

Optical determination of particulate abundance and production variations in the oligotrophic ocean

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Abstract—Observed diurnal variations of the beam attenuation coefficient at 660 nm (c) are used to estimate variations of particulate concentration and production in the open ocean. The diurnal cycles of c are found to be statistically significant throughout the euphotic zone (the upper 95 m), but not below this depth. Their amplitudes are nearly uniform with respect to depth with characteristic peak to peak values of $\sim 0.0065 \text{ m}^{-1}$. The minimum (maximum) of these daily variations occurs during local sunrise (sunset), indicating a daytime accumulation of particles. Specific particle production rates (r_0) calculated with beam transmissometer data alone have maximum noontime values of $\sim 0.5 \text{ d}^{-1}$ and are well-correlated with the incident solar radiative flux. The high correlation between the optically determined specific production rates and solar radiation allows r_0 to be decomposed into light-dependent and light-independent portions, which are interpreted as particle-specific growth and grazing rates. The resulting specific growth and grazing rates are balanced (i.e. net daily production is approximately zero) and are consistent with previous biological determinations for the open ocean. Daily mean specific growth and grazing rates are found to be $\sim 0.15 \text{ d}^{-1}$. The value of the water column integrated community production estimated using the optical data is $\sim 160 \text{ mg C m}^{-2} \text{ d}^{-1}$, which compares well with both simultaneous and seasonal mean carbon uptake rate measurements. This optical method should prove useful for *in situ* observations of particulate production in the oligotrophic ocean.

INTRODUCTION

THE estimation of the spatial and temporal variations of particulate production within the euphotic zone is an important factor in determining the ocean's role in the global balance of carbon (e.g. EPPLEY and PETERSON, 1979; BREWER *et al.*, 1986). To achieve this measurement goal, unattended *in situ* methods for determining primary production rates must be made (e.g. BREWER *et al.*, 1986; DICKEY, 1988). Several candidate methods, which utilize measurements of underwater radiation, presently are being developed and evaluated (TOPLISS and PLATT, 1986; BIDIGARE *et al.*, 1987; SMITH *et al.*, 1987; KIEFER *et al.*, submitted). Here, a method to determine particulate production rates that utilizes observed diurnal variations of the transmission of a collimated light beam at 660 nm is introduced. The diurnal transmission changes are used to estimate daily variations of particle concentrations and hence, rates of particulate production.

The percent transmission (T) of a collimated monochromatic beam of light over a distance Δz can be quantified in terms of the beam attenuation coefficient (c ; JERLOV,

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1976) or

$$T = 100 \exp(-c\Delta z). \quad (1)$$

For case I waters (i.e. in the absence of terrestrial influences), c is commonly partitioned into beam attenuation coefficients which can be attributed to pure seawater (c_w), living planktonic materials (c_{pl}), nonliving detrital materials (c_{de}), and dissolved materials (c_{di}).

$$c = c_w + c_{pl} + c_{de} + c_{di}. \quad (2)$$

The attenuation by dissolved material is generally negligible at the wavelength investigated (660 nm; BRICAUD *et al.*, 1981). Variations of c at 660 nm are caused by changes of c_{pl} and/or c_{de} and are observed to be related to changes of the concentration of suspended particulate materials (SPM) (BAKER and LAVELLE, 1984; GORDON *et al.*, 1984; BISHOP, 1986; SPINRAD, 1986). This linear relationship ($\Delta(c_{pl} + c_{de}) = A \Delta\text{SPM}$) has been verified during the present observations (KITCHEN *et al.*, 1983).

Diurnal variations of SPM concentrations have been observed in the open ocean (SHELDON *et al.*, 1973; POSTMA and ROMMETS, 1979; EPPLEY *et al.*, 1988). The phase of these variations indicates an increase of SPM during daylight hours. Diurnal variations are also observed in ultraplankton abundances (phytoplankton cells with diameters smaller than 5 μm ; SHAPIRO and GUILLARD, 1987) in the open ocean (CAMPBELL and CARPENTER, 1987; PRÉZELIN *et al.*, 1987; WATERBURY *et al.*, 1987). By taking into account the large (>50%) contributions ultraplankton populations can make to the primary production of the oligotrophic ocean (e.g. LI *et al.*, 1983; GLOVER *et al.*, 1986; ITURRIAGA and MARRA, 1988), it is likely that ultraplankton abundance variations contribute substantially to diurnal SPM variations.

