Biophysical forcing of particle production and distribution during a spring bloom in the North Atlantic

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Abstract—As part of the North Atlantic Bloom Experiment (NABE), CTD/transmissometer profiles were made on two cruises at 47°N, 20°W in spring 1989 to quantify the increase in particles during a phytoplankton bloom in relationship to biophysical forcing factors. Water samples were filtered to obtain particle mass concentrations for calibration of beam attenuation (beam c) from the transmissometer. Shipboard experiments demonstrated that beam c resulted primarily from the concentration of small particles (<20μm), with little signal coming from the aggregates or dregs that settle to the bottom of water bottles. Profiles of beam attenuation showed a three-fold increase in the surface mixed layer over a 2-week period. Superimposed on this increase were daily variations with evening highs and morning lows. Increases in beam attenuation resulted primarily from increases in particle mass generated through primary production. Some portion of the diel variation may be a physiological response to light. Nighttime decreases could be caused by remineralization, biological consumption and vertical migration, dilution by diurnal increases in the mixed-layer thickness, and large-particle production with subsequent settling (fecal pellets, aggregates). Linear regression of beam attenuation values versus time at multiple depths over the first 2-week period suggested a three-layer system with particle production in the top 50 m, particle loss down to 400 m (most rapid loss between 50 and 200 m) and a slow increase in particles from 400 to 2000 m. Caution is urged, however, in blindly treating the data as time-series measurements of conditions in a homogenous parcel of water, since the ship had to relocate as it followed buoys drogued at different depths drifting in divergent directions in a mesoscale eddy field.

Wind mixing, stratification and solar radiation were obvious influences on the rate of particle increase in surface waters. Depth-integration of beam attenuation over 20 and 50 m revealed that the increase in derived particle organic carbon (POC) can account for only about 18–28% of the drawdown of total CO2. Fluxes measured by drifting sediment traps at 150 m can be satisfied by the settling of only 2–4% day−1 of the standing crop in the upper 100 m, but the particles would have to be converted into larger, more rapidly settling particles to be collected effectively in sediment traps. Based on the drawdown of CO2 and the standing crop of particles, significant primary production must have occurred before we arrived on day 115. Our data demonstrate that the transmissiometer is an effective optical tool in monitoring the dynamics of particles in surface waters and its signal can be quantitatively related to biological processes in the ocean.

INTRODUCTION

The production and destruction of particles is a major control of biogeochemical cycles that influence the distribution of elements and compounds in the ocean. During biological production, nutrients and CO2 are taken up in surface waters and transformed into solid particles. Removal of particles results from grazing, sinking, dissolution and oxidation.
reactions. The degradation processes release nutrients, DOC and CO$_2$ in both surface waters and at depth, and consume O$_2$. Instruments have been developed to make continuous measurements of physical parameters such as temperature, salinity and depth, but most measurements of CO$_2$, nutrients, DOC and POC still require the acquisition and tedious analysis of discrete water samples. The measurement of total particle concentrations or of specific organismal abundance (phytoplankton, bacteria, etc.) has traditionally relied on acquisition of water samples for filtration and enumeration. In the open ocean biological production is the dominant source of particles in the near surface layer. The mass concentration of these particles is generally in the range of tens to hundreds of $\mu$g$^{-1}$ in the surface layer, decreasing rapidly with depth to 10–20 $\mu$g 1$^{-1}$ (BREWER et al., 1976). Interfacing optical instruments with CTDs has made it possible to collect continuous measurements of optical properties in seawater that can be related quantitatively to biological processes (DICKIE, 1991). For example, continuous fluorescence measurements are correlated with chlorophyll a concentrations, though photo-inhibition in surface waters necessitates calibration with discrete water samples (SMIT and BAKER, 1985; BARTZ et al., 1988). Continuous profiles of particle concentration can be obtained through a correlation with beam attenuation coefficients (beam c) from transmissometers (SPINRAD et al., 1983; BAKER and LAVELLE, 1984; GARDNER et al., 1985; MOODY et al., 1986; BISHOP, 1986). Because most particles in the surface ocean are of local biological origin, changes in particle concentration with time have been used to estimate primary production (SIEGEL et al., 1989; CULLEN et al., 1992) and compared with rates based on $^{14}$C incubation of water samples.

One of the goals of the Joint Global Ocean Flux Study (JGOFS) is to determine the rate at which CO$_2$ from the atmosphere is sequestered in the ocean. Quantitatively connecting aircraft- or satellite-derived chlorophyll concentrations to rates of primary production and then to particle export fluxes at various depths in different environments requires much more information about the parameters that affect each of those processes than presently exists. A satellite’s sensing depth in the ocean is a function of the penetration of solar radiation, which varies with particle concentration and type. The depth from which 90% of the satellite-detected irradiance is received varies from about 25 m in open ocean gyres to about 3 m in productive oceanic waters (SMITH and BAKER, 1978). In coastal waters non-biogenic particles decrease the sensing depth even further. As a result, the chlorophyll maximum is usually excluded from remote sensing. Continuous profiles of optical parameters from ships reveal detailed structure in vertical distributions of properties that can improve our understanding of biological and physical processes and their linkages. The North Atlantic Bloom Experiment (NABE) in 1989 provided an opportunity to make frequent profiles of beam c during the evolution of a phytoplankton bloom at the same time that a wide suite of other controlling parameters were being measured.

**METHODS**

_Cruise Atlantis II 119—leg 4_

The sampling strategy in NABE was to drift with a patch of water and monitor the changes in water properties and processes. In practice, two drifting buoys were deployed only 3 h apart when we arrived at 47°N, 20°W (Fig. 1). One was John Martin’s (MLML) 1500-m deep drifting sediment trap array and the other was Chris Langdon’s (LDGO)
Fig. 1. Contours of temperature at 100 m from CTD profiles during AI1 119—leg 4. Pluses indicate station locations. The wide grey line is the western eddy boundary based on satellite crossings between year days 111 and 127 (ROBINSON et al., 1993). The thin grey line trending SE and then curving NE is the track of a 1500 m drifting sediment trap array (MARTIN et al., 1993) and the solid black line spiraling clockwise is the track of a 90 m oxygen array (C. LANGDON, personal communication). The inset diagram shows the outline of the entire eddy for year days 111–127 (wide grey line) and for the western portion of the same eddy for days 128–144 (black line). The ship’s tracks for leg 4 (western track) and leg 5 (eastern track) are included in the inset.

