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Resolving the ocean's euphotic zone

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ABSTRACT

Measurements of net primary production (P) combined with calculated estimates of phytoplankton respiration (R_p) and gross primary production (G) are used to determine the depth of the ocean's euphotic zone, the autotrophic productive layer. The base of the euphotic zone, the compensation depth (where $P=0$ and $G=R_p$), is found to be consistently deeper than the traditionally assumed '1% light depth'. It is found to occur, however, at a depth that encompasses the depth range of all, or nearly all, autotrophic biomass. The estimated compensation depth also occurs near the depth of 1% of surface blue light (490 nm), supporting the determination of the ocean's productive layer from satellite ocean color sensors.

1. Introduction

The ocean's euphotic zone is the depth range where daily gross primary production (G) exceeds daily autotrophic respiration (R_p) and thus net primary production (P) exceeds zero (e.g., Falkowski, 1994). The depth at which $P=0$, the compensation depth, defines the base of the euphotic zone. The compensation depth is traditionally applied to autotrophic production, however, a somewhat shallower community compensation depth can also be identified as the depth at which net community production is zero, would include losses from heterotrophic respiration, and depending on time scale, grazing and sinking losses (Regaudie-de-Gioux and Duarte, 2010). The euphotic zone has been traditionally assumed to be the depth to which 1% of surface photosynthetically active radiation (PAR; $\lambda=400$–700 nm) remains, and "defining the water mass below which no appreciable photosynthesis can occur" (Ryther, 1956). The problems with using a percentage light depth given a variable solar irradiance have been pointed out by Lorenzen (1976), and more recently by Banse (2004).

The presence of internal waves can potentially influence the depth of the euphotic zone (Lande and Yentsch, 1988; Holloway and Denman, 1989), and other physical processes can alter its definition. When the surface ocean mixes vertically, the euphotic zone might be better described in terms of a 'critical depth', i.e., that defined by Sverdrup (1953), as the depth at which the integrated values of daily G and R_p are equivalent. Sverdrup's (1953) analysis, however, applied to the spring bloom biomass increases in the North Atlantic, appropriately includes zooplankton grazing and sinking losses.

There are no direct measurements in natural populations of the extent of the euphotic zone using strictly biological criteria. The reason is that while measuring P is relatively straightforward, measuring G and R_p in natural populations of phytoplankton poses substantial challenges. Carbon-based radiotracer methods have not discriminated between photosynthetic assimilation and respiratory loss. Oxygen- or CO_2-based methods cannot distinguish heterotrophic (bacterial, protistan) respiration from that of phytoplankton, and are in any case, sensitivity-limited in most of the open ocean. Nevertheless, oxygen-based methods have been used to directly estimate the community compensation depth (Regaudie-de-Gioux and Duarte, 2010). Najjar and Keeling (1997) and Siegel et al. (2002) report indirect estimates of this parameter.

Here we use a published method (Marra and Barber, 2004, hereafter MB04), using ^{14}C as a tracer, for estimating phytoplankton respiration and production at a daily time scale (see also Williams and Lefevre, 2008). From measurements of P, G, and R_p,

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we estimate directly the compensation depth for autotrophs, and define this as the euphotic zone. The experimental data come from an oceanographic voyage aboard the *RV Cape Hatteras* in summer of 2008, part of the Optical and Nutrient Dependence of Quantum Efficiency (ON DEQUE) program.

We point out the limitations of our analysis at the outset. The number of estimates is limited, however, the stations sampled cover a geographic range of oceanic conditions. Our data apply to stable, density-stratified water columns during summer where vertical excursions of phytoplankton are minimal. Also, we are unable to do a rigorous error analysis, given the range of instruments, analyses, and methods used to derive our estimates of the compensation depth. The relationships are approximate, but useful, and an improvement upon the '1% light depth' criterion. Our purpose is to present a promising approach to resolve the depth of the ocean's euphotic zone.

2. Methods

2.1. Sampling

Water samples were collected during CTD/Rosette casts, before sunrise each sampling day. Six or seven sampling depths were chosen from the near surface to below the fluorescence maximum. The bottles on the rosette had silicone internal closures. The CTD/Rosette, part of the operational capabilities of the *RV Cape Hatteras*, also included a fluorometer for observing *in vivo* chlorophyll-a fluorescence. Profile data were binned at 1-m intervals. *In vivo* fluorescence was also calibrated at sea to the concentration of chlorophyll-a, analyzed from extracts of water samples using standard methods.