Diurnal SPM variations can influence several optical parameters which can be easily measured (POSTMA and SPITZER, 1982). Preliminary analysis of moored transmissometer measurements from the Sargasso Sea (34°N, 70°W) shows amplitude and phase relationships consistent with the previously discussed biological variations (DICKEY *et al.*, 1987). Similar variations were observed from freely drifting transmissometer data taken in the California Current (ABBOTT *et al.*, 1987). Thus, diurnal variations of suspended materials may be ubiquitous in the open ocean (probably the result of ultraplankton abundance variations) and can be sensed using optical techniques.

MEASUREMENTS

Observations were made from the Research Platform (R.P.) *Flip* during the autumn of 1982 (20 October to 12 November 1982; Julian days 292–314). The measurements were made in the North Pacific Ocean (~33°N, 142°W) as part of the Optical Dynamics Experiments (ODEX). Conductivity–temperature–depth transmissometer (CTDX) profiles were obtained from the sea surface to ~250 m approximately eight times per day. Interpolated time series were computed ($\Delta t = 0.1$ d) for every 10 m of depth from 10 to 200 m. The data presently analysed (days 305–314) represent about one-third of those taken from the R.P. *Flip* during ODEX. This was done because of the irregular sampling intervals for CTDX deployments before day 305. A complete description of the data taken from the R.P. *Flip* during ODEX can be found in DICKEY and SIEGEL (submitted).

A 1 m pathlength beam transmissometer was used to determine the beam attenuation coefficient centered at a wavelength of 660 nm (BARTZ *et al.*, 1978). The volume of

seawater sampled by the transmissometer is estimated to be less than 200 ml. This limits the size of the particles that are continuously sampled because the probability of sampling particles with diameters $>50 \mu\text{m}$ is quite small (KITCHEN *et al.*, 1983). For example, characteristic open ocean concentrations of macrozooplankton, microzooplankton, and their nauplii (JACKSON, 1980) are not sampled continuously by the transmissometer. In addition, undetectable differences in the values of c were determined by comparing up and down profiles from several series of CTDX profiles. Thus, temperature hysteresis effects (BISHOP, 1986) were probably not important.

In addition to the CTDX profiles, water samples for nutrient and chlorophyll analyses were taken, spectroradiometer casts were made and a full suite of meteorological parameters was sampled. A SeaMarTech model 6000AR chlorophyll fluorometer was also interfaced to the CTDX system. Details of these and other measurements are found in SIEGEL and DICKEY (1987a) and DICKEY and SIEGEL (submitted).

Primary production measurements were made from the R.V. *Acania* using a simulated *in situ* ^{14}C bicarbonate uptake method (e.g. EPPLEY and HOLM-HANSEN, 1986 and references therein). Whatman 934AH filters were used in the determinations which may lead to underestimates in the total production (ITURRAGA and MITCHELL, 1986). Replicate samples at five light levels were incubated for periods from 6 to 9 h and corrected for dark incorporation of isotope. Sample irradiance was controlled using neutral density diffusing screens, resulting in transmittances from 2 to 50% of the surface irradiance. Results were scaled to the total daily photosynthetic available radiation (PAR_t) by multiplying the results from each incubation by $\text{PAR}_t/\text{PAR}_i$, where PAR_i is the amount of PAR for the incubation period. Estimates of the vertical profiles of production were made by interpolation onto scaled photosynthesis-irradiance curves based upon the fraction of PAR penetrating to depth (SIEGEL and DICKEY, 1987b). Values of integrated primary production were calculated using the vertical profile estimates.