90-m drifting array with oxygen sensors. Both were tracked by ARGOS satellite transmitters. A primary productivity array drogued to 125 m was deployed each morning and recovered at sunset by John Marra’s group (LDGO). CTD casts were made nominally at dawn and dusk by members of SIO’s Ocean Data Facility (ODF).

**Cruise Atlantis II 119—leg 5**

Leg 5 sampling began with a rendezvous at 46° 28’N, 17° 48’W with R.V. Meteor and R.V. Discovery. After 2 days of joint sampling the R.V. Atlantis II moved NW to retrieve and sample in the vicinity of the 1500-m trap array deployed during leg 4. Soon after the trap recovery a severe storm terminated CTD sampling for nearly 2 days. The ship returned SE to the vicinity of 46° 20’N, 17° 55’W where sampling proceeded for the next 10 days. A primary productivity array drogued to 125 m was deployed generally every other morning and recovered 24 h later. SIO CTD casts were usually made between 1100 and 2100 h.

Transmissometer data were collected on both legs using a Sea Tech (BARTZ et al., 1978) 25 cm pathlength beam transmissometer ($\lambda = 660$ nm) connected to SIO’s Neil Brown CTD and a 30-l bottle rosette (bottle design identical to Niskin bottles). Transmissometer windows were carefully cleaned prior to each CTD cast, and air calibrations of the units used were made in the laboratory at the beginning and end of each cruise to correct for any
decay of the LED beam intensity. Readings with the light path blocked and unblocked were made through the CTD electronics prior to several casts to test for any voltage losses through the CTD. Per cent transmission was recorded through the CTD and converted to a total beam attenuation coefficient ($c$) using the equation:

$$\frac{V}{S} = T = e^{-cz},$$

where $V$ is the instrument voltage output, $S$ is the maximum voltage of the transmissometer output, $T$ is per cent transmission, $c$ is the beam attenuation coefficient with units of m$^{-1}$, and $z$ is the optical pathlength in meters. Transmission was then corrected with the Sea Tech algorithm for the effects of temperature, salinity and pressure on the density of water and its effect on attenuation. An additional algorithm corrected for any non-linearities in the A–D board of the CTD as a function of temperature and voltage, which, for the SIO CTD, were very minor. No corrections were made for the small differences which can occur between down and up traces as a result of a time lag between internal and external temperatures, primarily because the temporal/spatial variability in attenuation between the down and up profiles was much greater than the calculated temperature correction (based on a modified scheme of that proposed by Bishop, 1986).

The beam attenuation coefficient in natural seawater is a summation of the beam attenuation coefficients for seawater ($c_w$), “yellow matter” ($c_y$), and particles ($c_p$) (Pack et al., 1988);

$$c = c_w + c_y + c_p.$$  

The contribution of $c_w$ is constant and is set at the factory to equal 0.364 m$^{-1}$ in particle-free water for this instrument. At 660 nm $c_y$ is assumed constant and negligible (Bricaud et al., 1981), but we performed an experiment at sea to verify this as will be discussed shortly. Therefore, since variations in beam attenuation result primarily from changes in particle concentrations, our beam attenuation data here are reported as $c_p$. To obtain $c_p$, $c$ was calculated from the corrected transmission values. The minimum value, $c_{min}$, for the 2 weeks at 47°N, 20°W was subtracted from all $c$ values to yield a pre-adjusted $c_p$ (beam attenuation due to particles alone). A linear fit was performed between the pre-adjusted $c_p$ values and the particle mass concentrations obtained from water filtered from the rosette water bottles (see below). The x-intercept value of $-0.0125$ m$^{-1}$ was subtracted from the pre-adjusted $c_p$ to obtain a $c_p$ that was zero for a particle mass concentration of zero.

During leg 4, between 1 and 20 l of water (usually 5–10 l in the surface 100 m, and 10–20 l in deeper water) were vacuum-filtered in-line from 30-l water bottles through pre-weighed 0.4 μm Poretics PCTE membrane filters (similar to Nuclepore filters). The filters were rinsed in a glove-box 10 times with distilled, deionized and 0.4 μm filtered water to flush the salt from the filter, then air-dried in the glove box and oven-dried for about 10 min at 60°C. At least one filter was put through this process during each cast without exposing it to seawater to establish an average blank value for methodological corrections.

After the water had been filtered down to the spigot level on several casts, the water remaining below the spigot was transferred through a tube to a polycarbonate flask, poured into a Millipore funnel filtration apparatus, filtered onto a Poretics filter, and treated as above. The volume of water below the spigot (referred to as the “dregs” volume) was generally about 1 l. The mass of particles in the dregs volume in excess of the concentration determined for water above the spigots was assumed to have been
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distributed evenly throughout the 30-l water bottle. Particle concentrations for both the “regular” and “dregs-corrected” samples were then determined (GARDNER, 1977). CTD cast 23-4 was a special cast where all bottles were tripped at about 50 m to test for a temporal effect on dregs concentrations. Upon arrival on deck, 1 l was drawn from several bottles and filtered onto a Poretics filter using a Millipore glass funnel filtration apparatus. The spigots were opened after increasing lengths of time, the bottles were drained, and the dregs water was removed and processed as above.

To compare in situ c with c in rosette water bottles, samples to 500 m from cast 19-2 were drawn through tygon tubing into a clean, 15-cm dia PVC cylinder. A transmissometer was inserted into the cylinder and beam c was calculated from the per cent transmission measured. A second sample from each bottle was filtered into clean, evacuated glass carboys. The filtered water was transferred into a clean PVC cylinder and c was determined. A comparison also was made of the constancy of c measured in several bottles tripped just below the surface by inserting a transmissometer directly into the water bottles on deck. Beam c in five bottles was 0.311 ± 0.008 m⁻¹. Rotating the bottles end over end several times to try to resuspend any settled dregs did not change c.

CTD data were recorded and reduced by the ODF group from SIO. Water samples were drawn from each bottle and analysed onboard ship for nutrients by the same group. Measurements of photosynthetically available radiation (PAR) were made by William Broenkow’s group (MLML) during legs 4 and 5. Wind measurements were made 21 m above the sea surface and averaged hourly by Taco deBruin (Netherlands) during leg 4. These data were correlated with ship-log estimates of Beaufort-scale wind force every 4 h to fill in some gaps in wind data during leg 4 and to estimate wind speed for leg 5.

