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Primary Production in the North Atlantic: Measurements, Scaling, and Optical Determinants [and Discussion]

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Primary production in the North Atlantic: measurements, scaling, and optical determinants

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SUMMARY

Productivity in the ocean is viewed from the perspective of its three components: biomass, yield (new production), and the rate of production. The three components are ordered along a time scale and a fundamental time scale is defined for the rate of production at the diel (24 h). Two optical properties, the absorption by phytoplankton and particle scattering, are presented and it is argued that they provide a means to unite the rate of production with biomass and yield at the diel scale.

1. INTRODUCTION

Of all the oceans, the North Atlantic is the most sampled and studied. Many oceanographic paradigms originate here, such as oceanic seasonality, the explanation for western boundary currents (the Gulf Stream), and circulation in the abyss. These physical phenomena naturally affect biological expression. Convective mixing in winter resets the seasonal production cycle, and springtime restratification induces a strong signal in productivity. The Gulf Stream redistributes mass, heat, and nutrients throughout the basin. These forcings and their effects are known in broad outline, but variability and interactions at all scales inhibit our understanding considerably.

Primary production in the North Atlantic has been expressed over a variety of scales and in a variety of ways, for example, as maps of carbon assimilation (see, for example, Koblentz-Mishke *et al.* 1970), from the balance of non-conservative properties (Riley 1951), from satellite imagery (Campbell & Aarup 1992), or from nutrient supply (Berger *et al.* 1989). In a variety of disciplines, the productivity of the ocean has on-going interest (see, for example: Jenkins 1982; Bishop 1989; Mix 1989). If we were to summarize the perspective of the scope of these studies, primary production might be thought of no more precisely than the collection of processes in the surface ocean, occurring between nutrient supply and export of organic matter to the deep sea. Here, I first try to establish a more coherent view of what we mean by primary production in the ocean, and out of that establish a central time scale – the diel – as a junction toward which we might direct our efforts. Finally, I discuss two kinds of measurement, having to do with optical variability, where I believe advances will be made in understanding the controls on primary production in the North Atlantic.

2. THE STUDY OF PRIMARY PRODUCTION

If we were able to take a snapshot of the North Atlantic, say with a satellite sensor such as the Coastal Zone Color Scanner, CZCS (or SeaWiFS), then we could show areas that appear to have more colour than others, and conclude that they are more productive. Similarly, if we were to collect data on the amount of fish caught during a particular time across the North Atlantic, we might also develop a crude map of productivity based on fish landings. These are two components that describe what we mean by the productivity of an ocean area (see Clark 1946). One is the biomass, the standing crop of the biota, and the other is (one part of) the yield of the ecosystem, the amount removed. The single satellite image gives us an indication of productivity by virtue of the relative distribution of biomass, and the fish-catch by virtue of the ocean's harvest. In modern parlance, the yield represents the 'new' production, which is commonly held to be the amount of organic matter exported from the surface ocean. Ecologically speaking, the yield is the same as the carrying capacity of the ecosystem.

From these two attributes alone we cannot know why the yield takes on the value it does, nor why a particular abundance of organisms exists. To understand them, therefore, we have to know the rates of production, the third component, since the same level of biomass could occur with either a rapid or a slow rate of increase to an equilibrium level. Similarly, the yield will depend not only on the supply of external substrate (e.g. a nutrient), but also on the relations in the foodweb (the biomass) of the system. If there has been any overall theme in plankton research in the last ten or so years, it is that biomass can be a poor indicator of the rate of primary production in the ocean, and that yield is not a simple function of nutrient supply.

Most rate measurements are based on physiology. However, in plankton systems, biomass and yield change rapidly enough such that the interrelations among the three might be effectively studied. To

