We collected blood from the freshly recovered living animals. The experiments described in this report were done on fresh vascular blood while we were on board the R.V. *Melville* at the hydrothermal vent site (except in the one case noted). The vascular blood was collected by dissection of the worm to expose the anterior section of the large dorsal vessel