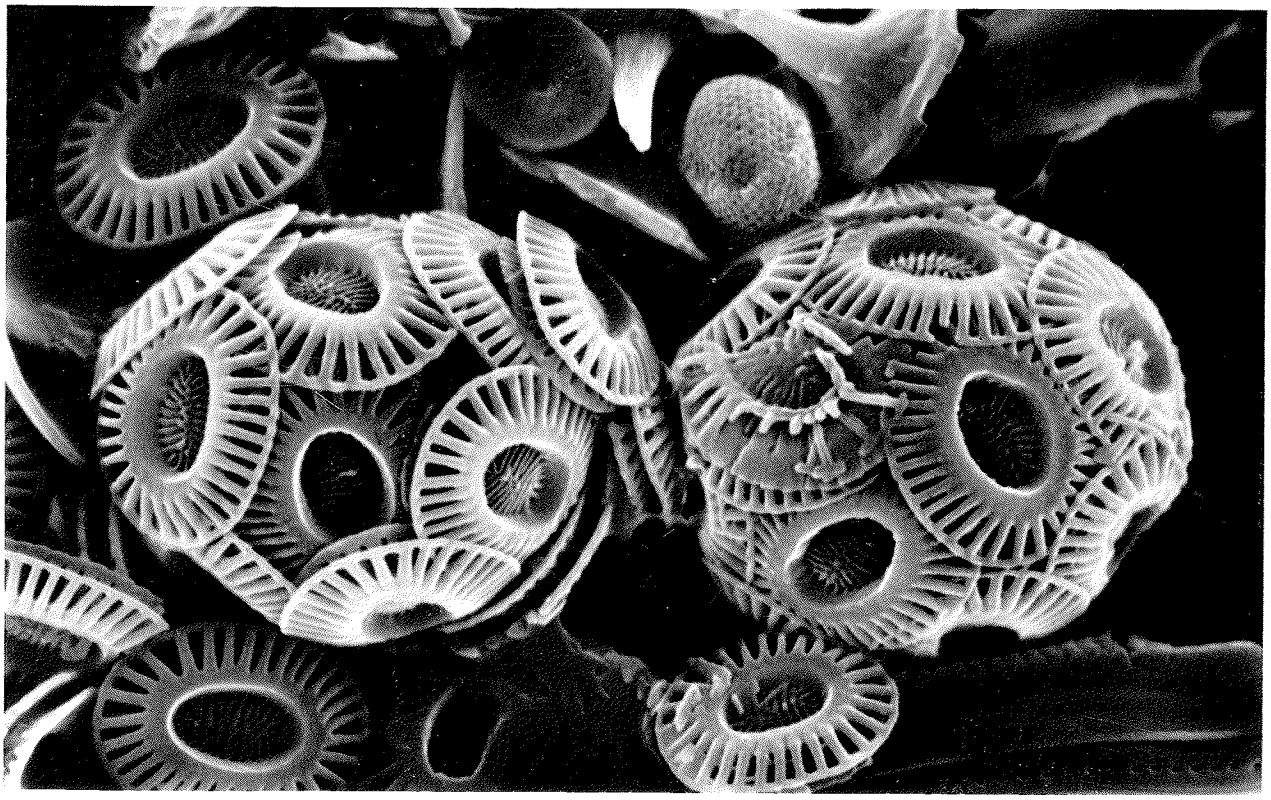
Calcareous Nannoplankton Biocoenosis:

Sediment Trap Studies in the Equatorial Atlantic, Central Pacific, and Panama Basin

John C. Steinmetz



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Explanation of Cover Photo: Two coccospheres of *Emiliania huxleyi* (Lohmann) from PARFLUX Station E in the western Tropical Atlantic Ocean collected at a trap depth of 389 m. *E. huxleyi* is the dominant species of coccolithophore in the world's oceans. Each coccosphere pictured here is 6 μm in diameter.

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Calcareous Nannoplankton Biocoenosis: Sediment Trap Studies in the Equatorial Atlantic, Central Pacific, and Panama Basin

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Abstract

Sediment traps deployed on three moored vertical arrays collected particles at various depths in the equatorial Atlantic (Station E), central Pacific (Station P_1), and in the Panama Basin (Station PB_1). The calcareous nannoplankton from the <63 μm size fraction were studied in order to characterize the flux of coccospheres and coccoliths, the taxa present, and their condition of preservation throughout the water column.