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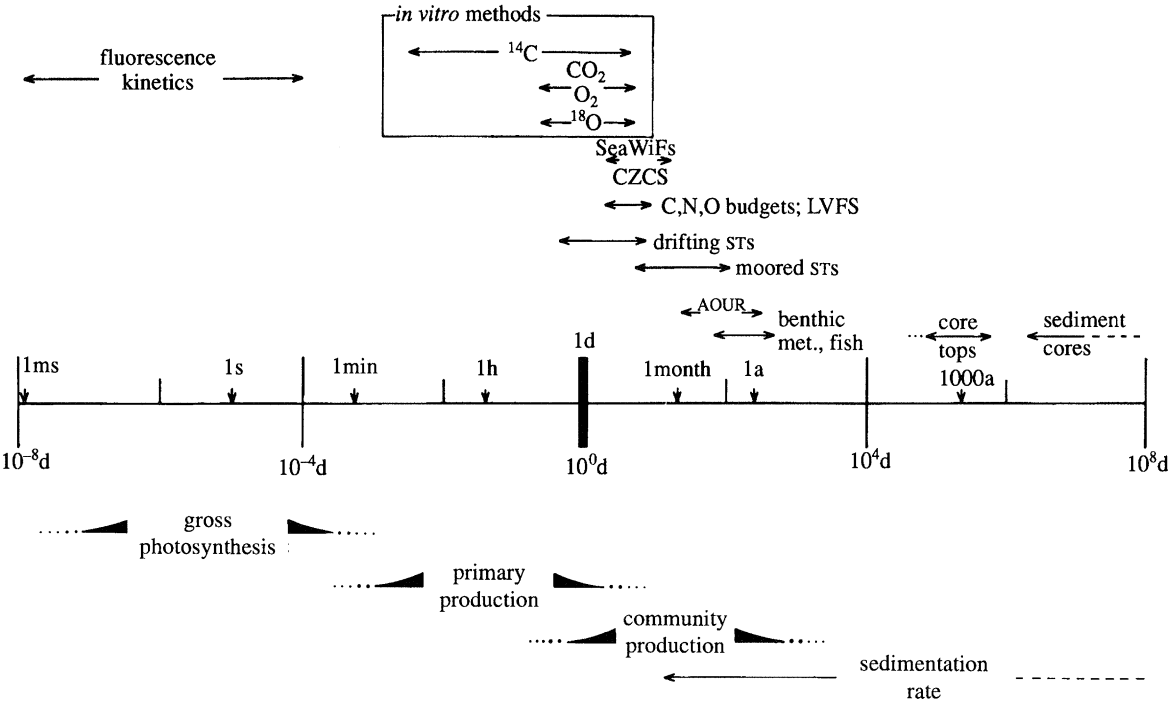

Figure 1. Time scales of primary production in the ocean. AOUR, apparent oxygen use rate. CZCS, Coastal Zone Color Scanner.

understand what I mean, we can examine the variability of physiological rates, biomass changes, and yield on a time scale (figure 1). From the fastest to the longest is about 16 orders of magnitude. To put that length into perspective, if a useful time scale in geology is one year, then the time scales of productivity in the ocean span a longer time than the age of the earth. Generally, we go from gross photosynthesis to geology (sedimentation rates), from the surface to full-ocean depths, and from small to large spatial scales. And, in the study of primary production, we can see that production goes from physiological rates, to rates of change of biomass (e.g. carbon, nitrogen budgets), to rates based on yield (AOUR). Nevertheless, the measurement techniques are what provide the data for the models of ecosystem dynamics in the ocean. Models also have a time scale, because these are the data that provide input to the models and are used to develop functional relations.

Beginning at the fast end, the realm of biochemistry, we can look at the fluorescence kinetics of the photosynthetic process, which has cycles of milliseconds (if not faster), and from this deduce rates of photosynthesis (Kiefer & Reynolds 1992). The time scale of hours to days has come to dominate phytoplankton and primary production studies, for the good reason that this is the time scale for phytoplankton growth. All of the *in vitro* techniques are at this scale, and it is clear that over periods of one day or less, solar irradiance will be the most important environmental variable. Going to longer time periods of measurement, there are time scales associated with water column budgets, sediment traps, and deep-water metabolism. Finally, geologists examine sediment cores for indications of how ocean productivity might have varied with past climates.

The processes listed in figure 1 have characteristic time periods for completion. At some point, the rate of production, P, is zero, or

$$\int_T P\,\mathrm{d}t = 0,$$

where T is a time period. At the scale of biochemistry, the characteristic time scale could be interpreted as the cycling between reduced and oxidized forms of energy-transferring molecules, fluorescence lifetimes, and the like. At longer times scales, we can easily label the solar day as a time period over which irradiance completes a cycle, and over which photosynthesis might balance respiratory losses. At longer time scales, there is seasonality, the time scale over which nutrients are recycled, and one strong characteristic of the North Atlantic.

