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Compensation irradiance for planktonic community metabolism in the ocean

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[1] The light compensation irradiance for planktonic metabolic balance, defined as the irradiance where gross planktonic primary production equals community respiration, is an important property describing ecosystem dynamics. Planktonic communities receiving irradiances above the compensation irradiance or compensation depth (i.e., the depth at which the compensation irradiance is received) are autotrophic and act as CO_2 sinks, whereas those at lower irradiances or located deeper in the water column act as CO_2 sources. However, this property is undefined for heterotrophic communities in which metabolic balance is not set by light availability. The compensation irradiance for planktonic metabolism in the ocean was quantified experimentally and calculated using data available in the literature to assess its variability and possible controls. Gross primary production by the oceanic planktonic communities examined here meet their respiratory requirements at irradiances of about 1.1 ± 0.4 mol quanta m^{-2} d^{-1} and tend to be autotrophic above a depth of 36 ± 9 m, on average. The depth of nitracline is closely correlated with the compensation depth for community metabolism across the studied areas, but the compensation depth tends to be located above the depth of the nitracline. This is expected from the facts that the underlying, net heterotrophic communities should act as sources of inorganic nutrients and that the nitracline cannot develop within the mixed layer where the compensation depth is often located. These results imply that the planktonic communities examined extending from 36 m depth, on average, to the bottom of the euphotic layer tend to be heterotrophic, acting as CO_2 and inorganic nutrient sources.

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1. Introduction

[2] The community metabolic balance, referring to the balance between the photosynthetic production of organic matter and its respiratory destruction, is a key trait of ecosystems affecting the carbon and nutrient budgets and the role of ecosystems on carbon sequestration and the CO_2 balance of the atmosphere [*Duarte and Agustí*, 1998]. Heterotrophic communities are those where primary production falls short of meeting the respiratory demands, and autotrophic communities are those where organic matter is produced in excess of respiratory demands, being available to be accumulated or exported from the ecosystem. Communities in productive aquatic ecosystems tend to be autotrophic, whereas those in unproductive aquatic ecosystems are often heterotrophic [*Duarte and Agustí*, 1998; *Duarte and Prairie*, 2005]. Hence, limitation of primary production by the supply of key resources, such as nutrients and irradiance, may drive aquatic ecosystems to net heterotrophy.

[3] Light limitation is arguably the factor most often conducive to heterotrophic community metabolism in the ocean [*Sverdrup*, 1953], responsible for the heterotrophic nature over most of the 95% of the ocean volume corresponding to the dark ocean. The euphotic layer of the ocean is defined as the layer receiving sufficient photosynthetically active radiation (PAR) for net photosynthesis to occur. It is conventionally defined as the layer receiving more than 1% of the PAR incident below the ocean surface [*Ryther*, 1956]. This conventional definition, however, may not necessarily refer to the irradiance required for the planktonic community to be autotrophic, as its definition only considers the respiration by the autotrophs, which typically comprise a modest fraction of the community respiration [*del Giorgio et al.*, 1997].

[4] The compensation irradiance for community metabolism (E_{com}, units mol quanta m^{-2} d^{-1}) is defined as the irradiance at which gross community primary production (GPP) balances respiratory carbon losses (R) for the entire community [*Gattuso et al.*, 2006]. The compensation irradiance is an important property for planktonic metabolism as it helps determine the depth below which planktonic

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metabolism becomes heterotrophic as well as the impact of changes in light penetration on the planktonic metabolic balance. *Sverdrup* [1953] defined this depth as the critical depth and derived equations to calculate this. However, Sverdrup's calculations assumed that the only loss of photosynthetic carbon in the community was through phytoplankton respiration [*Nelson and Smith*, 1991], which would grossly underestimate the irradiance necessary for photosynthesis to balance whole-community respiration. Hence, instead of using the equations developed by *Sverdrup* [1953], daily E_{com} is typically inferred from the relationship between daily net community production (NCP) at different depths and concurrent measurements of daily irradiance [*Gattuso et al.*, 2006].

[5] *Gacía et al.* [2005] experimentally determined the compensation irradiance for metabolic balance of a Philippine seagrass meadow to be close to 80% of the incident light. *Gattuso et al.* [2006] reviewed the compensation irradiance for metabolic balance of benthic communities (macroalgae, seagrass, and microphytobentos) to range between 0.24 and 4.4 mol quanta m^{-2} d^{-1}. To date, few estimates of the compensation irradiance for planktonic metabolism are available, and basic properties such as its regional variability and patterns of variation have not yet been established.