2.2. Dilution experiments

Near-surface water (5–10 m) was gravity-filtered through a Millipore HA filter (effective pore size=0.45 μm), placed beneath a glass–fiber pre-filter. The filtered seawater was added to sterile, 270 ml tissue culture flasks. Six flasks were filled completely, and six others up to 203 ml. An additional six flasks were kept empty, and three other flasks were filled with filtered seawater. Raw seawater from the same depth was then added to the partially filled and empty flasks, resulting in six flasks each with 100% filtered seawater, 25% raw seawater, and 100% raw seawater. Each sample was inoculated with (nominally) 10 μC ^{14}C as $Na_2{}^{14}CO_3$ dissolved in sterile carbonate solution. The uptake for the diluted samples was corrected for the uptake in filtered seawater. ^{14}C uptake in filtered seawater averaged 2% of that in the raw seawater, with a range of 0.8–5%. The filtration will not have removed viruses, however any effect is likely to be within the error of our measurements (Wilhelm and Suttle, 1999). The flasks were incubated on deck in an incubator screened to about 50% with neutral density screening to simulate near surface *in situ* irradiances, and plumbed with running seawater for temperature control. Three replicate samples from each treatment were removed at dusk (dawn–dusk) and assayed, and the remaining samples were removed after overnight incubation (24 h).

2.3. In situ productivity

The method followed closely the protocols designed for the Joint Global Ocean Flux Study (Barber et al., 2001), with dawn-to-dusk incubations at the sampled depths, followed by incubations of replicates overnight in a darkened, deck incubator. Thus, half of the replicates were assayed for C assimilation after dusk, and the other half before dawn the next day. Details of the ^{14}C assay can be obtained from Barber et al. (2001). In addition to a time-zero correction, we used a 'dark' uptake from the photosynthesis-irradiance experiment at the same station and depths, and extrapolating that short incubation value to the daytime and 24 h time periods. The samples were counted at sea on a scintillation spectrometer. Carbon assimilation values are reported as the mean of two replicates.

2.4. Daily surface irradiance

Above-surface PAR was measured with PUV-501 UV-PAR radiometer [Biospherical Instruments, Inc. (BSI), San Diego, CA] calibrated for use in air and mounted on the ship's equipment mast. Irradiance was measured at 1 s intervals and averages were logged at 1 min intervals to a computer using BSI software. All records from pre-dawn to post-dusk were integrated over time to calculate total daily PAR, $E_0(PAR)$ as mol quanta m^{-2} day^{-1}.

2.5. Subsurface irradiance

Submarine spectral irradiance, $E_d(\lambda)$ was measured using a 14-wavelength free-falling optical Profiler II (Satlantic Inc., Halifax, NS, Canada) equipped with two upward-directed OCR-500 cosine irradiance sensors with 7 channels each, for a total of 14 channels spanning the wavelengths 380–779 nm, each with 10 nm bandwidth. Triplicate casts were done near solar noon on each day off the ship's stern taking care to avoid ship shadow and reflection. Photosynthetically active radiation as downwelling irradiance, E_d(PAR), was calculated as the photon flux integrated between 400 and 700 nm. Measurement of irradiance immediately beneath the ocean surface, $E_d(\mathrm{PAR}, 0^-)$, was estimated by extrapolating E_d(PAR) from the upper several meters, where good data were available, upward to $Z=0$ m, by calculating the intercept of the least-squares curve fit of the exponential relationship between E_d(PAR) and depth (Kirk, 1994). The diffuse attenuation coefficient for PAR at depth Z, $K_d(\mathrm{PAR}, Z)$, was calculated at 1-m intervals,

$$K_d(\mathrm{PAR}, Z) = \ln(E_d(\mathrm{PAR}, 0^-)/E_d(\mathrm{PAR}, Z)). \quad (1)$$

We are aware that K_d based on PAR may not be depth independent (e.g., Lee, 2009). Inspection of profiles of ln(PAR) against depth in our data (not shown) reveals this relationship to be very close to linear (see Kirk, 1994, p. 136). A depth-dependent K_d would not affect our results, since K_d is used both for our estimates of the compensation depth and the 1% isolume. In any case, we argue below (see Section 4) that PAR is not the best optical index on which to base the depth of the euphotic zone. Thus, we adopt a depth-averaged K_d for each station. Except where noted, K_d will refer to K_d(PAR).

2.6. Calculations

Phytoplankton daily respiration (R_p) is calculated from the difference between the carbon assimilation after a dawn-to-dusk incubation (A_L) and carbon assimilation after 24 h ($A_{L\&D}$). Since we assume the same respiration day or night (see Section 3), we need to extrapolate the extra overnight dark loss ($A_L - A_{L\&D}$) to a whole day. MB04 used a factor of 2 to account for the equal day and night periods. Here, we use the proportion of the 24 h day that is in darkness. This factor f, accounts for seasonal and latitudinal differences in the dark fraction of each day, and is mathematically equivalent to the factor used in MB04. Thus,

$$R_p = (A_L - A_{L\&D})/f, \quad (2)$$