The average calculated flux of coccospheres ranged from a low value of 24 coccospheres/m^2 /day in the central Pacific, to an intermediate value of 4725 in the equatorial Atlantic, to a high of 8030 in the Panama Basin. In general, the coccosphere flux decreased with depth at all three sites.

Coccolith fluxes and flux profiles were significantly different at each of the three sites. At Station E, the flux decreased regularly with depth but increased sharply at the lowermost trap (724 m above the bottom). The average flux for the entire column was 316 × 10^6 coccoliths/m^2/day. At Station P_1, the flux was low in the shallowest two traps and increased markedly in the three deepest traps. This increase is due mainly to a suspected Umbilicosphaera sibogae *bloom which occurred shortly before the traps were deployed in September 1978. The highest coccolith flux was recorded in the Station PB_1 traps averaging 910 × 10^6 coccoliths/m^2/day. The flux profile at this station was essentially constant in the shallowest four traps and decreased almost 59% in the lowermost two traps. The average coccolith carbonate fluxes for the entire columns for the Stations E, P_1, and PB_1 are, respectively, 2.53, 2.68, and 7.28 mg/m^2/day. These fluxes represent minimum values, since coccospheres and coccoliths were also contained in fecal pellets and other particles larger than the size fraction studied (<63 μm).*

Scanning electron microscopic examination of the trap samples revealed 56 species belonging to 33 genera of calcareous nannoplankton. Three new species are described and illustrated: Alisphaera spatula *n. sp.,* Umbilicosphaera calvata *n. sp., and* Umbilicosphaera scituloma *n. sp.*

A census of taxa present, including their relative frequency and state of preservation, is presented together with a photographic atlas of the taxa. Station E is the most diverse with 50 species, and is the best preserved of the three sites. Station PB_1 the least diverse with 26 more poorly preserved species. In general, the best preserved specimens were observed in the shallowest sample at each of the three sites; diversity and state of preservation diminished with increasing depth.

Introduction

Calcareous nannoplankton, or coccolithophores, are pelagic, single-celled, golden-brown algae that secrete calcite plates or shields. Nannoplankton are one of the major constituents of marine phytoplankton and are, therefore, important primary producers in the food chain (e.g. Haq, 1978). Together with planktonic foraminifera and pteropods, they constitute the major contributors of calcium carbonate to the water-column and the sea-floor.

Calcareous nannoplankton characteristically form spherical cells known as coccospheres. Each coccosphere is covered with a layer or several layers of calcite shields called coccoliths. Coccoliths are secreted internally and then extruded to the surface of the coccosphere where they form a coating or armor around the cell. Coccoliths range in size between 1 and 10 μm in diameter, and the average coccosphere is between 5 and 20 μm in diameter. Occasionally coccoliths are sloughed off or lost, or they may be freed when a coccosphere disaggregates.

Much of our knowledge regarding the geographic distribution and preservation of calcareous nannoplankton is derived from plankton-tow, water-casting and surface-sediment studies. Plankton-tow or water-casting studies have provided us with qualitative and quantitative information regarding the vertical distribution and seasonal variation in abundance and composition, and with standing stock estimates of nannoplankton. Such measurements, however, do not translate directly into sedimentation rate, accumulation rate, or even preservational state of nannoplankton on the sea-floor. Surface-sediment studies may yield information concerning the spatial distribution of calcareous nannoplankton in the overlying waters; however, they provide little to the understanding of rates of coccolith production and vertical transport. Until recently, oceanographers have not had a means to investigate the processes by which these minute particles settle to the sea-floor.

Simple, yet elegant, calculations by Honjo (1976), using the Stokes' relationship for the settling of particles in a fluid, have shown that an individual coccolith from a coccosphere would take several tens of years to settle unassisted in the open ocean. Certainly, within a fraction of that time, a calcite particle would likely drift far beyond its original latitudinal zone distribution and would undergo marked, if not complete, dissolution. Yet, well-preserved coccolith ooze is present on the deep-sea floor beneath an overlying euphotic community that is identical to it in assemblage composition.

Nannoplankton populations in the open ocean are under high grazing pressure from zooplankton and are therefore likely to be consumed before completing their life cycle (Honjo, 1975). Nannoplankton are among the flora consumed by grazing zooplankton and commonly pass through the gut of these tiny organisms with no mechanical or chemical effect on the calcite coccoliths. Fecal pellets of zooplankton occasionally consist almost exclusively of coccoliths. Often delicately preserved, intact coccospheres are found within pellets (Honjo, 1975, 1976; Honjo and Roman, 1978). Fecal pellets and other oceanic macroaggregates are believed to be responsible for the rapid vertical transport of the majority of coccospheres and coccoliths through undersaturated waters to the sea-floor (Honjo, 1975, 1976; Honjo and Roman, 1978). Such a transport mechanism also explains why coccoliths occur below the calcite saturation depth and may exhibit little or no effect of progressive dissolution.