When speaking of environmental factors, we can see that irradiance and nutrients in the North Atlantic operate on different time scales. The greatest variability for phytoplankton will be on the diel, when irradiance exhibits its maximum change. Nutrient supply is regulated most strongly on the seasonal time scale through convective mixing in winter. For models describing events on the short term, therefore, irradiance becomes the most important factor, while for longer time scales (say, weeks or months), the growth equations for autotrophs are based on nutrient kinetics (see, for example, Fasham *et al.* 1990).

To summarize, over the diel scale, population photosynthesis is driven by irradiance. Over the annual cycle, community production is essentially zero, and is driven by nutrient cycles. Over global-ocean scales, climate is the driving force, producing major redistributions of nutrients and plankton, and variability in ecosystem structure.

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The central time scale, I submit, is that for phytoplankton growth: the diel (or at most a few days). Rate measurements shorter or longer than this involve extrapolations to this scale. Naturally, one goal would be to connect the time scales and that way link physiological rates with biomass changes and yield. I will suggest a means of proceeding on this problem from the point of view of the optical properties of the phytoplankton. In short, I suggest that the absorption of irradiance by phytoplankton helps to define the physiological rates, while the scattering properties of phytoplankton (and similar-sized particles) will reveal rates of change in biomass.

3. OPTICAL DETERMINANTS TO PRIMARY PRODUCTION

I will illustrate the optical determinants to diurnal production in phytoplankton by considering data from three sites in the North Atlantic. The first is Biowatt in the North Sargasso Sea (34° N 70° W). The other two are more familiar to those in JGOFS (Joint Global Ocean Flux Study), the location used for the North Atlantic Bloom experiment (NABE) in 1989 at 47° N 20° W and the Marine Light–Mixed Layers program (ML–ML) site at 60° N 20° W. ML–ML, due north of the 47° N site, was also used as one of the major stations for the NABE. The major field program in ML–ML occurred in 1991. Like most of the North Atlantic, all three sites exhibit seasonality, but differ in degree, for example, in the magnitude of the seasonal range in sea-surface temperature and in the reservoir of nitrate available to be mixed into the surface layers in winter.

(*a*) *Phytoplankton absorption*

Phenomenologically, photosynthesis can be expressed as the product of the fraction of irradiance that is absorbed by the plants, and the efficiency of the photosystems in using the absorbed irradiance to fix carbon. The relation is

$$P = \phi a_{\mathrm{ph}} E, \qquad (1)$$

where E is the irradiance and is typically represented as the total number of photons integrated over the wavelength region of photosynthetically active radiation (PAR), 400–700 nm, expressed as mol photon $m^{-2}\,s^{-1}$. The absorption of irradiance by phytoplankton is also usually averaged over PAR (or else weighted by the spectrum of irradiance at the depth sampled), and is represented by the coefficient, $a_{\mathrm{ph}}\,(m^{-1})$. The quantum yield, ϕ, represents the efficiency for the conversion of absorbed irradiance into (in this case) fixed carbon (mol C [mol photon]$^{-1}$).

Equation (1) is wonderfully simple, but seldom used. The reasons are threefold. First, the measurement of submarine irradiance has not been accorded the same kind of care and precision typical, for example, for nutrients. Second, the absorption coefficient for phytoplankton, a_{ph}, has been difficult to separate from absorption by other particulate matter. (Now the measurement of submarine irradiance is becoming routine, and great progress has been made in the determination of absorption by phytoplankton (see, for example, Bidigare *et al.* 1992).) Finally, ϕ cannot be measured directly, that is, independent of irradiance absorption. In equation (1), the quantum yield is usually estimated and modelled based on laboratory studies (Kiefer & Mitchell 1983), using an equation of the form

$$\phi = \phi_{\mathrm{m}} f(E),$$

where $f(E)$ is a function for the irradiance, and ϕ_{m} is a maximum value for ϕ. Given the chemistry, ϕ_{m} will have a theoretical maximum of 0.125 (in terms of oxygen evolved). Metabolic demands, other pathways and losses, and expression in carbon units, however, make the realized values less by about 50 %.

