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Estimating the compensation irradiance in the ocean: The importance of accounting for non-photosynthetic uptake of inorganic carbon

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ABSTRACT

The compensation irradiance, the irradiance at which net photosynthesis is zero over a 24-h period, was estimated at station ALOHA (22°45′N, 158°W) from analysis of ^{14}C uptake rates measured from 8 January 1989 to 13 June 1990 at depths ranging from 5 to 175 m. The estimates were made on the basis of linear regressions of the difference between light bottle and dark bottle ^{14}C uptake in the light-limited region of the euphotic zone and determination of the depth at which the difference between the uptake rates was zero. About half of the non-photosynthetic ^{14}C uptake at the compensation irradiance could be attributed to chemolithoautotrophy; the remainder was presumably due to anaplerotic processes. Deriving the compensation irradiance by extrapolating dawn-to-dawn light-bottle uptake above the compensation irradiance to zero resulted in underestimation of the compensation irradiance by a factor of 2. We estimated the compensation irradiance at station ALOHA to be 0.054 mol-photons m^{-2} d^{-1}, about 0.11% of surface 400–700 nm radiation and 1% of surface 475-nm (blue) light.

1. Introduction

In oceanography the compensation depth is defined as the depth in the water column at which net photosynthesis is zero over the course of one day (Falkowski and Raven, 2007). For many years it has been customary to assume that the compensation depth corresponds to the depth at which photosynthetically active radiation (400–700 nm light) is reduced to 1% of its value at the surface. However, as noted by Falkowski and Raven (2007), (p. 329), "The actual compensation depth is variable and certainly difficult to measure" (Banse, 2004; Falkowski and Owens, 1978; Platt et al., 1990; Ryther, 1954).

Since the development of the ^{14}C method to estimate photosynthetic rates in the ocean more than 60 years ago (Steemann Nielsen, 1951, 1952a, 1952b), measurements made by this method have provided much of the information on which the current understanding of photosynthetic rates in the ocean is based (Barber and Hilting, 2002). In addition, these measurements have been used to calibrate satellite-derived algorithms that are now being used to estimate marine primary production on a global scale (Behrenfeld et al., 2002). When measurements are made by the ^{14}C method, it is invariably the case that uptake of ^{14}C occurs in the absence of light, i.e., in bottles incubated in the dark. Uptake of inorganic ^{14}C in the dark clearly cannot represent the result of photosynthetic processes but instead may be attributed to anaplerotic carbon fixation and chemolithoautotrophy (Li, 1986). In the early years of the ^{14}C method the radioactivity assimilated in the organic matter in dark bottles was therefore subtracted from that in light bottles to correct for non-photosynthetic uptake of CO_2 (Steemann Nielsen, 1952b). The rationale for making this correction, however, has been questioned by several authors (Li, 1986; Morris et al., 1971). Li (1986), for example, has argued that much of the non-photosynthetic uptake of ^{14}C may be due to heterotrophic picoplankton and that the activities of heterotrophic picoplankton may be reduced in the light, the implication being that ^{14}C uptake in the dark would overestimate anaplerotic CO_2 uptake in the light. However, if the compensation point occurs where the irradiance is roughly 1% of the surface photosynthetically active radiation (PAR), it seems reasonable to postulate that non-photosynthetic uptake of ^{14}C is virtually the same in light and dark bottles at irradiances equal to or less than the compensation irradiance (I_C). In other words, it seems reasonable to assume that the reduction of the activities of heterotrophic picoplankton by light is a continuous function of irradiance, and in the limit of dim light becomes negligible. If this assumption is correct, then the compensation point occurs at the shallowest depth at which uptake of ^{14}C is the same in light and dark bottles incubated for

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one day (Letelier et al., 1996). Here we examine the implications of this assumption with the use of archived ^{14}C uptake data collected at the start of the Hawaii Ocean Time-series (HOT) program (Karl and Lukas, 1996) at station ALOHA (22°45′N, 158°W). Our hypothesis was that the failure to account for non-photosynthetic uptake of ^{14}C would lead to significant underestimation of the compensation irradiance.

2. Materials and methods

Water samples were collected on a total of 16 cruises from 8 January 1989 to 13 June 1990. The sampling and incubation protocols have previously been described by Karl et al. (1998). Briefly, water samples were collected using clean techniques (Fitzwater et al., 1982; Karl et al., 1996; Letelier et al., 1996) at sunrise, in most cases from a total of eight depths: 5, 25, 45, 75, 100, 125, 150, and 175 m. Prior to July 1989 simulated in situ incubations were carried out using an on-deck system that simulated both in situ photosynthetically active radiation (PAR) and temperature (Lohrenz et al., 1992). In situ incubations using a free-floating productivity array began in July 1989 (Karl et al., 1996; Letelier et al., 1996). Typically, three light and three dark 500-ml polycarbonate bottles were filled with seawater from each depth and spiked with ^{14}C-bicarbonate. The light bottles were incubated in situ for a total of 24 h. The dark bottle incubations were terminated after approximately 12 h. The specific activities of the dissolved inorganic carbon concentrations were determined from the total ^{14}C activity in 250-μl subsamples from the incubation bottles and measurements of dissolved inorganic carbon made by means of CO_2 coulometry (Winn et al., 1994). For the total activity measurements, β-phenylethylamine was used as an inorganic carbon trapping agent.