Individual coccoliths found at depth in the water column have either descended very slowly to that point (very unlikely) or have been released from a fecal pellet that transported

them to that depth (Honjo, 1976). In this paper, the term "free-coccolith" is used, and is here defined as a coccolith found separate or free in the water column or retained in a sediment trap. Free-coccoliths are likely to have been liberated (released) from fecal pellets (or similar aggregate particles) which have broken or biodegraded and spilled their contents. Fresh coccoliths or coccospheres are thus replenished at all depths by descending fecal pellets (Honjo, 1976). If coccoliths are released from the host fecal pellets, their rate of descent decreases a thousand-fold, and they are fully exposed to undersaturated deep water (Honjo, 1975). Upon their release from a fecal pellet, their residence time at depth in the water column is relatively short and they are quickly remineralized. Thus, free-coccoliths dissolve before they arrive at the sea-floor and do not disturb the bio-thanatocoenosis correspondence between the surface water community and the surface sediment assemblage (Honjo, 1976).

With the advent of sediment-trap technology, scientists are now able to deploy anchored or floating collecting devices for days to months in the open ocean. Once retrieved, the quantities and identities of these particles can be ascertained, and particle fluxes directly calculated (Wiebe et al., 1976; Honjo, 1978, 1980; Spencer et al., 1978; Soutar et al., 1977; Knauer et al., 1979; Rowe and Gardner, 1979; Thunell and Honjo, 1981). By measuring the flux of calcareous nannoplankton to the sea-floor we can determine how the biocoenosis (living assemblage) is transformed into the thanatocoenosis (death, or sedimentary, assemblage). We can then better estimate the importance of calcareous nannoplankton to the calcium carbonate cycle in the oceans.

To date, little assessment of the assemblage composition, amount, and preservational condition of calcareous nannoplankton from sediment trap experiments has been attempted. Honjo (1976) reported on a study of the contents of zooplankton fecal pellets collected in a sediment trap (Wiebe et al., 1976). The trap was deployed at 2,200 m for two months in the Tongue of the Ocean, Bahamas. He found that about 80% of the pellets contained hard skeletons of phytoplankton (coccoliths and diatoms) and clay mineral-like particles. The preservation of the coccoliths was excellent. Honjo (1976) determined that the average fecal pellet collected contained 0.8 μg of $CaC0_3$, which he estimated to be equivalent to approximately 1×10^5 coccoliths or 5,000 average-size coccospheres. He also calculated the horizontal drift of an average fecal pellet descending through a 5,000 m water column and estimated the resolution of replication of the bio- and thanatocoenosis to be better than 200 km.

Sediment trap experiments are particularly important in obtaining information about the transport of material through the water column. The Particulate Flux Experiment (PARFLUX) was designed to measure total particulate flux to the sea-floor (Honjo, 1980). A part of the program involved deploying a series of sediment trap arrays in different oceanographic conditions. Material collected provides an unusual opportunity to measure and compare total coccosphere and coccolith fluxes in regions of vastly different surface productivity, as well as to document the biocoenosis of calcareous nannoplankton at these locations.

Time-series PARFLUX sediment traps were utilized by Samtleben and Bickert (1990) to collect coccoliths at monthly increments for a year at three locations in the Norwegian Sea. Results of the analyses are an important contribution to our understanding of coccolith seasonality, species composition, and selective preservational processes in high-latitude waters.

The purpose of this article is to document the character, quantity, and preservation of coccospheres and coccoliths recovered from three vertical sediment-trap arrays deployed in different water masses. Presented for the first time are measured flux values for coccospheres and coccoliths in tropical areas. These values are presented in both flux of particles, as well as in flux of equivalent calcium carbonate to their respective locations in the water column. An atlas of calcareous nannoplankton illustrates the taxa recovered at the three trap sites.

