

# The Compensation Irradiance for Phytoplankton in Nature

John Marra

Lamont-Doherty Earth Observatory of Columbia University, Palisades, New York

**Abstract.** The compensation irradiance for phytoplankton is calculated from the time course of fluorescence-derived chlorophyll-*a* measured on moored sensors in the North Atlantic in spring. Following the initiation of the spring bloom, the time at which chlorophyll-*a* begins to decrease at a particular depth in a stratified water column is used to compute the compensation irradiance from the critical depth criterion. Over the depth range of 50-110 m, the compensation irradiance is estimated to be in the range from 0.1-0.3 mol photons m<sup>-2</sup> d<sup>-1</sup>.

## 1. Introduction

The compensation irradiance,  $E_c$ , is defined as the irradiance where photosynthesis equals respiration.  $E_c$  is difficult to measure in the laboratory; usually, its value is estimated indirectly from an extrapolation to zero growth in a series of cultures grown at different irradiances [e.g., *Langdon, 1987*]. In nature,  $E_c$  is nearly impossible to estimate. It is nevertheless important, however, to understanding seasonal cycles in the ocean, and phytoplankton productivity.  $E_c$  is central to the idea of the critical depth [*Sverdrup 1953*], the criterion for the initiation of the spring bloom in many regions of the ocean.

In 1989, as part of the Marine Light – Mixed Layers (ML-ML) project [*Marra, 1995*], we conducted a mooring experiment in the North Atlantic about 300 km south of Iceland. The mooring consisted of a surface buoy with meteorological instrumentation, and current meters coupled with bio-optical sensors arrayed at depth intervals of 20-30 m over the top 250 m of the water column. The mooring failed about 50 days after it was deployed. The current meter housings were later recovered (in August 1990), and they held intact the data recorded during the 1989 experiment. Initial descriptions of the data along with some analysis are in *Dickey et al. [1994]*. That publication describes the changes over the initial stratification of the water column and the bio-optical response. *Ho and Marra [1994]* analyze the intermittency of chlorophyll-*a* (Chl-*a*) accumulation in the surface layers (as indicated by in vivo fluorescence) and water column mixing during mid-April to mid-May, the early part of the record. Here, I analyze the chlorophyll fluorescence data from the later portion of the record, where the spring bloom had begun, and which shows behavior with respect to the sequence of the temporal response occurring over depth that can be used to estimate the compensation irradiances. To my knowledge this is the first time the compensation irradiance has been observed in a natural population at these time scales. However, the use of time series data from a mooring means the data have other sources of variability, adding uncertainty to the analysis.

## 2. Observations

The mooring was deployed at 59°29.5'N, and 20°49.8'W. The sensors began collecting data on 13 April 1989 (Day No. 103), and stopped on 12 June 1989 (Day 163). The array of

sensors along the mooring line and pertinent to this investigation are Multi-Variable Moored Systems [MVMS; see Dickey *et al.*, 1991] at nominal depths of 10, 30, 50, 90, 110, 150, and 250 m. The MVMS consists of a vector-measuring current meter (VMCM), a beam transmissometer, fluorometer, scalar irradiance sensors (for photosynthetically active radiation, or PAR), and dissolved oxygen sensors. The MVMS at 90 and 150 m varied from the above package in having downwelling irradiance sensors (at 488 nm) instead of PAR sensors. The surface buoy had a suite of meteorological sensors, and solar radiation (300-3000 nm in  $\text{W m}^{-2}$ ). The sensors were calibrated according to the protocols given in previous publications [e.g., Marra *et al.*, 1992; Weller *et al.*, 1990]. Chl-*a* is determined from in vivo fluorescence, which is also subject to other forms of variability. The most important source of variation is non-photochemical quenching, caused by high irradiance [Marra, 1997]. There is some evidence of non-photochemical quenching occurring early in the records examined here, but it becomes unimportant later as Chl-*a* increases, and irradiances decrease in the water column. Non-photochemical quenching occurs in these waters for irradiances  $> 200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  [Marra, 1997] and irradiances never exceed this value at 10 m (the topmost fluorometer) after day 140.