RESULTS

Particles and beam c

The properties of particles that affect beam attenuation are their concentration, size distribution, index of refraction and shape, with the first two being most important. If the size distribution, index of refraction, and shape of particles are constant, beam attenuation is linearly related to particle concentration (SPINRAD et al., 1983; BAKER and LAVELLE, 1984; MOODY et al., 1986). Although characteristics of particles in the ocean are very diverse, empirical studies have shown that in the open ocean beam attenuation is linearly correlated (r = 0.85–0.97) with filtered mass concentrations or particle volume concentrations below the surface 100 m (SPINRAD et al., 1983; GARDNER et al., 1985; BERGLUND, 1989; WALSH, 1990), so particle mass can be estimated with transmissometers. In surface waters there is significantly more scatter in correlations between the attenuation coefficient and particle volume or particle mass (r = 0.77–0.88), and the slope may change with depth, but the trend is still linear (GARDNER et al., 1985; BISHOP, 1986; SPINRAD et al., 1989).

Our correlations between c and particulate matter concentrations (PMC) for data from the North Atlantic demonstrate the strongly linear trend below the surface waters (Fig. 2B) and a marked increase in scatter when surface waters are included (Fig. 2A). The beam c data were decimated at 2 dbar intervals, and for consistency we used the c value at the first depth below the bottle trip depth. Although the value used was never more than 2 dbar away, there were some cases at the base of the mixed layer where c changed by over 0.1 m⁻¹ in 2 m, possibly contributing to scatter in the correlation. Some scatter certainly
results from obtaining $c_p$ during the down cast of the CTD and tripping the water bottles during the up cast, thus introducing spatial/temporal variations. However, an analysis using preliminary up $c_p$ data did not significantly improve the correlation. Biological diversity and patchiness in surface waters, where organisms are actively growing, result in changes in size, shape and composition, which also contribute to the scatter. Scatter within a single station was less than for the combined data, and the slopes of correlations for different stations varied by as much as a factor of 2, but the limited data points for each station provide poor statistical reliability to determine differences. A large change in slope between Stas 18-11 (day 123.86) and 20-6 (day 125.83) was separated by high winds which mixed the upper 40 m followed by low winds, full sun, and a large increase in $c_p$ during day 125.

ACKLESON et al. (1990) have found that in laboratory cultures of phytoplankton $c_p$ can increase substantially in 2 h without any change in cell concentration, when illumination goes from dark to light. The effect differs with plankton species and nutrient availability.
but a similar reaction in the field could account for some of the scatter between \( c_p \) and PMC, which occurs primarily within the photic zone. Separating our samples by morning and evening did not improve the correlation or reveal any trends, but stations were not taken in a manner to test adequately a photo effect based on \( c_p \). Morning casts with filtered water were made between 0430 and 0600 GMT, while evening casts with filtered water were made between 2000 and 2200 GMT, so all samples were taken in the dark. On day 126, however, PMCs from casts at 0432 h (Sta. 21-2) and 2200 h (Sta. 21-7) increased from 260 to 743 \( \mu g \) l\(^{-1}\) in the surface sample with smaller increases (<25%) in the upper 100 m. This is evidence of real increase as opposed to a photo response.

Water samples also were filtered for particulate organic carbon (POC) (Ducklow et al., 1993; Slagle and Heimerding, 1991). Because of the need for large volumes of water for accurate POC and PMC measurements in the open ocean, there were only eight bottles from which both total PMC and POC samples were taken at 47°N. All of the samples were below 700 m where concentrations were low and errors tend to be larger. PMC and POC concentrations in these samples (uncorrected for dregs; see later discussion) tended to be about equal, whereas one would expect total PMC to be about twice the POC concentration. A comparison of POC concentrations and PMC obtained from casts about 1 h apart on leg 4 showed that, as expected, PMCs were about twice the POC concentrations, except for Sta. 19 where the concentrations were about equal. On two occasions POC was measured during a morning cast and PMC was measured during an evening cast. In these cases the PMC(dusk)/POC(dawn) ratio was about 4, indicating an increase in PMC during the day. This provides further evidence that diel increases in particle concentrations based on \( c_p \) were more than a photo-induced physiological change. However, the data of Ackleson et al. (1990) showed no decrease in \( c_p \) in the laboratory cultures even 2 h after the lights were turned off, so more studies are needed to unravel any photo effects.

For POC measurements made from the CTD rosette samples, values of \( c_p \) are also available. Only a few such samples were analysed during leg 4 when PMC measurements also were made, but numerous rosette samples were measured during leg 5. The correlation of \( c_p \) with POC (\( r^2 = 0.90; \) Fig. 2D) was much better than with PMC (\( r^2 = 0.70; \) Fig. 2A), strengthening the argument that changes in \( c_p \) are well correlated with biological processes. The greater scatter in PMC suggests much greater diversity and patchiness in the non-organic carbon components of the total particle load.

A linear regression of the leg 4 POC and \( c_p \) data yields a slope of 378 compared with the PMC vs \( c_p \) slope of 1022 (Fig. 2A and D). The ratio of the two slopes, 2.70, is the ratio of PMC to POC during that time. This is much smaller than the ratios of 7.8, 5.1 and 3.9 for Total Mass flux to Organic Carbon flux measured for three consecutive time periods at 150 m in floating traps by Martin et al. (1993). Thus, the sinking material is greatly depleted in carbon compared with the total particulate material in the water column, but as the bloom progressed the sinking particles became more enriched in organic carbon.

A final factor we considered to explain the variability in \( c_p \) vs PMC was dregs. Dregs correction factors (the ratio of corrected to uncorrected PMC; Gardner, 1977) varied from 1.02 to 2.0 at 47°N (Fig. 3) and was 2.3 at a station at 53°N. Settled dregs also affect concentrations of POC, PON (Gundersen et al., 1991) and specific elements (Calvert and McCartney, 1979). In reality the problem may be much greater than correction factors imply. PMCs in water below the spigot were between 2 and 60 times greater than above the spigots. Specific particle types (e.g. large aggregates, foraminifera, diatoms, etc.) are likely to be fractionated preferentially, resulting in even larger particle-specific
correction factors. In turn, this could affect measurements of chlorophyll and other pigments, total primary production, and size-fractionated measurements of primary production. The data collected during this and our previous cruises suggest that many of the dregs result from the rapid sinking of aggregates collected in the water bottles, implying that the contribution of large particles or aggregates to the total PMC in the water column is much larger than predicted by McCave (1975).