Oceanographic Setting of the Sediment-Trap Stations

The PARFLUX experiment was designed to measure, characterize, and compare the flux of particulate matter in different oceanographic regions having significantly different levels of productivity. Of the three locations discussed here, the Panama Basin has the highest level of primary productivity. The levels of biological productivity in this region of upwelling exceed an annual average of 1,000 mg $C/m^2/day$ in the euphotic zone (Forsbergh, 1969; Love, 1970, 1971; Moore et al., 1973). Station P_1 in the central Pacific lies within the area of lowest level of biological productivity of the three regions considered. The station is north of the eastern equatorial Pacific high productivity region and exhibits a productivity of less than 100 mg $C/m^2/day$ (Koblentz-Mishke et al., 1970; van Andel et al., 1975). Station E in the western tropical Atlantic displays a level of primary productivity that is somewhat intermediate between those of the Panama Basin and central Pacific stations.

Station PB_1 is located in the northeast quadrant of the Panama Basin. The Panama Basin lies in the eastern equatorial Pacific Ocean and is bounded on the east by the Isthmus of Panama between Central America and South America, on the northwest by the Cocos Ridge, and on the south by the Carnegie Ridge. The hydrography of the east tropical Pacific region adjoining the Panama Basin is dominated by the Equatorial Current system. Here lies the eastern terminus of the Equatorial Counter Current and the place of origin of the westward flowing North and South Equatorial Currents (Smayda, 1966). Surface circulation in the Panama Basin is characterized by a counterclockwise eddy, except during February and March. During these months of the upwelling season, the southernmost loop of the eddy continues directly into the South Equatorial Current (Cromwell and Bennett, 1959; Smayda, 1966), instead of flowing eastward toward the coast of South America and then northward into the Gulf of Panama as the Columbia Current (Wooster, 1959).

Annually, the region is successively influenced by the movement of the Trade Winds-Calm Belt (Doldrums) climatic system. From January through April, the dry, northerly, offshore winds of the northeast Trade Winds prevail over the area and induce upwelling. During upwelling, the surface waters are displaced offshore and replaced by colder, more saline and nutrient-rich water. In late April or May, the northeast Trade Winds usually weaken and dissipate, move northward, and are progressively replaced by the Doldrums and the southeast Trade Winds. The rain-bearing southeast Trade Winds are southwest, relatively light and shallow onshore winds that usually persist until mid-December. For 8 months, heavy rains diminish ocean mixing. The surface waters become warm, diluted, and nutrient-impoverished. A slight resurgence of northerly winds during July and/or August may induce mixing or even cause a slight upwelling. During the rainy season, a progressive southerly migration of the Trade Winds-Calm Belt (Doldrums) system re-establishes the northeast Trade Winds in the region by December (Wooster, 1959; Smayda, 1966).

Details of the oceanography of the Panama Basin have been described in reports by Wooster and Cromwell (1959), Wyrtki (1967), Forsbergh (1969), and Stevenson (1970). Upwelling in the Panama Basin is largely responsible for the high productivity of the waters. Productivity is highest near the coastal margins and over the Carnegie Ridge (Moore et al., 1973). The sediments in the Basin are dominated by biogenous components, except near the coast where terrigenous input is high. The character and distribution of the sediments are discussed by Kowsmann (1973), Moore et al. (1973), van Andel (1973), Heath et al. (1974), and Yamashiro (1975).

Station P_1 is located between the Molokai and Clarion Fracture Zones in the east Hawaii Abyssal Plain, one of the largest basins in the North Pacific Ocean. The area exhibits unusually monotonous flat topography, and no significant submarine features (ridges, seamounts, or volcanoes) occur within 450 km of the station (Honjo, 1980). The nearest continental landmass is 3,350 km away (Monterey, California). Station P_1 lies within the main axis of the westward-flowing North Equatorial Current (Tchernia, 1980). Bottom sediments in the area consist of consolidated clay with alternating thin ferro-manganese laminations (R/V KANA KEOKI Cruise Report, September 1978, Hawaii Institute of Geophysics). Calcium carbonate comprises less than 10% of the sediment (Berger et al., 1976).

Station E is located in the western tropical Atlantic at least 750 km from the nearest landmass (Guyana coast). The station is situated within the north westward-flowing North Equatorial Current (Tchernia, 1980). The underlying Demerara Abyssal Plain has a gentle topography, is relatively flat, and gradually deepens northward toward the eastern end of the Puerto Rico Trench.

Logistics

The samples used in this study were collected from sediment trap arrays located in the western equatorial Atlantic (Station E), the central North Pacific (Station P_1) and the Panama Basin (Station PB_1) (Figure 1 and Table 1). At Station E (13°31′N, 54°00′W) four sediment traps were deployed at various depths between 389 and 5,068 m in 5,288 m of water for a period of 98 days from November 1977 to February 1978. At Station P_1 (15°21′N, 151°28′W) five sediment traps were deployed between 378 and 5,582 m in 5,792 m of water for a period of 61 days from September to November 1978. The third array, at Station PB_1 (5°21′N, 81°53′W), consisted of six traps placed at depths between 667 and 3,791 m in 3,856 m of water for 112 days from July to November 1979.