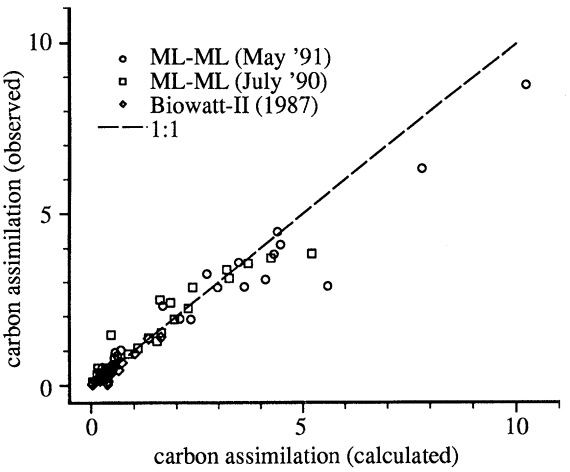

Figure 2. Optical calculations of carbon assimilation. The observed values are from dawn-to-dusk, *in situ* measurements of carbon assimilation by the ^{14}C technique. The calculated values are obtained from equation (1) in the text, carbon assimilation being calculated at each of the observed depths by means of estimates of $E(z)$, the chlorophyll-specific absorption coefficient for phytoplankton (a^0_{ph}), and a model for ϕ which assumes a ϕ_{m} of 0.055 (Biowatt) or 0.060 (ML–ML) and an irradiance saturation function (Kiefer & Mitchell 1983).

The published data which use equation (1) as a bio-optical calculation of carbon assimilation are shown in figure 2, from ML–ML (Marra *et al.* 1993, 1994) and from Biowatt (Marra *et al.* 1992). The environmental conditions span 8–26 °C in the water temperature in which the experiments were done and from undetectable levels of nitrate (Biowatt) to 12 μM (ML–ML). Overall, the estimate of carbon assimilation is fairly good, but with some notable underestimates in the observed values relative to that calculated, especially at higher rates of production. In one experiment during ML–ML (1991), a completely clear day (63 mol photon $m^{-2}\,d^{-1}$) in a stratifying water column immediately followed several days of clouds, storms, and water column mixing (Marra *et al.* 1994). Observed carbon assimilation is lower than predicted in this case, we think because of the time needed to adapt, to photoacclimate, to the abrupt change to new conditions. Other improvements in the relation shown in figure 2 may come with greater reliance on spectral

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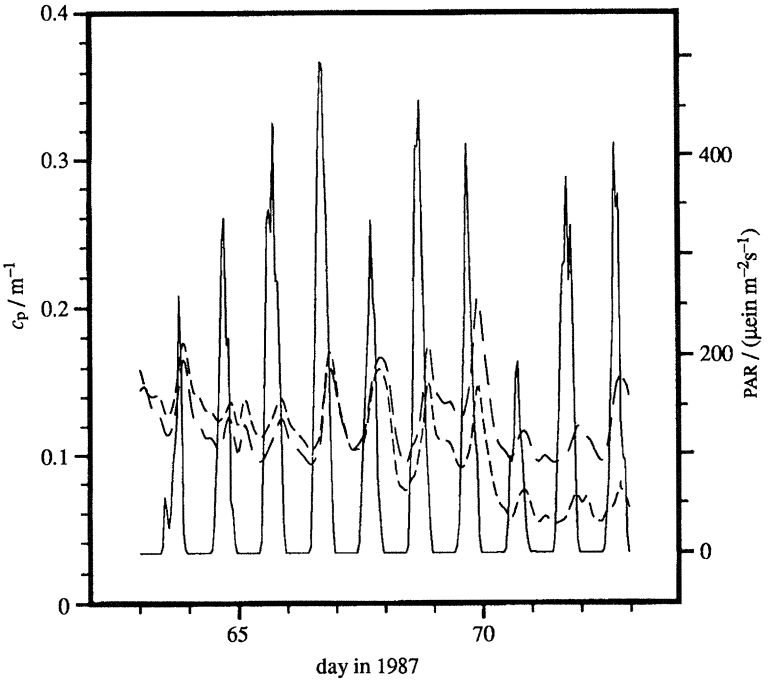

Figure 3. The diel variability in particle attenuation (c_p) at 10 and 20 m, along with E_{PAR} (at 10 m) from the Biowatt mooring experiment (34° N 70° W) in 1987.

irradiance (rather than the broad-band PAR) and improved estimates of phytoplankton absorption.