To test for the effect of dregs on the correlation we plotted both regular and dregs-corrected particle concentrations against beam attenuation coefficients (Fig. 2B and C) for samples below 122 m (samples were all below the mixed layer). The fit between $c_p$ and PMC is extremely good ($r^2 = 0.91$), suggesting that below that depth the small particles, which constitute most of the attenuation signal, are quite uniform in optical properties and composition. The addition of dregs does not improve the correlation significantly ($r^2 = 0.93$), but it does change the slope of the fit from 725 to 1024. Since the $c_p$ we obtained by inserting a transmissometer directly into the water bottles at varying times after they were on deck matched exceedingly well with the in situ $c_p$ recorded through the CTD, we concluded that the best correlation to use for $c_p$ data is the one without a dregs correction.

There was a slow increase in the dregs correction factor with time. Most (75%) of the correction factor reached after 3 h existed after 1 h. Since it usually takes more than 1 h from the time bottles are tripped at depth to recover and process CTD bottles for particles, our dregs correction factors should be fairly independent of depth of sample and time for processing (Fig. 4A). More tests need to be made on the time dependence of dregs at slightly deeper depths where correction factors are higher. The shaking of samples.
however, did not seem to affect the $c_p$ signal, presumably because this did not break up the aggregates. Therefore, we assert that $c_p$ is better correlated with the concentration of small particles in the ocean. The concentration and dynamics of large particles must be addressed with different instrumentation (WALSH and GARDNER, in preparation). The substantial drop in $c_p$ between unfiltered and filtered surface water confirms that most of the particles which generated the $c_p$ signal are removed from seawater with a 0.4 $\mu m$ Poretics filter (Fig. 5). We would expect the $c_p$ of filtered water to be zero, but the sources

![Graph](image1)

**Fig. 4.** (A) Dregs correction factor vs time since each water bottle was tripped at 50 m at Sta. 23-2; and (B) particle mass concentration in water above and below the water-bottle spigots.

![Graph](image2)

**Fig. 5.** Beam $c_p$ vs depth for water from Sta. 19-2 (day 124, 0450 GMT) *in situ*, on deck unfiltered, and on deck after the water was filtered. Filtered water yields a nearly uniform $c_p$ value with depth.
of contamination in transferring water between bottles and open containers are larger than the ability to filter the water and make it cleaner. The difference between in situ $c_p$ and unfiltered laboratory $c_p$ in the surface sample may be significant and will be discussed later.

The difficulty in correlating $c_p$ with PMC uniformly through the water column is that data from the surface waters have a different slope and intercept than for deeper samples. To avoid a discontinuity in the estimation of particle concentrations across that boundary, we fit the data with a single empirically derived equation:

$$\text{PMC} = 1022 c_p \gamma,$$

where PMC is particulate matter concentration in $\mu g \ l^{-1}$ and $\gamma = 1$ for $c_p > 0.1$ and $\gamma = (c_p/0.1)^{0.5}$ for $c_p \leq 0.1$. This equation was used for all conversions for mass calculations in this paper.

**Spatial and temporal variability**

Toward the end of leg 4 we received a preliminary analysis of satellite altimeter data showing the presence of three cold-core mesoscale eddies between 46 and 51°N (ROBINSON et al., 1993). An estimate of the eddy locations was made for days 111–127 and 128–144. The first composite corresponded roughly to the period of sampling during leg 4 of AI1 119 (Fig. 1) and the second composite was primarily for the time between legs 4 and 5. Although it is tempting simply to superimpose the ship tracks from the two legs onto the composite eddy fields to determine sampling position with respect to the eddies, analysis of the shipboard hydrography makes this approach questionable. Simple superposition would lead one to conclude that the ship drifted SSE into a cold-core eddy for the first 6 days, moved just west of the eddy for the next 5 days, and then moved east back to the center of the eddy for the last 3 days (Fig. 1 insert). However, if we treat the 2 weeks of sampling as a geographic survey rather than a time-series and make an objective analysis contour plot of temperature at a constant depth (100 m, for example, as in Fig. 1), it appears that the ship was in three separate and distinct hydrographic areas with respect to the eddy field, being outside the eddy for the first 11 days and then near the eddy front for the final three days. This interpretation results from the fact that temperature at 100 m gradually decreased with time (or space) for the first 6 days, dropped 0.4°C after moving to the west, and dropped another 0.5°C after relocating to the east (Fig. 6). Had the ship moved out of an eddy, temperature at a given depth should have increased due to doming of isotherms within a cold-core eddy. Salinity exhibited a similar decrease with time (space), creating a spatial map similar to the temperature map. Values at the 100 m depth we analysed (Fig. 1) may be influenced by surface-layer dynamics (McGIllicuddy, personal communication) but a similar mapping at 200 m shows the same basic property distribution. An analysis of the altimetry and shipboard data by ROBINSON et al. (1993) details the complexity of hydrography and eddies in the region and demonstrates that spatial variability must be carefully considered in all data interpretations during the study.

Mesoscale variability is demonstrated in the tracks of the two drifting arrays deployed at the beginning of the survey. The two arrays moved in roughly parallel paths to the SSE for a few days and then diverged to spiral in opposite directions (Fig. 1). The motion of the 90-m array suggested either the presence of a small warm-core eddy, or a decoupling between surface-layer motions and deeper currents in the larger eddies. The average speed of the 90-m array was 28 cm s$^{-1}$, but ranged from 5 to 55 cm s$^{-1}$ (LANGDOn, personal
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Fig. 6. Time-series of (A) integrated particle load down to four depths; (B) beam $c_p$; and (C) temperature at four depths during *Atlantis II* legs 4 and 5. Vertical lines indicate significant changes in ship positions (see Fig. 1), including after the storm on day 142.

Communication). While the speed of the 90-m array correlated positively with the wind speed measured on board ship, the direction of drift did not match wind direction, even moving into the wind as it traveled west. We drifted in the rough proximity of the 1500-m array for 6 days as we followed the daytime deployment of the 125-m primary productivity array. We then moved 75 km NW to retrieve the 90-m array and stayed in that vicinity for 5 days. Our final relocation was 130 km E to retrieve and redeploy the 1500-m array where we made measurements for three more days. The 1500-m array seems to have moved across streamlines calculated for the upper 500 m (Robinson et al., 1993), which suggests different currents existed between 500 and 1500 m. In reality we drifted and sampled in three different locations because of our relocations during leg 4.