I focus on the MVMS data from Day No. 135 through Day 161 (the end of useful data collection), 27 days. The temperature records at the depths from 10-150 m are shown in Fig. 1. There is incipient and intermittent stratification between days 136 and 143 (Fig. 1a), where during the day, there are increases of  $\sim 0.1^\circ\text{C}$ . After that, the top three sensors (at 10, 30 and 50 m) show increases that build until about day 148, when the water column becomes stratified over the top 90 m. There is some evidence that the water column exhibits a two-layer structure during days 143-148, with the division between 50 and 90 m. Stratification becomes stronger over 10-50 m after day 148, and by day 157 (Fig. 1b) there is evidence of the advection of slightly cooler temperatures past the mooring. The current vectors at this time (not shown) abruptly change for days 155-157, but until this point, the stratification can be regarded as a local process [Dickey *et al.*, 1994]. Given the stratification of the water column, I treat each depth horizon separately, and calculate optical characteristics for each depth range defined by the sensor locations.

The data from the fluorometers, presented as Chl-*a*, in raw form are noisy, although the signals can still be discerned (Fig. 2). The variability in the beam transmissometer data (not shown) follows that of Chl-*a* until day 156 [Dickey *et al.*, 1994]. Chl-*a* increases together at all depths, beginning at day 138 (and after a mixing event on day 137), but almost immediately thereafter, the shallower depths (10-50 m) begin to increase faster, probably reflecting incipient stratification of the water column shallower than 90 m (Fig. 1a). At 110 m, Chl-*a* stays constant, and then by day 144 begins to decline. The behavior at 90 m is very similar with a parallel increase and decline, although the Chl-*a* may be sustained for  $\sim 1$  day longer. Chl-*a* at shallower depths continues to increase, but by day 147, the 50 m signal begins to decline, followed by the 30 m signal at day 153. I interpret the record of 30 m after day 153 and 10 m after day 155 to result largely from advective influences (see below). The simplest explanation for the overall behavior of the Chl-*a* data indicate self-shading of the

populations, with populations at shallower depths growing at the expense of those deeper as the bloom progresses.

Superimposed on the data in Fig. 2 are 4-d running averages, to determine objectively the point at which Chl-*a* begins to decline. The running average will smooth over short-term, as well as day-night variability. I will use the running averages to define the point at which Chl-*a* begins to decline, and this will mark the critical depth. From the critical depth, the compensation irradiance can be calculated.

Surface irradiance (from the meteorological buoy; not shown) exhibits variability associated with changing weather, but remains more or less constant averaging  $30 \text{ mol photons m}^{-2} \text{ d}^{-1}$ . Attenuation coefficients for PAR ( $E_{\text{par}}$ ) for each depth range are calculated according to

$$k(z_2-z_1) = \ln(E_{\text{par}_2}/E_{\text{par}_1})/(z_2-z_1) \quad (2)$$

where  $k$  is calculated at each depth range between sensors (10-30, 30-50, and 50-110 m), and  $z_2$  and  $z_1$  refer to the depths of the respective sensors. Values of  $k$  for the three depth ranges (Fig. 3) increase beginning after day 142. (Suspect data from days 143 and 144 for 30 m have been excluded.)

### 3. Analysis

I now assume that the successive decreases in Chl-*a*, at shallower and shallower depths, are because the phytoplankton become progressively self-shaded, which eventually leads to their being at greater than the critical depth. Other losses are possible, such as zooplankton grazing, or sinking, however, these are difficult to reconcile with the data without changing known behaviors in the zooplankton or exceeding typical values for sinking. Furthermore, it is possible to reproduce the general changes in Chl-*a* shown in Fig. 2 (up until day 155 when water column changes occur) by employing a simple photosynthesis model for phytoplankton, an average irradiance for the top three sensors (approximating the mixing depth), and typical values for respiration [Geider, 1991]. The simplest explanation, therefore, is progressive self-shading of the phytoplankton, and consequent inhibition of growth.

Assuming that the phytoplankton in a stratified water column are at the critical depth when they begin to decline, I can calculate the compensation irradiance. The critical depth [Sverdrup, 1953] is defined as,

$$D_{\text{cr}} = E_0/(E_c \cdot k) (1 - \exp(-k \cdot D_{\text{cr}})), \quad (3)$$

where  $E_0$  is the incident irradiance,  $E_c$  is the compensation irradiance,  $k$  is the attenuation coefficient, and  $D_{\text{cr}}$  the critical depth. If the depth of mixing is less than the critical depth, the phytoplankton can increase. In the case of the data presented here (Fig. 2), the phytoplankton increase, but then decline successively at shallower depths. Equation (3) can be rearranged to

$$E_c = -E_0(-1 + \exp(-k \cdot D_{\text{cr}}))/(k \cdot D_{\text{cr}}). \quad (4)$$

I now assume that the  $D_{\text{cr}}$  can be assigned to the depths of the various sensors. And if that is the case,  $E_c$  can be computed for each of the various depths. The point at which the Chl-*a*

begins to decrease, then, corresponds to the critical depth, and the compensation irradiance can then be calculated. Since there is no PAR sensor at 90 m, I assume that the  $k$  from 50-110 m applies to the depth range 50-90 m, and from 90-110 m.  $E_c$  defined this way can be thought of as a single time point in the record. I have determined this point by differencing the data at each depth, and noting when the value crosses zero. For the 90 and 110 m sensors this occurs on or about day 144, and for 50 m, it occurs near day 148. In Table 1, I show these days, plus 1 day on either side to account for variability in the data.