On another tack, we can examine how the biological terms in equation (1) are likely to change in response to environmental conditions. The primary means by which phytoplankton respond to irradiance is to alter their absorption properties, either in the quantity or types of pigments, or in how pigments are distributed in the cell. The absorption term in equation (1) may actually hide considerable complexity.

For example, under summertime or tropical conditions, the phytoplankton community living near the surface commonly have pigments that serve a photoprotective function (Bidigare *et al.* 1992). These pigments are one mechanism used to shield the photosystems from irradiances that are too high. The size distribution of the phytoplankton also assumes importance, as well as the distributions of the chloroplasts (pigment) within the cell. Collectively, these latter modifications to pigment absorption are termed the 'package effect', referring to the fact that absorption by pigments takes place in discrete units rather than in solution (Kirk 1994). One typical manifestation of the package effect is the reduction in pigment-specific absorption when the cells manufacture more pigment on encountering lower than optimal irradiance. Even so, the majority of absorption in the cell is by the most abundant pigment, chlorophyll *a*. The particulate absorption spectra still retain the primary characteristics of that expected if chlorophyll were the only pigment. Thus, locally, the chlorophyll-specific absorption,

$$a^0_{ph} = a_{ph}/\mathrm{Ch},$$

stays relatively constant.

How quantum yields could change in response to environmental forcing is largely unknown. The effort here has been directed towards ϕ_m since that parameter is accessible to estimation through the measurement of α, the initial slope of photosynthesis–irradiance curves (see, for example, Cleveland *et al.* 1989). If it is assumed that the rate of photosynthesis at low light occurs at maximum efficiency, then

$$\alpha = \phi_m a_{ph}.$$

Whether variability in α is caused by adjustments in ϕ_m or a_{ph} is an area of active research. Most laboratory data support the idea that changes in ϕ_m come about through absorption and that ϕ_m is independent of irradiance (see Geider 1993). The data from natural populations are uncertain either because it is difficult to isolate factors or because the measurement of α entails procedural variability which masks environmental effects (Marra & Bidigare 1994).

In summary, while the data (figure 2) suggest that changes in ϕ_m are secondary, equation (1) may possibly be affected by environmental conditions: the quantity of nutrients available or the temperature of the water. Thus far, however, no practical method has been devised to incorporate these potential effects into equation (1). Recalling the differing scales of variability for nutrients and irradiance mentioned above, I believe that the nutrient supply to the euphotic zone governs the absorption properties of the phytoplankton, and irradiance governs the physiological rates. A corollary hypothesis is that nutrient supply sets the level of biomass in the system and therefore the absorption properties. Unfortunately, in the North Atlantic, nutrients and irradiance confound one another. Generally speaking, at large scale, one is low while the other is high. Although the North Atlantic has been the birthplace of many paradigms in oceanography, we will have to look elsewhere for a test of how nutrients interact with irradiance in these physiological relations.

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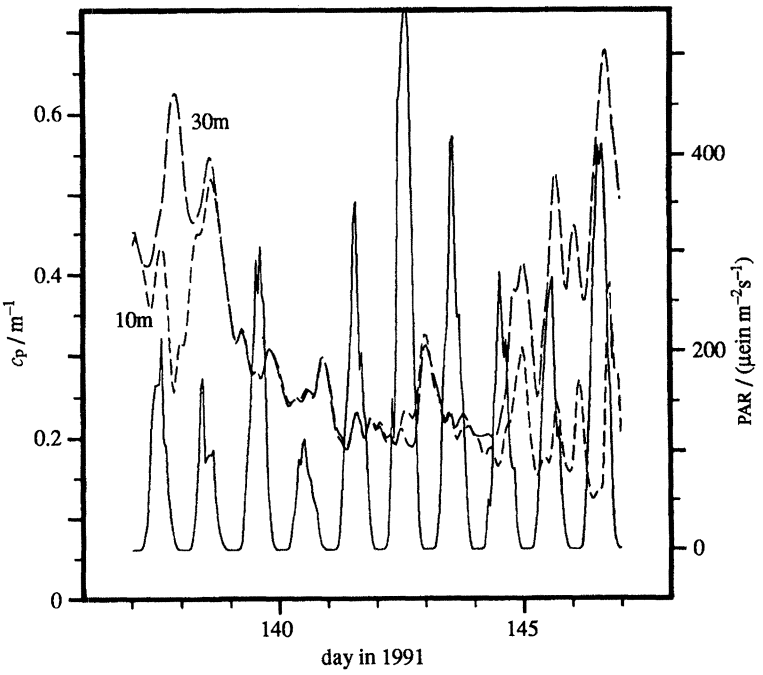