During leg 5 the 1500-m trap array drifted due east at <3 cm s$^{-1}$ for 10 days after the storm. Superposition of the location on the satellite-derived maps of Robinson et al. (1993) indicate it was near the outer portion of an eddy (Fig. 1. insert), but their later detailed analysis of stream lines based on hydrography (Figs 12 and 15 of Robinson et al.,...
plus the slow movement of both the 1500-m array and the daily productivity array indicate the leg 5 data were taken in the vicinity of a weakly circulating ring.

**Surface mixing and beam attenuation**

C. Goyet (WHOI, personal communication) calculated mixed-layer thickness using the equations of Millero and Poisson (1981) that determine the depth of the density corresponding to a 0.02°C change in temperature from surface water. We examined high-resolution CTD plots and measured the depth at which there was a break in slope of T or density profiles. The two methods yielded identical depths 50% of the time while 25% of the Goyet calculations were thicker than ours and 25% were thinner. A sharp drop in beam c also can be used to predict mixed-layer thicknesses and yields results very comparable with the other two methods. The particles which constitute the beam c signal act as tracers on this time scale.

Because the $c_p$ data were collected through the CTD, the vertical resolution of $c_p$ data matched that of temperature. Figure 6 shows the temporal evolution of temperature and $c_p$ at 10, 40, 100 and 200 m. The relationships between $c_p$ and temperature at 10, 20, 30 and 40 m, and wind, light and mixed layer depth (Fig. 7) demonstrate how closely changes in small-particle concentration were coupled with environmental conditions.

Nitrate values were nearly 6 $\mu$M 1$^{-1}$ in the mixed layer at the beginning of leg 4 and decreased to <3 $\mu$M 1$^{-1}$ before the ship left the area. Nine days later when the ship returned, NO$_3$ was <1 $\mu$M 1$^{-1}$. After the 2-day storm beginning day 141, nitrate increased slightly, but gradually was drawn down to nearly zero by day 152. Silicate decreased from 2.4 $\mu$M 1$^{-1}$ to almost zero during leg 4, and was zero for 2 days when the ship returned on leg 5. After the storm silicate values ranged between 0.2 and 0.4 $\mu$M 1$^{-1}$. Despite the intense mixing that had to occur to raise the nutrient levels, there was no indication of a thickened mixed layer by the time the first CTD profile was taken after the storm (Fig. 7b). The intense solar radiation, diminished winds, and strongly stratified surface water prevented significant sustained thickening of the mixed layer. Note, however, that following day 145 when solar radiance was low for four days and winds were moderately high, mixed layer thickness nearly tripled.

**DISCUSSION**

Clearly the presence of eddies with their associated fronts complicates the interpretation of the bloom as reflecting solely temporal changes in a homogeneous parcel of water. Yoder et al. (1993) report spatial changes of about a factor of two in aircraft-sensed chlorophyll concentrations in the vicinity of the ship over length scales <100 km. With a maximum horizontal velocity in the eddies computed to be from 10–15 cm s$^{-1}$ (Robinson, et al., 1993) to 28 cm s$^{-1}$ (mean drift rate computed for the 90 m drifter), one could anticipate factor-of-two changes in chlorophyll over the period of 4–10 days in the same geographic location, although the objective was to drift with the surface water. In crossing the "standard" eddy to the northeast of the "small" eddy where the ship was located, aircraft-sensed chlorophyll concentrations changed by a factor of two within 10 km. Changes greater than a factor of two in related variables can be presumed to be real, not just advection of patchy features.
Changes in ship location caused large changes in temperature and $c_p$ in the upper 200 m, which must be attributed to spatial changes. After relocations on days 121 and 126, $c_p$ decreased at 40 m, but remained nearly constant at 100 and 200 m (Fig. 6). Conversely, temperature did not change much in the upper 40 m (the surface warming that occurred during sunny day 125 apparently affected both locations), but dropped as much as 0.4° at 100 and 200 m. Despite little change in surface temperature during the 100 km shift on day 140, $c_p$ decreased by nearly 50%. This matches the factor-of-two variations in regional chlorophyll concentrations observed by YODER et al. (1993) during aircraft overflights.

**Particle increases**

Beam attenuation due to particles ($c_p$) in the mixed layer (at 10 m for this discussion) increased by a factor of three from 0.17 to 0.51 m$^{-1}$ over a 2-week period (Fig. 7a). Superimposed on this increase were diel variations (0.06–0.12 m$^{-1}$) with evening highs and morning lows, which are related to the intensity of wind mixing, solar radiance, and a decrease in nutrient levels (Fig. 7). The diel variations we observed were much larger than those observed by SIEGEL et al. (1989) in the Pacific (0.01 m$^{-1}$), but were of the same order as those measured at 9 m on a buoy drifting in a cold filament off northern California (ABBOTT et al., 1990). SIEGEL et al. and ABBOTT et al. assumed that increases in beam attenuation resulted primarily from increases in biomass and organic detritus through primary production. OLSON et al. (1990) and ACKLESON et al. (1990) have suggested that some of the diel change may be a physiological response. ACKLESON et al. demonstrated that beam $c$ increased when laboratory cultures (such as the diatom *Thalassiosira pseudonana* and the coccolithophorid *Emiliania huxleyi*) are exposed to light with no increase in cell concentration (number l$^{-1}$). The cell index of refraction decreased (which would decrease $c$) but the increase in mean cell diameter was sufficient to increase $c$. In the case of *Thalassiosira* the increase was 0.4 m$^{-1}$ in 2 h when nutrients were abundant, but there was no net change when the culture was nutrient limited, even though the mean diameter increased by the same amount in both cultures. We note, however, that the mass per cell could increase during photosynthesis so that total mass could increase even if the cells l$^{-1}$ remained unchanged. We also note that the laboratory data showed no decrease in $c_p$ after 2 h when the lights were turned off, indicating it is not a reversible effect within that time period.

We cannot make a direct comparison with the laboratory experiments of ACKLESON et al. (1990), because, although diatoms were abundant in the water during leg 4 (SIERACKI et al., 1993), we do not know what species were present. However, the increase in $c_p$ between the values we measured in situ and in unfiltered water onboard ship suggests a physiological effect due to light (Fig. 5). The cast was made at 0450 GMT (dark), but the shipboard measurements were made an hour later in a lighted laboratory. Any particle settling between sample collection and laboratory measurements would decrease $c_p$, but $c_p$ in the laboratory surface sample increased 0.05 m$^{-1}$ over the in situ value. We also have clear evidence that the increases in $c_p$ reflect real increases in POC and PMC based on filtration data at dawn and dusk as discussed earlier. Therefore, while some of the diel variation observed in $c_p$ (at least increases) might be photo-induced, biological production must still be dominant. Otherwise we could not account for the three-fold increase in $c_p$ over the 2-week period, which was matched by a three-fold increase in the integrated particle load based on filtered samples.
Fig. 7a and b.  (A) Wind speed and incident solar radiance; (B) mixed layer depth (C. GOYET, personal communication); (C) nitrate concentration in mixed layer; (D) temperature at four depths; and (E) beam $c_p$ at four depths for legs 4 and 5 of Atlantis II 119. Note scale changes for temperature and $c_p$ between legs 4 and 5.