MEAN VERTICAL VARIATIONS

The mean c profile exhibits a well-mixed region throughout the upper 50 m and a subsurface maximum at about 65 m (Fig. 1a). Observations indicate that this particle maximum, although varying in intensity, shape and depth, is a ubiquitous feature of the oligotrophic ocean (JERLOV, 1976; PAK *et al.*, 1988; MITCHELL and KIEFER, 1988; DICKEY and SIEGEL, submitted). Below the particle maximum, the value of c decreases rapidly. The mean mixed-layer depth is ~ 55 m (Fig. 1b). A relatively strong seasonal pycnocline is found between 55 and 90 m (mean buoyancy frequency ~ 8 cycle per hour; cph) and stratification is reduced below 90 m (~ 4 cph; DICKEY and SIEGEL, submitted).

Chlorophyll a concentrations within the mixed layer are relatively low ($\sim 0.07 \text{ mg m}^{-3}$; Fig. 1c). Below the mixed layer, Chl a concentrations increase rapidly until a subsurface maximum is encountered at 85 m. The value of Chl a concentration at the subsurface maximum is $\sim 0.2 \text{ mg m}^{-3}$. From spectroradiometer measurements, the depth of the euphotic zone ($z_{1\%}$; the depth where PAR is 1% of the PAR just beneath the sea surface) is ~ 95 m (SIEGEL and DICKEY, 1987b). Further, nitrate concentrations were below detectability above ~ 120 m. These conditions are characteristic of the oligotrophic North Pacific Central Gyre in the autumn (e.g. EPPLEY *et al.*, 1973; HAYWARD *et al.*, 1983; MITCHELL and KIEFER, 1988; DICKEY and SIEGEL, submitted).

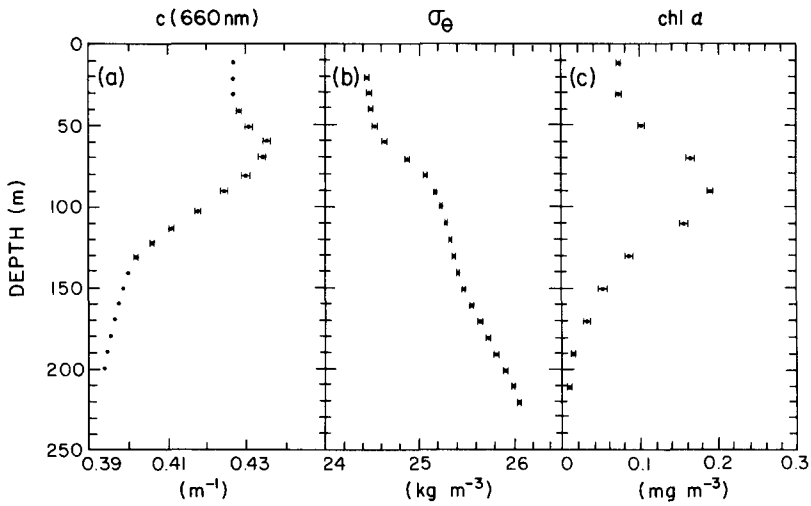


Fig. 1. Vertical mean profiles of (a) the beam attenuation coefficient at 660 nm (c) in units of m^{-1} , (b) the potential density (σ_θ) in units of kg m^{-3} and (c) the extracted chlorophyll a concentration (Chl a) in units of mg m^{-3} . Error bars represent 95% confidence intervals for the estimated mean values. After DICKEY and SIEGEL (submitted).