Figure 4. As for figure 3, but for the ML–ML experiment (and at 10 and 30 m) (60° N 20° W) in 1991.

(*b*) *Diurnal changes in the attenuation of particulate matter*

Interpreting of the results from standard primary production methods with changes in water column properties at the diel scale has been accomplished only recently (Williams & Purdie 1991; Bender *et al.* 1993; Chipman *et al.* 1993; Marra *et al.* 1994), however, to match *in vitro* physiological rates with changes occurring in the water column must be a goal, to unite rates with biomass and yield. Once measurements exclude the incubation container, other processes are included in the assessment of production, such as air–sea exchange, advection (including internal waves), and diffusion, making the problem formidable indeed.

Measurement of the beam attenuation of light in seawater, however, holds promise to record the change in biomass of particle populations and particulate organic carbon. Beam transmissometers supply data quickly and continuously; thus the method provides both the depth and time resolution sufficient to interpret changes in terms of environmental forcing. Transmissometers have a long tradition in optical oceanography in measuring particle abundances in terms of the attenuation coefficient, c (m^{-1}). Now they can be employed dynamically. The attenuation data from the NABE (Gardner *et al.* 1993), for example, suggest a somewhat different means to express growth and production of phytoplankton populations on a diel time scale.

The attenuation coefficient of light, c, is the sum of the absorption and scattering coefficients. In the ocean, attenuation can also be expressed as the sum of three major components, that from particles (c_p), that from dissolved organic material (c_d) and attenuation from the water itself (c_w), i.e.

$$c_{tot} = c_p + c_d + c_w,$$

where c_{tot} refers to total attenuation at 660 nm. The attenuation from dissolved material is small enough at this wavelength that it can be ignored, and c_w is reasonably well known. A further point is that at these longer wavelengths, attenuation is overwhelmingly caused by the scattering of light rather than by absorption. Finally, given the optical path, and the nature of oceanic particulates, c_p largely represents particles of 0.8–20 μm in effective diameter, the size range of the most abundant forms of phytoplankton.

From a highly resolved series of profiles in the Pacific, Siegel *et al.* (1989) were the first to report that c_p undergoes a regular diel variability. They argued that the observed changes are due to the production of particles, but variations in particle attenuation can only be interpreted as such provided that the size, shape, and refractive index of the particles also do not vary coincidentally (see, for example, Spinrad 1986). Siegel *et al.* (1989) did not have the supporting measurements to evaluate those particle characteristics, but Stramski & Reynolds (1993), using laboratory populations, find that while the attenuation and scattering parameters change by 80% over a diurnal period (indicating changes in particle characteristics), much smaller changes occur when these are normalized to cellular carbon content. Thus, if the observed increase in scattering is associated with carbon incorporation and cell division, then it constitutes a method for looking at biomass changes directly, *in situ*, with the additional advantages of rapidity in sampling and inspecting results. In natural populations, correlations between c_p and particulate organic carbon are very good (Gardner *et al.* 1993; Marra *et al.* 1994), but to create a relation with generality will require knowledge of particle size distributions and the refractive index (Spinrad 1986).