If the analysis works perfectly, the compensation irradiance for each depth record of Chl-*a* should agree. The appropriate value for  $E_c$  is that which occurs when the chlorophyll begins to decline, as defined by the zero-crossings of the first-differences of the smoothed Chl-*a* record (Fig. 4). Accordingly,  $E_c$  is likely to be in the range of 0.06-0.3 mol photons  $m^{-2} d^{-1}$  (Table 1) although it is possible that the range could be extended to 0.02-0.4. Taking an average at each of the three depths gives a range 0.1-0.3 mol photons  $m^{-2} d^{-1}$ . As stated above, the 10 and 30 m sensors exhibited declines, but late enough that water column changes or other processes cannot be ruled out. Other processes at these times could include herbivory or sinking, or changes in population structure. There is a change in the current vectors around day 157 [Dickey *et al.*, 1994], which might signal a change in water mass, however, the current speeds tend toward zero, and thus advection of different water properties would not appear to be an explanation.

While the data do not indicate a single value for  $E_c$ , the relatively small range should still be a useful observation. The Sverdrup criterion has important assumptions, such as constant respiration as a function of depth, and photosynthesis directly proportional to irradiance. Given the restricted depth ranges, and applying the criterion to the lower parts of the euphotic zone provides some justification for these assumptions.

Siegel *et al.* [2002] calculate the  $E_c$  from an indication of bloom initiation in the North Atlantic from ocean color and an estimate of the mixed layer depth from climatology. Their value of 1.7 mol photons  $m^{-2} d^{-1}$  (for 60°N) is over five times the estimate here, however, their analysis averages over much longer time and space scales, where other loss factors would have to be included. Values for the compensation irradiance in laboratory populations are few and highly variable depending on species. Langdon [1987] suggests a range of 0.06-1.8 mol photons  $m^{-2} d^{-1}$ , with the high value for a large dinoflagellate, *Gonyaulax tamarensis*. Hobson and Guest [1983] and Falkowski and Owens [1978] report compensation irradiance values of 0.2-0.3 mol photons  $m^{-2} d^{-1}$  for *Skeletonema costatum*. The large range in  $E_c$  derives from differences in respiratory demands in different phytoplankton genera. Given the range in life modes among phytoplankton, variation in respiratory demand is not unexpected; it may help explain why species exist in different depth horizons in the ocean [Bidigare *et al.*, 1990], and does not necessarily affect the operational definition of the euphotic zone. Irradiance at the surface for these data varies from about 20-50 mol photons  $m^{-2} d^{-1}$ . If we consider these as representative of the average value for surface irradiance, then the values I calculate, ~0.1-0.3 mol photons  $m^{-2} d^{-1}$ , are about 1% of that, and support current definitions of the euphotic zone.

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**Figure 1.** Temperature records from the shallowest six MVMS' units. To see the temperature variations more clearly, the records are divided into two sections, days 135-150 (a) and days 150-161 (b) each having different ranges. Note the mixing event near day 137.

**Figure 2.** Chl-*a* (from in vivo fluorescence) at each of the mooring depths, 10 m, (dashed line) 30 m (solid line), 50 m (dotted line), 90 m (heavy dashed line), and 110 m (dot-dashed line). (The data from 150 and 250 m are omitted.). The heavy, smooth lines are running averages for the data used in the analysis.

**Figure 3.** The attenuation coefficient (*k*) for Epar, computed from Equation (2), for each depth range. Etot data from days 143 and 144 are suspect and were excluded from the calculations for *k*.

**Figure 4.** First differences calculated for the (smoothed) Chl-*a* data recorded at 50 m (dashed line), 90 m (solid line), and 110 m (dash-dot line). The vertical lines mark the times when the values cross the zero line. The data at 30 m (not shown) did not cross zero until late in the record, that is after other changes occurred in the water column. The zero-crossing at ~day 137 results from water column mixing leading to isothermal conditions (see Fig. 1a), and was not included in consideration of Ec.