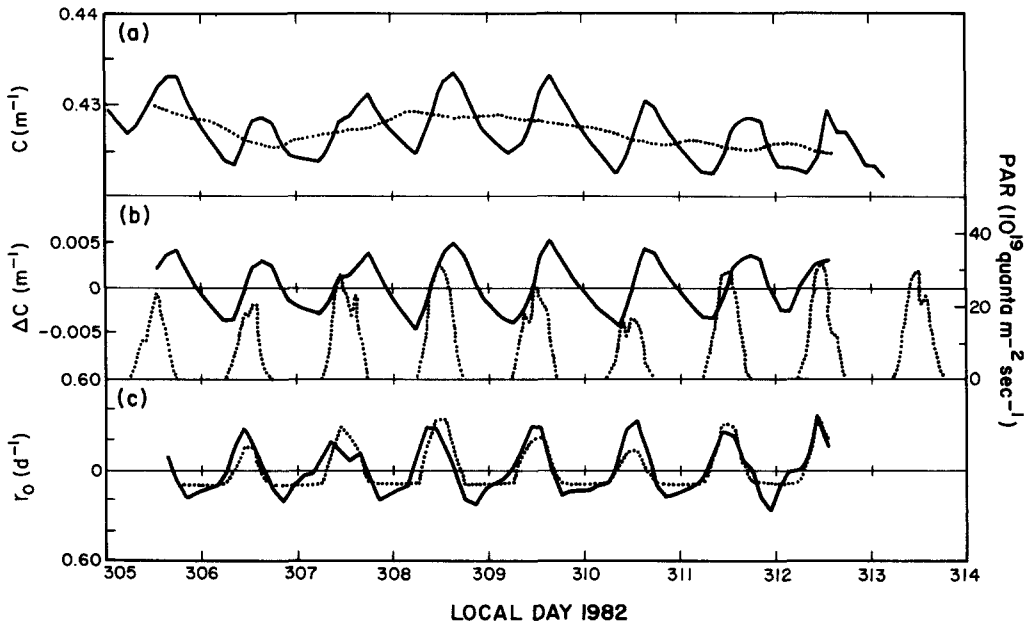


Fig. 2. (a) Temporal variation of c (20 m) (solid) and $\bar{\epsilon}$ (20 m) (dashed), in units of m^{-1} . Days are in local time. (b) Time series of Δc (20 m) (solid) and PAR(20 m) (dashed). PAR (20 m) is in units of 10^{19} quanta $\text{m}^{-2} \text{s}^{-1}$ and is calculated following SIEGEL and DICKEY (1987b). (c) Time series of the sampled (solid) and modeled (dashed) specific production rates (r_0 and θ_0) for 20 m, in units of d^{-1} .

TEMPORAL VARIATIONS OF THE BEAM ATTENUATION COEFFICIENT

Temporal variations of the beam attenuation coefficient at 20 m are clearly dominated by diurnal oscillations with amplitudes as large as 0.01 m^{-1} (Fig. 2a). Variations of the running daily mean $c(20 \text{ m})$ (\bar{c}) are primarily a consequence of thermohaline water mass variations (WASHBURN *et al.*, accepted; DICKEY and SIEGEL, submitted) and generally have smaller amplitudes than the diurnal scale variations. The diurnal variability can be illustrated better by using the deviation of c from the daily running mean ($\Delta c = c - \bar{c}$; Fig.

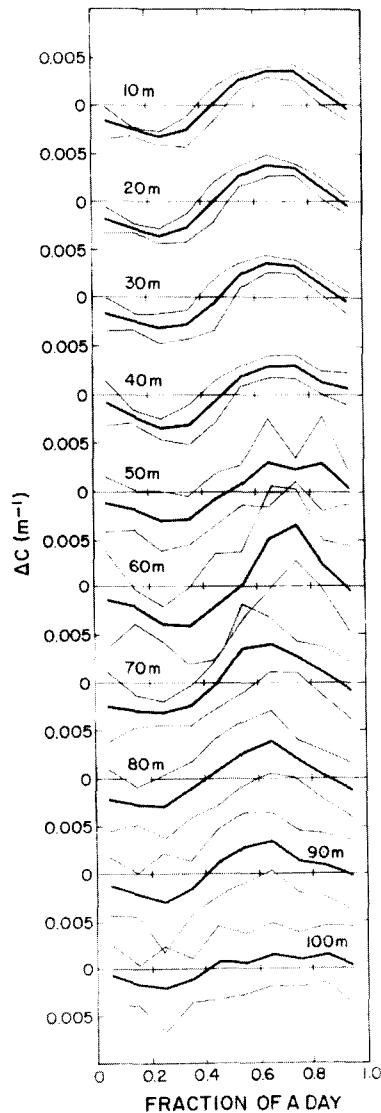


Fig. 3. Mean diurnal cycles for Δc for depths from 10 to 100 m in 10 m increments. Units are m^{-1} . The gray regions represent 95% confidence intervals for the mean diurnal cycle. These diurnal cycles are statistically significant from the sea surface to 90 m.