Two examples show the variability of the *in situ* diel behaviour of particle attenuation. For Biowatt, diel variability persists throughout the nine-month record

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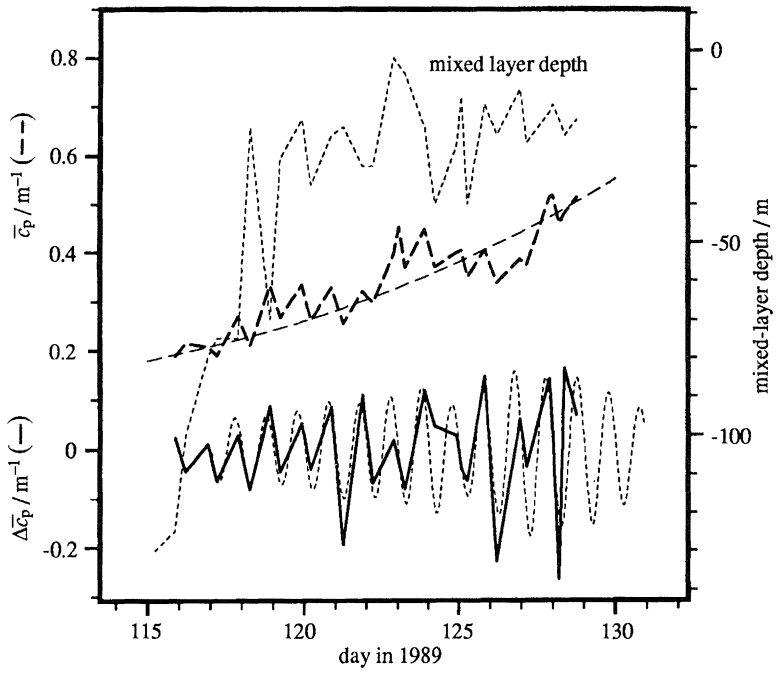

Figure 5. Particle attenuation in the mixed layer during the U.S. JGOFS cruise (25 April–7 May 1989) as part of the NABE at 47° N 20° W. Mixed layer depths are identified. The middle set of data is the particle attenuation averaged over the mixed layer ($\bar{c}_p$), and the bottom data ($\Delta\bar{c}_p$) is the first difference of the $\bar{c}_p$ data and includes the compensation for changes in mixed-layer depth described in the text. The $\bar{c}_p$ data are fitted (long-dashed curve) to the equation, $\bar{c}_p = 0.018\ e^{0.075t}$ (where t is time in days). The $\Delta\bar{c}_p$ data are fitted to the equation

$$P^C = p_1\, e^{p_2 t} \cos(2\pi t + p_3),$$

where $p_1 = 0.012$, $p_2 = \int_{t-48}^{t} E_{PAR}\, dt$, $p_3 = 1.4$ and E_{PAR} is the surface irradiance.

of the mooring in the near-surface sensors, with a near-dawn minimum and a maximum at sunset (figure 3). The relation is steady and predictable. A contrasting situation occurs for ML–ML in spring (figure 4). Here, there is little discernible regular relation between the variability in c_p and the daily cycle of irradiance. The first five days of this sequence were dominated by storms and mixing. It was not until the last two to three days that the water column stabilized.

We also examined the NABE c_p data (Gardner *et al.* 1993) in greater detail (figure 5). (This analysis was done in collaboration with my associate, Cheng Ho.) Although the temporal resolution is much poorer, extensive ship-board data help to interpret the observations, and the water column was restratifying, leading to the spring bloom. We confined our analysis to the mixed layer since this is where the plankton grow in the spring. There is a hint here of the spatial variability in the development of the bloom; the ship repositioned on the nights of 120–121 and 124–125 (see McGillicuddy *et al.* 1994). Nevertheless, fitting the overall time sequence gives a specific growth rate of 0.075 d^{-1}. (This might underestimate the true growth rate because detrital particles are included in the measurement.) We are interested more, however, in how the daily rate of production varies as a result of environmental forcing, particularly irradiance. Therefore, we calculated the first differences of the data, which because the samples were collected near dawn and dusk each day, become estimates of daytime particle production and nighttime particle loss. But the changes in the mixed layer have to be incorporated into the change in particles. As pointed out in Chipman *et al.* (1993), when the mixed layer depth shoals over the time step, the biomass left beneath should be included in the calculation of growth. Conversely, when the mixed layer depth deepens, the biomass imported into the mixed layer depth is excluded from the growth calculation.