**Particle loss and the mixed-layer pump**

Factors that could cause decreases in beam attenuation are biological consumption, large-particle production with subsequent particle settling (fecal pellets, aggregates), or bioactive transport by organisms migrating to deeper depths (WALSH et al., 1988). A previously undiscussed factor that could cause a decrease in $c_p$ during the night is an
increase in mixed-layer thickness. From leg 4 CTD profiles made at dawn and dusk, we often can discern a diurnal variation in mixed-layer thickness: increasing at night and decreasing during the day (Fig. 7a). From days 115 to 117 the mixed-layer thickness decreased from 127 to 20 m as solar heating induced stratification. During the following 3–4 days winds were moderate and relatively constant. Under these uniform wind conditions the thickness of the mixed layer varied from about 20 m in the evening to 30–40 m the following morning (Fig. 7a). Mixed-layer thickness responds not only to wind mixing, but also to convective cooling during the night (Price et al., 1986).
What effect might the change in mixed-layer thickness have on nutrients and particles? During this period of uniform winds the surface NO$_3$ concentration exhibited a slight diel variation with morning concentrations about 0.2 μM$^{-1}$ higher than the previous evening. Because overnight regeneration of NO$_3$ is unlikely, the nighttime thickening of the mixed layer must entrain nutrients from below the mixed layer. The evening cast on day 119 had NO$_3$ concentrations of 5.2 μM$^{-1}$ at 3 m and 5.9 μM$^{-1}$ at 42 m with a 20-m mixed layer. The morning cast of day 120 had a mixed layer of 36 m. Simple mixing could account for the measured value of 5.3 μM$^{-1}$.

Beam $c_p$ was 0.34 m$^{-1}$ in the upper 20 m on the evening of day 119 and about 0.13 m$^{-1}$ at 30–40 m. Simple mixing of the water would predict the same beam $c_p$ of 0.25 m$^{-1}$ that was measured in the mixed layer that morning. Mixing rates certainly vary with the wind, so it is difficult to extract the mixing signal from the data, but these simple calculations suggest a substantial portion of the nighttime loss of particles could be due to downward mixing by thickening of the mixed layer. During the day heating reduced the mixed-layer thickness and particles were apparently isolated below the level of maximum turbulent mixing. The immediate fate of these particles is uncertain. Beam $c$ profiles show stepped structures as the thinning mixed layer isolated particles below (Fig. 8). Perhaps aggregates form in this region, which could speed their sinking rate or decrease their chance of being detected.
with a transmissometer (Gardner and Walsh, 1990). We assume the particles mixed downward are permanently lost from the mixed layer unless there is some mechanism by which phytoplankton can induce a net upward motion in the mixed layer as it shallows, but it is hard to imagine such a mechanism could dominate over vertical mixing. Dinoflagellates can move upward toward light (Margalef, 1978), but their abundance and contribution to movement during this study is unknown.

Changes in mixed-layer thickness due to stratification or diurnal variations could "pump" particles out of surface waters. For example, on day 115 at 47°N PMC in the mixed layer was uniform at about 174 μg l⁻¹ (based on both filtration and beam $c_p$). The mixed-layer thickness dropped from 127 to 20 m the following day, isolating the astounding mass of 18.6 g m⁻² from surface mixing. This is almost 30 times the daily flux measured at 150 m (0.67 g m⁻²) with drifting sediment traps during that time (Martin et al., 1993). From dawn to dusk on day 119 the mixed-layer thickness shallowed from 30 to 20 m. At a particle concentration of 255 μg l⁻¹, this leaves 2.55 g m⁻² isolated in the 10 m below the mixed layer between morning and night.

Environmental influence on primary production

The beam $c_p$ signal demonstrates how closely changes in small-particle concentration are coupled with environmental conditions of solar radiation, wind and nutrients (Fig. 7). If the increases in $c_p$ are from increases in biomass through primary production, it is most likely to occur when the sea is calm and stratified, and solar radiance is abundant, especially following mixing events which entrain nutrients from deeper water. Mixing events are discernible from wind records during leg 4 on days 117, 120–122, 124 and 129, and the mixed-layer concentrations of nitrate and silicate were 0.3–0.4 μM l⁻¹ higher after those events due to entrainment of nutrient-rich water below the mixed layer. The largest wind event was during days 140 and 141. After the storm abated, the ship returned to the geographic location it had occupied on day 139. In the first CTD profile taken after the storm the mixed layer was only 10 m thick (Fig. 7b), though the sea was less stratified in the upper 40 m than it had been at that location before the storm (day 140). Stratification decreased even further the following day (day 143), but was quickly re-established with heating during the next three sunny days.

The value of $c_p$ increased to its highest levels during the 2 days after the storm (Fig. 6). Initially one would assume that production was rapid after the injection of new nutrients with sunny skies and calm seas (Fig. 7b). Note, however, that the high $c_p$ was restricted to the upper 10 or sometimes 20 m. Beam $c_p$ actually decreased dramatically at 30 and 40 m (Fig. 7b). The standing stock of particles integrated to 40 m only increased by 25% between days 143 and 145, while the integrated value to 10 m increased 100%. One could still argue for rapid production in surface waters, with particles below the mixed layer rapidly settling out. An alternative hypothesis is that a physiological response in phytoplankton to adjust to an optimum light level might dominate over mixing once the winds diminished, with the result that plankton could rise from below 10 m to cause what appears to be rapid growth in surface waters and a loss at depth. A similar increase in surface waters and decrease in subsurface waters can be seen in the data of Dickey et al. (1991). A third argument for the rapid increase in $c_p$ is that the storm broke aggregates into small particles, but the increase in $c_p$ did not begin until after the storm. Herndl and Peduzzi (1988) found that very large aggregates break up in storms in shallow water and reform within a
week under calm conditions. In any case, PMC reached levels in surface waters that significantly decreased the sunlight penetrating to deeper depths to support primary production (Walsh and Gardner, in preparation).