2b). The peak to peak Δc amplitudes range from 0.006 to 0.010 m^{-1} . The minimum occurs near sunrise while the maximum occurs at approximately sunset, indicating a daytime accumulation of particles.

Vertical variations of the mean diurnal Δc cycle (Fig. 3) are statistically significant (at the 95% confidence interval) from the sea surface to 90 m. The amplitudes of these daily cycles show small vertical variations, with characteristic peak to peak amplitudes of $\sim 0.0065 \text{ m}^{-1}$. The lack of significant diurnal Δc cycles below 90 m is consistent with the observed mean depth of the euphotic zone ($\sim 95 \text{ m}$). This suggests that the observed diurnal particulate variation is controlled, at least in part, by the photosynthetic production of particles.

ESTIMATION OF SPECIFIC PRODUCTION, GROWTH AND GRAZING RATES

Temporal variations of particle production can be examined by defining a specific particle production rate (r_0), or

$$r_0 = \frac{1}{c - c_w} \frac{\partial c}{\partial t}, \quad (3)$$

where c_w is taken to be 0.36 m^{-1} (BISHOP, 1986). The time series of $r_0(20 \text{ m})$ (Fig. 2c) shows maximum values ($\sim 0.4 \text{ d}^{-1}$) at noon, while night-time values are more uniform with values of $\sim -0.2 \text{ d}^{-1}$. The variations of $r_0(20 \text{ m})$ are relatively peaked near noon and flat during evening hours, appearing similar in shape compared with the *in situ* PAR at 20 m (Fig. 2b). Significant mean diurnal cycles of r_0 are observed from 10 to 80 m (Fig. 4), and no significant amplitude or phase variations with depth are observed. Also, the daily mean specific production rate is not significantly different from zero indicating that particulate production is balanced (i.e. average daily particulate growth equals grazing).

It should be noted that (3) should underestimate the true specific production of living materials because the beam attenuation due to detritus (c_{de}) is not taken into account ($c - c_w \geq c_{pl}$; EPPLEY, 1981). Assuming that detrital attenuation is one-half of the total particulate attenuation ($c_{de} = c_{pl}$), the present specific production underestimates the production of viable materials by a factor of two. Unfortunately, little is known about the relative contribution of detrital material to the particulate beam attenuation coefficient at 660 nm.

The specific production rate at 20 m is well predicted by the *in situ* PAR (explaining 71% of the variance; the artificial prediction skill (S_A) is approximately 22%; $S_A \approx 22\%$; DAVIS, 1976; SIEGEL and DICKEY, 1986), enabling r_0 to be modeled statistically as the sum of a light-dependent growth term (μ_0) and a light-independent grazing term (g_0)

$$\hat{r}_0 = C_1 \text{PAR} - C_2 \quad (4a)$$

$$\hat{r}_0 = \mu_0 - g_0. \quad (4b)$$

The modeled production rate ($\hat{r}_0(20 \text{ m})$) is shown in Fig. 2c (dotted curve). The maximum specific growth rate for 20 m approaches 0.7 d^{-1} while the grazing rate is 0.16 d^{-1} . The daily particulate growth rate is 0.16 d^{-1} as particle production is balanced. These specific growth and grazing rates compare favorably with previous specific rate determinations (SHELDON and SUTCLIFFE, 1978; EPPLEY, 1981; LANDRY and HASSETT,