The results of calculations for production in the mixed layer (and which incorporate changes in mixed layer depth) show interesting behaviour (figure 5, bottom curve). First, night-time losses are high, the highest nearly matching daytime gains. Second, the ship movements (nights of 120–121, 123–124) do not appear to have unduly influenced the calculations. (The anomalous behaviour during day 124, also noted by McGillicuddy *et al.* (1994), remains, thought by those authors to be caused by unexpected water movements.) Third, and most interesting, as daytime production increases as the bloom develops, nighttime losses also accelerate. These data agree with the supposition that respiratory losses may be larger than previously thought (Langdon 1993).

The oscillating behaviour of production in all these studies suggests a periodic model, and so the data were fitted to the equation with irradiance (see Marra & Ho 1993) as the forcing variable,

$$P^C = p_1\, e^{p_2 t} \cos(2\pi t + p_3). \qquad (2)$$

The fitting constant p_1, p_2, and p_3 may be thought of (respectively) as an initial production rate, a growth constant, and a lag. The initial production rate can be considered to be that which obtains under constant

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conditions. The parameter p_2 has been modelled as a function of the light history, in this case the integrated irradiance over the previous 48 h. The periodic component describes the phase shift in the production rate and the nighttime losses. For the NABE data, the infrequency of the sampling makes p_2 highly uncertain and heavily influenced by the sampling time. Nevertheless, we have found some agreement in the data (figure 5).

The above equation is atypical, but we require some form that allows the observed acceleration in the change in the production rate on a diel basis, and as the mixed layer shoals. Equation (2) may be thought of as a solution to the logistic equation, but with an explicit time-dependent growth term,

$$\mathrm{d}[N(t)]/\mathrm{d}t = r(t)\,N(t).$$

Clearly, we are not at a stage where the change in beam attenuation can be regarded as definitive in terms of biomass changes in the phytoplankton. Yet the apparent ubiquity of the diurnal signal, the vertical and temporal resolution that can be obtained, and near real-time availability of results make the method attractive in quantifying relations among environmental forcing, the biomass and the rate processes (photosynthesis and respiration). What is needed now is further understanding of the relation between attenuation and phytoplankton and particle characteristics.

3. CONCLUSION

In the past, the solution to the problem of poor sensitivity of the local measurements of primary production and the unpredictability of water motions was to broaden the scale of study (see, for example, Riley 1951). The inception of the ^{14}C technique allowed estimates of photosynthetic rates, but did not permit a measurement of loss processes, and led us away from *in situ* population dynamics. From recent studies, the consensus annual rate for primary production in the North Atlantic is 10–15 mol C m^{-2} (Campbell & Aarup 1992; Marra *et al.* 1992; Lohrenz *et al.* 1992). Greater detailed knowledge of loss processes through the optical properties of the plankton will allow us to put this value in the context of biomass and yield.

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Discussion

H.W. Ducklow (*Department of Chemistry, Woods Hole Oceanographic Institution, U.S.A.*). The North Atlantic Bloom Experiment (NABE) was one of the first attempts at an international standardization of trace metal-free incubations for primary production estimates by ^{14}C. Are the NABE estimates of N. Atlantic productivity greater than older estimates in the historical archive? How are we to consider the earlier estimates of productivity in this basin?

J. Marra. The ^{14}C has three characteristics. It is easy, it always returns a 'positive' result, and it is extremely sensitive. The characteristics mean that lots of determinations are possible, the method always seems to work, and it is difficult to verify. All three should warn us, and we owe a debt to John Martin, George Knauer, and their colleagues who, in the 1970s, argued for more careful technique.

My guess is that the productivity data from the NABE is indeed higher, but more importantly, they compare well with *in situ* (mixed layer) changes in ΣCO_2. Over the past few years, estimates of annual production in the North Atlantic have about doubled the older values, from 6 to 12 mol C m^{-2}.

How should we consider the earlier data? With scepticism, I think. Certainly there are examples of careful methods in the past (the International Indian Ocean Expedition's sampling method comes to mind), but more often the detailed protocols are not sufficiently known to be evaluated. Further complicating the issue is the possibility of long-term (decadal) changes in oceanic conditions which may have affected the level of primary production irrespective of the methods used. I note that for two years at the Bermuda Atlantic Time Series station, the annual estimates differed by 24%.