Why did $c_p$ at 10 m decrease by 50% over the next 2 days? If the bloom crashed, how could the particles be removed so rapidly from surface waters? The small particles cannot suddenly sink unless they are rapidly transformed into aggregates large enough to settle out of the mixed layer, or escape quantitative detection by the transmissometer. Measurements of aggregates during leg 4 suggested there were diel changes in aggregate abundance with more aggregates during the day (Walsh and Gardner, in preparation). If a diel variation in aggregate abundance was confirmed with more measurements in the future, it would demonstrate an important process in the removal of small particles from surface waters.

Grazing is another route to remove small particles and decrease $c_p$. DAM et al. (1993) measured mesozooplankton abundance in the mixed layer (to 30 m during leg 5) and found an increase in zooplankton during the time $c_p$ decreased after day 145. The increase was most notable (50–100%) in the 0.2–0.5 mm zooplankton. From the data of DAM et al. (1993, Figs 1 and 3) we calculate that between days 145 and 151 the mesozooplankton grazed on the order of 1 mg C m$^{-3}$ day$^{-1}$, or 2 mg total mass m$^{-3}$ day$^{-1}$ if we assume 50% of the particle mass is organic C. With a total particle mass on the order of 1000 mg m$^{-3}$ in the surface mixed layer at the peak concentration, it is obvious that mesozooplankton grazing played a minor role in the 50% decrease in particle mass which occurred in 2–3 days. This is the same conclusion DAM et al. reached in evaluating the removal of primary production by mesozooplankton.

Some of the variability could have been spatial. As noted earlier, during an aircraft overflight Robinson et al. (1993, Figs 3 and 16) found variations in remotely sensed surface fluorescence of up to a factor of 2 in 10 km in the interior of an eddy adjacent to the “small” eddy in which the ship was located. A change in $c_p$ might be expected if the ship moved relative to the eddy in which it was located (Fig. 15 of Robinson et al., 1993). The ship was drifting 4–6 km day$^{-1}$, about the speed of motion within the eddy, and we have no information about spatial variations in the “small” eddy.

The most likely cause for the decrease, however, seems to be wind mixing. After day 145 wind levels and mixed-layer depths increased and light levels decreased (Fig. 7a). This would mix particles and decrease the surface maximum while not changing the standing stock drastically.

**Three-layer model**

If we treat leg 4 at 47°N as a time-series, we can test for cruise-length trends by performing linear regressions of data for specific depth horizons against time (data for some depths are shown in Figs 6, 7D and E). A plot of the slopes of the regressions for each depth horizon reveals surprisingly smooth profiles for $T$, $S$ and $C_p$ (Fig. 9). $R^2$ values go to zero when slopes go to zero and below 700 m, at which depth Mediterranean water moved into the study area midway during the cruise.

With no large sources or sinks in surface waters, salinity regressions exhibit a fairly constant rate of decrease in salinity over time down to 700 m. The temperature regression plot is similar, with the exception of the upper water column where the influence of solar radiation is seen. The surface 10–20 m heated over the 2-week period. Below that depth
Particle production and distribution

Fig. 9. Slopes of linear regressions of (A) salinity; (B) temperature; and (C) beam \( c_p \) for the 2-week period of leg 4. Depth horizons for regressions are every 10 m down to 200 m, every 20 m from 220 to 500 m, and every 50 m below 500 m. The inset plots are the \( R^2 \) values of the regressions, indicative of goodness-of-fit. \( R^2 \) approaches zero as the slope changes from positive to negative.

there was a cooling trend in the water which increased down to 90 m, below which the cooling trend was fairly uniform until the above-mentioned Mediterranean water was encountered.

Particles in the upper water column can be both produced and removed. The regressions of the \( c_p \) data show a three-layer model: rapidly increasing particle concentrations in the upper 50 m, decreasing concentrations between 50 and 400 m, and increasing concentrations below 400 m (data end at 1000 m). We interpret the surface increase as net production in the upper water column. The apparent "loss" of particle mass between 50 and 400 m could result from (1) upward mixing of clearer, cooler water; (2) aggregation and removal by settling or consumption; or (3) biased data due to changes in the water mass measured (i.e. movement of the ship into a cold-core ring). Increases below 400 m could result from net disaggregation of fast-settling particles.

The cooling trend seen between 30 and 700 m would suggest upwelling of cold water during the sampling period such as would occur in a cold-core ring. However, the rates of upwelling required to sustain the apparent decrease in temperature are on the order of 14 m day\(^{-1}\), which is unreasonably high. Examining the entire temperature time-series at four depths in Fig. 6C, the trends of warming and cooling are obvious. Warming or cooling trends are much less apparent, however, if restricted to the segments between the vertical bars, which represent times of major ship repositioning.

Trends of increasing or decreasing PMC at different depths are more consistent than temperature trends whether they are viewed either as short segments or as a 2-week trend. This is because the biological and gravitational processes that produce and remove particles are superimposed on the mesoscale hydrographic features in the open ocean, and, while certainly not independent of hydrography, they proceed regionally despite changes in hydrography or location. Nevertheless, we urge caution in interpreting the leg 4 data as a true time-series of processes in a uniform water parcel because of changes in ship location and because the drifting buoy tracks and the analysis of Robinson et al. (1993)
suggest complex eddy structures that can create significant spatial variability in the study region.

Regressions on temperature, salinity and beam $c_p$ data for leg 5 do not exhibit the distinct trends seen during leg 4. The large peak in beam $c_p$ after the storm biases the trend in surface water. Thermal stratification appears well established by leg 5, so temperature changes are not rapid. Drift rates of surface buoys and the ship are very small during this time, so it appears that the data after the storm can be viewed more plausibly as a time-series within the same water mass.

**CO$_2$ drawdown and integrated particulate matter standing crop**

During biological production CO$_2$ is converted to POC and particulate inorganic carbon (PIC). Chipman et al. (1993) calculated that the drawdown of CO$_2$ in the mixed layer during the day equaled about 75% of the rate of primary production measured by $^{14}$C incubations; a good correlation considering measurements were not made in a closed system. POC and PIC can be lost from surface waters in three ways; respiration or remineralization of carbon back to CO$_2$, transformation to the dissolved pool (DOC, DIC), or removal of particles from surface waters. An apparent loss of carbon could occur if the small particles measured in $c_p$ are converted to large aggregates not sensed quantitatively in $c_p$. Replenishment of CO$_2$ from the atmosphere during leg 4 was about 10% of the biological uptake rate (Chipman et al., 1993), but CO$_2$ could be replenished from deeper waters through wind mixing and diurnal variations in mixed-layer thickness.