Following the incubations, subsamples of 100–500 ml were filtered onto 25-mm-diameter Whatman glass fiber GF/F filters. The filters were placed in liquid scintillation vials, 1 ml of 2 M HCl was added, and the vials were vented for 24 h to allow degassing of $^{14}CO_2$. An aliquot of 10 ml of Aquasol-II was added to each vial, and the vials were stored for approximately 30 days to allow for desorption of dissolved organic carbon from the filter matrix (Karl et al., 1998). The ^{14}C activities in the vials were measured on a Packard model 4640 liquid scintillation counter. The dark bottle uptake during 24 h was estimated by multiplying the uptake at the end of the dark incubation by 24 and dividing by the duration in hours (typically 12) of the dark bottle incubations.

We assumed that in the light-limited region of the euphotic zone (1) the photosynthetic rates were proportional to irradiance, and (2) the irradiance was linearly related to the logarithm of depth. To estimate the compensation depth on each cruise, we therefore plotted photosynthetic rates versus the logarithm of depth. We fitted a regression line to the linear portion of the data and estimated the compensation depth from the intercept of the regression line, i.e., the depth at which the photosynthetic rate estimated from the regression line equaled zero (Fig. 1). We estimated photosynthetic rates in two ways: (1) by subtracting the 24-h dark bottle uptake from the 24-h light bottle uptake, and (2) by ignoring the dark bottle uptake and basing the estimate entirely on the 24-h light bottle uptake.

Since the beginning of the Hawaii Ocean Time-series (HOT) program in 1988, measurements of surface PAR have been routinely made at 10-minute intervals on cruises with a LI-COR data logger (model LI-200 for the first 12 years and model LI-1000 since 2001) equipped with a Biospherical Instruments cosine collector. In

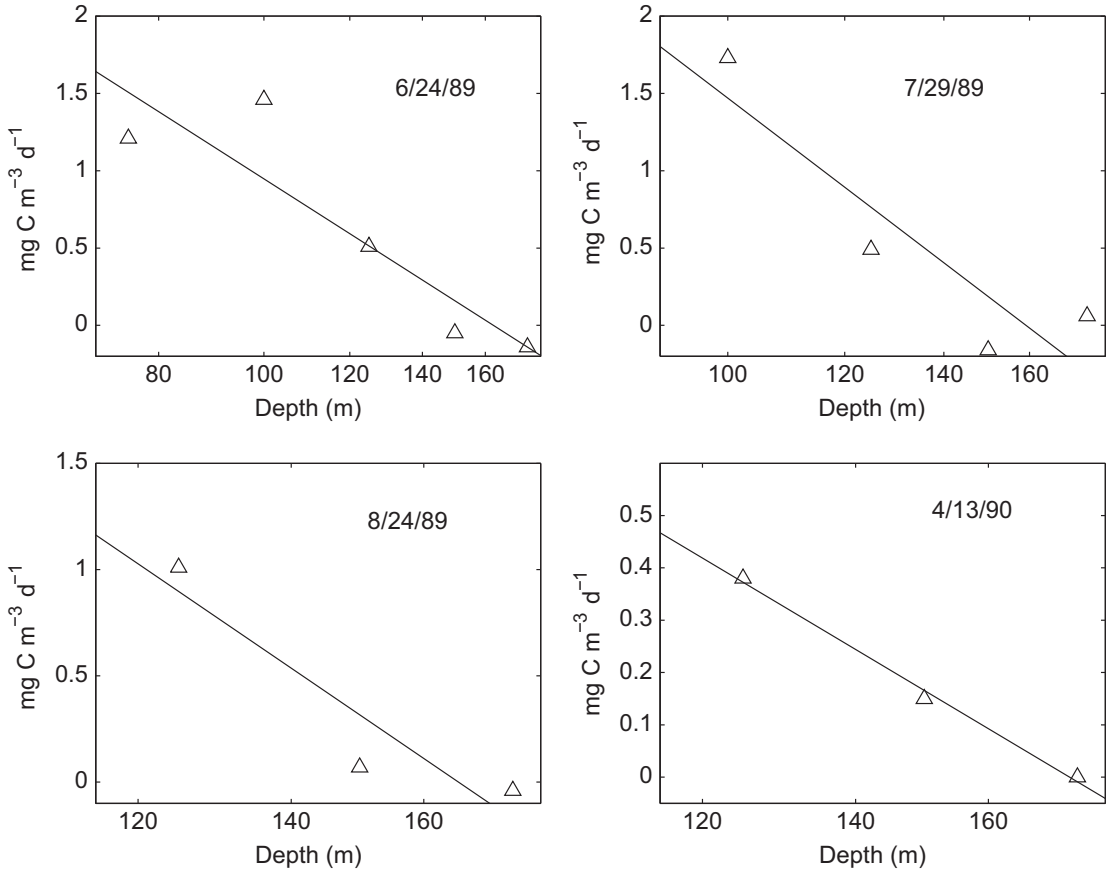

Fig. 1. Graphs of the difference between 24-h CO_2 uptake in light bottles minus dark bottles versus the logarithm of depth in the light-limited region of the euphotic zone on 4 of the 16 HOT cruises. The straight lines are model I least squares regressions fit to the data.