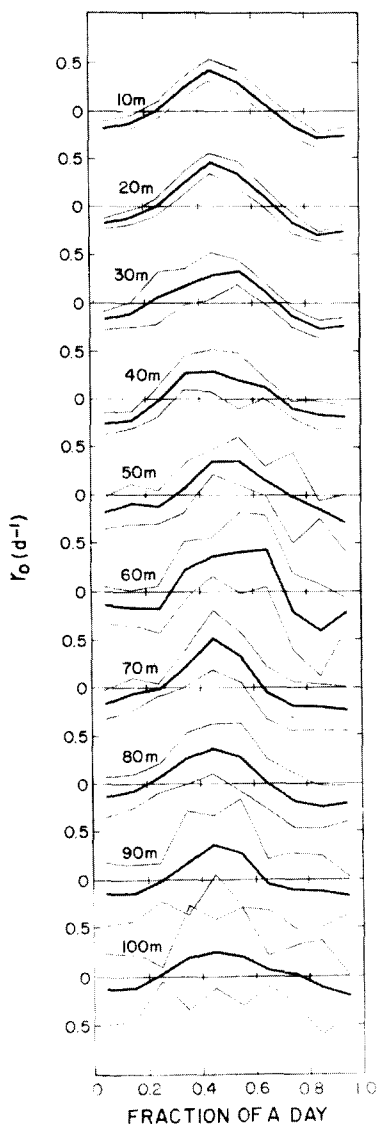


Fig. 4. Mean diurnal cycles for r_0 from 10 to 100 m in 10 m increments. Units are d^{-1} . The gray regions represent 95% confidence intervals for the mean cycles. Cycles are observed to be statistically significant to a depth of 80 m.

1981; PLATT *et al.*, 1983; ITURRIAGA and MITCHELL, 1986; WELSCHEMEYER and LORENZEN, 1986). Similarly at all depths where the mean diurnal c variations are significant (10–80 m), r_0 is well explained by values of PAR (predicting 23–71% of the observed variance, $S_A \leq 22\%$). Daily particulate growth rates have a mean value of about $0.14 d^{-1}$ with insignificant vertical variation.

A HYPOTHESIS FOR THE OBSERVED DIURNAL VARIATIONS

It is presently hypothesized that the diurnal production of particulates is due to photosynthetic production of ultraplankton and is offset by losses of these particles through microzooplankton ingestion. Similar microplankton food webs have been postulated for the open ocean (BEERS and STEWART, 1971; SHELDON and SUTCLIFFE, 1978; JACKSON, 1980; ITURRIAGA and MITCHELL, 1986; WELSCHMEYER and LORENZEN, 1986).

Other biological processes may contribute to the diurnal variations of the beam attenuation coefficient. However, these processes can be shown to be of lesser importance than those related to ultraplankton growth and microzooplankton grazing. As discussed previously, sensing of macrozooplankton diurnal vertical migrations is not likely because of the relatively small sampling volume of the transmissometer.

Diurnal-scale photoadaptation of cellular pigment concentrations cannot contribute to the observed diurnal beam attenuation variations, because the observed diurnal Chl *a* pigment concentration variations at 10 m are out of phase with beam attenuation variations (minimum during solar noon; DICKEY and SIEGEL, submitted). Further, mean diurnal variations of *in situ* chlorophyll fluorescence are insignificant below 45 m (SIEGEL and DICKEY, in preparation), whereas the mean diurnal variations of Δc are significant to a depth of 90 m (Fig. 3).

In the oligotrophic ocean, contributions by macrozooplankton to phytoplankton grazing are considered to be relatively unimportant (generally less than 10% of the total) compared with microzooplankton grazing rates (e.g. WELSCHMEYER and LORENZEN, 1986). It should be noted that predation of microzooplankton by diurnally migrating macrozooplankton and micronekton migrators may contribute to the observed variations (J. BISHOP, personal communication, 1988). Diurnal predation of ultraplankton grazers implies that the present growth and grazing rates may be underestimated. However, diurnal predation cannot control the observed Δc cycles because micrograzer abundances are not sampled by the transmissometer. As discussed previously, the present growth and grazing rates are also underestimated because of unknown amounts of detrital materials.

The simple particulate growth/grazing model (4) is consistent with the ultraplankton production/microzooplankton grazing hypothesis. This is true if microzooplankton feeding is independent of time of day and synchronized cell division is unimportant relative to solar-induced cell division. Presently, there is little consistent information concerning temporal variations of microzooplankton grazing (e.g. ANDERSON *et al.*, 1987). However, any diurnal variability in the ultraplankton grazing only affects the magnitude of the resulting rate (which is surely underestimated due to detrital attenuation).