The PARFLUX Mark II sediment trap was used at all three locations. The details of the design and engineering were presented in Honjo (1980) and Honjo et al. (1980). The trap opening is 1.5 m^2 and contains hexagonal baffle cells to minimize water turbulence in the trap. The sediment receiving cup is located at the bottom of the trap. Sodium azide (NaN_3) bacteriocides diffuse through a series of porous membranes to prevent degradation of organic matter in the cup. Each receiving cup was automatically sealed 3 days prior to recovery.

Table 1: Sediment Trap Logistics.

	PARFLUX E	PARFLUX P_1	PARFLUX PB_1
Location	13°30'N, 54°00'W	15°21'N, 151°28'W	5°21'N, 81°53'W
Ocean/Basin	Equatorial Atlantic/ Demerara Abyssal Plain	Central Pacific/ E. Hawaii Abyssal Plain	Eastern Pacific/ Panama Basin
Term	11/77–2/78	9/78–11/78	7/79–11/79
Duration	98 days	61 days	112 days
Trap Depths	389 m 988 m 3,755 m 5,068 m	378 m 978 m 2,778 m 4,280 m 5,582 m	667 m 1,268 m 2,265 m 2,869 m 3,769 m 3,791 m
Ocean Depth	5,288 m	5,792 m	3,856 m

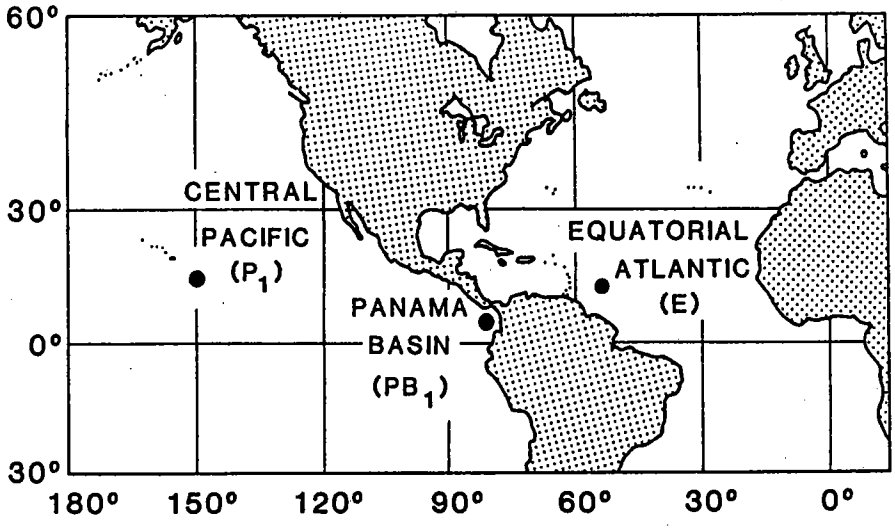

Figure 1: Geographical locations of the three sediment-trap sites.

Laboratory Procedures

Sample Preparation

The sediment trap samples were processed, split, and stored according to the methods discussed in Honjo (1980). The <63 μm size-fraction from each sediment trap sample was wet split into aliquots using a precision rotary splitter (Honjo/Erez splitter, Honjo, 1978). The laboratory procedures were performed on the following fractional aliquots: Station P_1 samples: 1/256 aliquot; Station E samples: 1/256 aliquot; and Station PB_1 samples: 1/1024 aliquot. Using pipettes, subsamples in the fractional aliquots were taken for the three assessments to be described (i.e., coccosphere studies, coccolith studies, and SEM studies). The coccospheres and coccoliths were enumerated using separate procedures. This is because of the size differences between coccospheres and coccoliths, but particularly due to the frequency of coccoliths that was several orders of magnitude greater than that of coccospheres.

The total liquid volume of each sample was between 60 and 160 ml. Each sample was stored in a 1-liter bottle. The size of the bottle and amount of liquid in each were such that the sample could be gently swirled and thoroughly agitated to disperse and randomize the solid particles within the liquid without losing sample. A few crystals of mercuric chloride ($HgCl_2$) were added to each bottle to inhibit bacterial growth.