To balance the total CO$_2$ drawdown in surface waters with the increase in small-particle mass during the two cruises, we integrated the decrease in total CO$_2$ over 20 m (a rough approximation of average mixed-layer thickness) and 50 m (the depth to which particle production was positive throughout leg 4). Our calculations reflect the loss of total CO$_2$ from day 115 so that we would assess only changes from the time we began sampling (squares in Fig. 10). In addition, POC based on $c_p$ was calculated by a linear regression to the leg 4 data in Fig. 2D (circles in Fig. 10). This allows a direct comparison of the carbon lost (from total CO$_2$) to the carbon gained in particles (Fig. 10). The calculated mass equivalents were compared over the same depths for the same period of time. Integrations over both depths showed that the increase in POC based on $c_p$ was only 18–28% of the amount needed to account for the drawdown of total CO$_2$ (Fig. 10). The large difference between these two calculations suggests that particles quickly settle out or are converted to the dissolved pool, leaving only a portion of the generated particles in surface waters.

The trap fluxes of 545–774 mg m$^{-2}$ day$^{-1}$ measured at 150 m during legs 4 and 5 (Martin et al., 1993) can be satisfied by the settling of only 2–4% of the standing stock in the surface 100 m. The total mass fluxes measured at 1000 m from the end of April to the end of May were 90–140 mg m$^{-2}$ day$^{-1}$ (Honjo and Manganini, 1993). This requires only 0.2–0.8% of the particles measured in the surface 100 m during leg 4 to have settled to 1000 m.

DOC recently has been shown by Sugimura and Suzuki (1988) to have much higher values than previously reported, especially in the upper 400 m of the water column. Based on the new measurements of DOC, Toggweiler (1989) suggests that much of the organic carbon may be transferred to the DOC pool in the upper water column rather than passively sinking in particulate form. Once POC is transferred to the DOC pool it moves with the surrounding water mass until the carbon is remineralized into CO$_2$ or is utilized by bacteria and re-enters the food chain and the POC pool. In this regard aggregates may be
excellent microenvironments for remineralization depending on the rate of pore-water exchange (Silver et al., 1978; Allredge and Cohen, 1987; Logan and Hunt, 1987; Allredge and Silver, 1988; Herndl, 1988), so their distribution and dynamics may be very important (Walsh and Gardner, in preparation).

Aggregates can also be important sites of primary production, accounting for anywhere from 1 to 90% of total primary production depending on location and conditions (Knauer et al., 1982; Prezelin and Allredge, 1983; Herndl, 1988). If the dregs found in standard water sampling bottles result from aggregates settling after bottle closure, estimates of primary production based on $^{14}$C incubations could increase significantly; perhaps enough to account for the difference between estimates of primary production based on different methods (Jenkins, 1982; Platt et al., 1989).

When did the bloom begin?

Weather charts indicated a major storm had just passed over the 47°N site with the wind waning as we arrived on station. The mixed-layer thickness was over 120 m on our first CTD profile. The surface waters stratified and particle concentration increased rapidly during the following days, which may mislead us into thinking we arrived “just in time” to witness the onset of the bloom. When moored sediment traps were deployed at this site on day 103, surface NO$_3$ concentrations were 9.4 µM $^{-1}$ (50% higher than when we arrived on day 115), mixed-layer depth was 248 m, and PMCs were about 35 µg $^{-1}$ in the surface 100 m for an integrated particle standing stock of 3.5 g m $^{-2}$ (Hongo et al., 1989). On day 115 PMC throughout the upper 127 m was 174 µg $^{-1}$ (17.4 g m $^{-2}$ integrated to 100 m).
Likewise, total CO$_2$ in surface waters integrated to 100 m was undersaturated by about 71 µM cm$^{-2}$ (data from Chipman et al., 1993). Based on the drawdown of CO$_2$ and the large standing crop of particles, significant primary production must have occurred before day 115. In fact the increase in small-particle mass in the upper 100 m during the 12 days prior to our arrival on day 115 was about 14 g m$^{-2}$ (a five-fold increase) while the increase was about 30 g m$^{-2}$ (a three-fold increase) in the 13 days after day 115. Given that increases in $c_p$ were greatest during periods of stratification and high solar radiation during our sampling (Fig. 7), we surmise that the region had experienced some stratification and rapid production prior to day 115. The small density gradient in the surface waters, however, was not sufficient prior to day 120 to inhibit deep mixing. Only after strong solar heating during leg 4 was the density gradient sufficient to maintain stratification even through intense storms.

**Significance**

The high-vertical resolution data from transmissometers provides improved ability to quantify biophysical processes in the ocean. Our data suggest that:

1. Long-term increases in beam $c_p$ in the surface water reflect increases in particulate matter concentration resulting from primary production.

2. The diel signal in beam $c_p$ results primarily from daytime increases in PMC due to primary production, but photo-induced physiological effects in plankton cells may exert some influence and need further evaluation; nighttime decreases in PMC result from grazing, dilution by diurnal variations in the mixed-layer thickness, aggregation, settling, remineralization, and bioactive transport.

3. Mixing events, stratification of the water column, and solar radiation are primary controls on the changes in PMC and standing stock in the near-surface water column.

4. Some of the apparent temporal changes during leg 4 may actually be spatial changes sampled in the area as the ship moved with respect to the mesoscale eddy field. Interpretation of all data collected in the project needs to consider this likelihood.

5. Deep mixing/restratification and diurnal changes in mixed-layer thickness act as a "hydrographic pump" that may be significant in removing particles from surface waters as well as adding nutrients and CO$_2$ to the mixed layer.

6. Particles are an important component in the surface layer carbon cycle through which carbon passes before it settles out or enters the DOC pool. The large difference in POC calculated from $c_p$ and the drawdown in total CO$_2$ suggests that particles quickly settle out of surface waters or are converted to the dissolved pool, leaving only a portion of the generated particles in surface waters.

7. Settling of particles within water bottles can cause measurements of particle mass to be low by up to a factor of two. This causes errors in all measurements based on concentration (e.g. particle types) or reaction rates (e.g. primary production) and needs more attention in future programs.

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with other data sets meticulously collected and graciously shared by scientists in JGOFS-NABE. "The sum is greater than the parts."

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