Synchronous cell division has been observed for ultraplankton populations (specifically cyanobacteria) in both laboratory and field studies (CHISHOLM, 1981; CAMPBELL and CARPENTER, 1987; WATERBURY *et al.*, 1987). However, the high degree of correlation between the specific production rate and PAR suggests that the cell division rate is a simple function of light intensity and that synchronous division is probably not important for the present case. Unfortunately, the growth/grazing hypothesis cannot be rigorously tested using the present data because simultaneous growth, grazing, optical and particulate observations are not available.

ESTIMATION OF COMMUNITY PRODUCTION

Water column integrated production can also be estimated using the transmissometer data. The peak to peak Δc amplitudes denote a net accumulation of particles during the day; thus production calculated in this manner should represent the net community production (PLATT *et al.*, 1984). A value of Δc of $\sim 0.0065 \text{ m}^{-1}$ (Fig. 3), which is nearly constant throughout the depth of the euphotic zone (95 m), is used. The conversion from c variations to particulate organic carbon (POC) variations can be made by using values for the SPM specific beam attenuation coefficient [$1020 \mu\text{g kg}^{-1} \text{ m}$ (assuming a specific gravity for SPM of 1.05 g ml^{-1}); KITCHEN *et al.*, 1983] and the percentage of POC in SPM ($\sim 25\%$; HOBSON, 1967; BISHOP *et al.*, 1986). The resulting water column community production is $\sim 160 \text{ mg C m}^{-2} \text{ d}^{-1}$. Using a value for the SPM specific beam attenuation coefficient taken from the Sargasso Sea and North Atlantic Ocean ($1150 \mu\text{g kg}^{-1} \text{ m}$; BISHOP, 1986), a community production of $\sim 180 \text{ mg C m}^{-2} \text{ d}^{-1}$ is obtained. Although it is difficult to ascribe a confidence interval to the production estimate, the difference between the two rates suggests that the estimate of $160 \text{ mg C m}^{-2} \text{ d}^{-1}$ is probably accurate to within 25%.

The value of optically determined community production compares well (although it is somewhat higher) with nearly simultaneous carbon uptake production determinations made from the R.V. *Acania* ($116 \pm 27 \text{ mg C m}^{-2} \text{ d}^{-1}$; $n = 7$). The optical community production is also consistent with summer mean values from the North Pacific Ocean ($106 \pm 43 \text{ mg C m}^{-2} \text{ d}^{-1}$; HAYWARD *et al.*, 1983). The difference between the optical and carbon uptake community production rates may be attributed to the filters used in the uptake experiments. It should be noted that recent primary production measurements in the oligotrophic Pacific Ocean show values that are two to three times greater than either of the previously denoted carbon uptake determinations (MARRA and HEINEMANN, 1987; LAWS *et al.*, 1987).

CONCLUSION

An optical technique is introduced to determine variations of particulate abundance and production in the open ocean. Values of specific production rate and integrated community production are consistent with previous and simultaneous determinations. Specific rates of primary and secondary production may also be estimated by assuming that grazing activity is independent of time of day. The present method appears to have significant potential and its use may facilitate determinations of both spatial and temporal variations of particulate production from unattended instrumentation.

It should be noted that the present analysis is limited by uncertainties in the estimation of particulate (and more importantly phytoplankton) properties using variations of the beam attenuation coefficient. Better knowledge of particulate optical properties of both phytoplankton and detritus is needed to be made before these shortcomings are alleviated.

Finally, diurnal variations of the beam attenuation coefficient (c) may influence the quality and interpretation of synoptic spatial maps of c . The present observations show peak to peak variations of c to be as large as 0.01 m^{-1} . Within the euphotic zone, horizontal attenuation variations will be significant only if their magnitudes are greater than this amount. Spatial distributions of c at the attenuation maximum (roughly 60 m)

made from the R.V. *Acania* during ODEX show values ranging from 0.43 to 0.45 m⁻¹ (STOCKEL *et al.*, 1986). Thus, diurnal *c* variations can account for up to 50% of the observed "spatial" variations, limiting the utility of synoptic maps of *c*.

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