Coccosphere Studies

The Utermöhl or Inverted Microscope Method (Utermöhl, 1958; Lund, Kipling and LeCren, 1958) was used to count coccospheres. In order to concentrate the particulate material, a 5-ml aliquot of liquid was withdrawn from an agitated sample container and deposited in a 10-ml-capacity glass settling chamber. The particles were allowed to settle to the bottom of the settling chamber for two hours and were then identified and counted from beneath, using an inverted microscope.

Samples observed to be too dense were diluted with buffered, filtered sea-water to either 1/10 or 1/20 their original volume. Five diameter-transects of the settling chamber were counted, and based on the average number of coccospheres per transect, the total number of coccospheres in the entire chamber was estimated. The following rationale was used in making this calculation: The ratio of the whole settling chamber bottom area to the area of a one-diameter transect is:

$$\frac{\pi r^2 2}{2rw} = \frac{\pi r}{2w}$$

where **r** is the radius of the chamber and **w** is the width of the diameter transect. The total number of coccospheres in the entire chamber equals:

$$\frac{\pi r}{2w} \times N$$

where **N** is the average number of coccospheres in a one-diameter transect.

In this study, for example, the 10-ml-capacity settling chamber had a diameter of 25 mm, and the width of the transect (defined using a ×40 objective lens) was 0.54 mm. Therefore, the ratio of the whole bottom area to the area of one diameter transect was 36.36.

Only complete coccospheres or obviously ruptured spheres were counted; aggregates or clumps of coccoliths were not. The estimates of the numbers of coccospheres per milliliter represent a minimum; coccospheres less than about 10 μm were not recognizable using a $\times$40 objective lens ($\times$400 total magnification). Therefore, all small coccospheres, especially *Emiliania huxleyi*, were not accounted for in the estimates. Thoracospheres and individual scyphospheres also were not counted.

The total number of coccospheres in the original sediment trap sample was calculated by taking the product of the number of coccospheres per milliliter, the original volume of liquid sample in the fraction aliquot, and the inverse of the fractional aliquot. The coccosphere flux was calculated by dividing the total number of coccospheres by the area of the sediment trap opening (1.5 m^2), and by the number of days the trap was deployed (see Table 1).

Coccolith Studies

Experiments were performed using various cell-counting chambers in order to find the most appropriate for counting coccoliths at the magnification required for their identification. The Sedgwick-Rafter and Palmer-Maloney types provide for small volumes of liquid (1.0 ml and 0.1 ml, respectively), but the densities of coccoliths present were too great to count practically. The hemocytometer with improved Neubauer ruling was found effective for counting coccoliths, considering the magnification required and the density of individuals per sample volume. The hemocytometer has two counting chambers consisting of nine ruled squares, each 1.0 mm on a side. Each 1 mm^2 area is further equally subdivided into twenty-five squares. With the coverslip in place, the chamber is 0.1 mm deep and the volume of a 1 mm^2 area is 1 mm^3. Since 1 ml = 10^3 mm^3, the volume of one 1 mm^3 area is 0.0001 ml. Similarly, the volume of a 1/25 mm^2 area is 0.000004 ml (= 4×10^{-6} ml). The conversion factor used to obtain the number of coccoliths per milliliter, from the average number of coccoliths in a 1/25 mm^2 area is 4×10^6.

Sample preparation for the hemocytometer consisted of withdrawing a 2-ml aliquot of liquid from the agitated sample container and depositing it in a test tube. The tube was agitated for thirty seconds on a vortex mixer at its highest speed setting to disarticulate coccospheres and aggregates. A drop of liquid containing the sample was then introduced into each of the two chambers of the hemocytometer. Rapid, continuous diffusion beneath the coverslip ensured that the distribution over the counting grid was even. The coccoliths in the liquid were allowed to settle 2–4 minutes before enumeration.

A 1/25 mm^2 area of the hemocytometer fills the field of view of a compound microscope set for a magnification of $\times$250 with a $\times$20 objective. Coccoliths are readily visible at this magnification. The coccoliths in twenty to forty 1/25 mm^2-areas in each of the two chambers were counted, with the aid of a hand tally, and an average number of coccoliths for each area calculated.

Immediately following a counting procedure, the chambers were rinsed with fresh water, followed by ethyl alcohol, and wiped dry with lens paper. This ensured rapid and smooth distribution of the next sample.

The total number of coccoliths in the original sediment trap sample and the coccolith flux were respectively calculated in the same manner as those for coccospheres. The coccolith carbonate flux was calculated by assuming coccoliths to be pure calcium carbonate with an