[6] The goal of this study is to quantify the compensation irradiance for planktonic metabolism in the ocean and assess its variability and possible controls. We do so by experimentally estimating E_{com} during three different cruises (subtropical Atlantic Ocean, eastern Arctic Ocean, and Southern Ocean) and searching the literature and databases for data on planktonic metabolism at various irradiances suitable to derive E_{com} estimates. We then combined the two data sets (experimental and reported) to derive estimates of E_{com} for different regions of the ocean and search for patterns in its distribution across the ocean.

2. Methods

[7] The experimental studies were conducted in the RODA II cruise in the subtropical Atlantic Ocean (−30°E to −15°E; 18°–28°N) in February 2007, in the ATOS-Arctic cruise in the eastern Arctic Ocean (−30°E to 12°E; 78°–81° N) in July 2007, and, finally, in the ATOS-Antarctic cruise in the Antarctic Ocean (−75°E to −51°E; −69°N to −61°N) in January–February 2009. For the first cruise, the compensation irradiance was determined at seven different stations. Seawater was sampled at 5 m depth and incubated at different irradiances, using neutral screen material, over 24 h in an on-deck incubator at in situ temperature, continuously flushed with surface seawater (5 m depth). For the second and third cruise, the compensation irradiance was determined at 8 and 15 different stations, respectively. Seawater was sampled at three different depths (surface layer, deep chlorophyll maximum depth, and an intermediate depth) and incubated as described above. NCP was measured at those different depths at each station. Seven replicates were used to determine the initial oxygen concentration, and seven replicated transparent Winkler bottles were incubated in the light. The bottles were suspended in seawater and incubated on the deck for 24 h at the in situ temperature at 5 m depth, under natural sunlight, with neutral density screening set as to mimic the incident irradiance at the sampled depths. During these two cruises, the thermocline was located deeper than the sampled depths, which showed a uniform temperature distribution, thereby avoiding temperature effects on metabolism rates during the incubation time. The use of neutral screens is expected to reproduce the total irradiance reaching at different sampled depths but cannot reproduce its spectral quality. For instance, the borosilicate glass material of the Winkler bottles excludes UVB irradiance, which may affect primary production in surface waters, and the light field would be progressively deprived at depth of the red and green fields [*Kirk*, 1994] relative to that in the incubation system. However, experimental evaluations of the action spectra of phytoplankton photosynthesis have shown that the differences in total photosynthetic rates associated with differences in the spectral composition of irradiance are generally modest [*Kirk*, 1994]. In addition to potential artifacts of bottle incubations on photosynthetic rates, community respiration may also be underestimated, as the larger components of the heterotrophic community is typically omitted from incubation bottles, although this generally involves a modest error [*Robinson and Williams*, 2005]. Whereas confinement-free techniques would potentially be free of these sources of error, the techniques available yield estimates for the mixed layer (triple O_2 isotope techniques or others [*Luz and Barkan*, 2000; *Grande et al.*, 1982; *Bender et al.*, 1987]), and are thus far unable to resolve the NCP at depth, required to estimate the compensation irradiance.

[8] NCP was measured by monitoring oxygen concentration changes in light bottle incubations [*Carpenter*, 1965; *Carritt and Carpenter*, 1966]. Oxygen concentrations were analyzed by high-precision Winkler titration using a potentiometric electrode and automated endpoint detection (DL28 titrator; Mettler Toledo). NCP was calculated from the changes in dissolved oxygen concentration after incubation of samples in the light.

[9] The light extinction coefficient was calculated, at each station sampled, from the vertical profile of irradiance derived by deploying a Satlantic OCP-100FF irradiance profiler, fitted with a PAR sensor, down to 100 m depth. The compensation irradiance was estimated as the irradiance at which NCP = 0, calculated from the relationship between NCP and PAR irradiance (Figure 1), derived by fitting the regression equation

$$\mathrm{NCP} = a + b\log(E), \tag{1}$$

where NCP is the net community production (mmol O_2 m^{-3} d^{-1}), E is the corresponding PAR irradiance (mol quanta m^{-2} d^{-1}), and a and b are the fitted intercept and slope, respectively. The compensation irradiance, E_{com} (mol quanta m^{-2} d^{-1}) was calculated by solving the equation for NCP = 0 (GPP = R) as

$$E_{com} = \exp^{\left(-\frac{a}{b}\right)}. \tag{2}$$

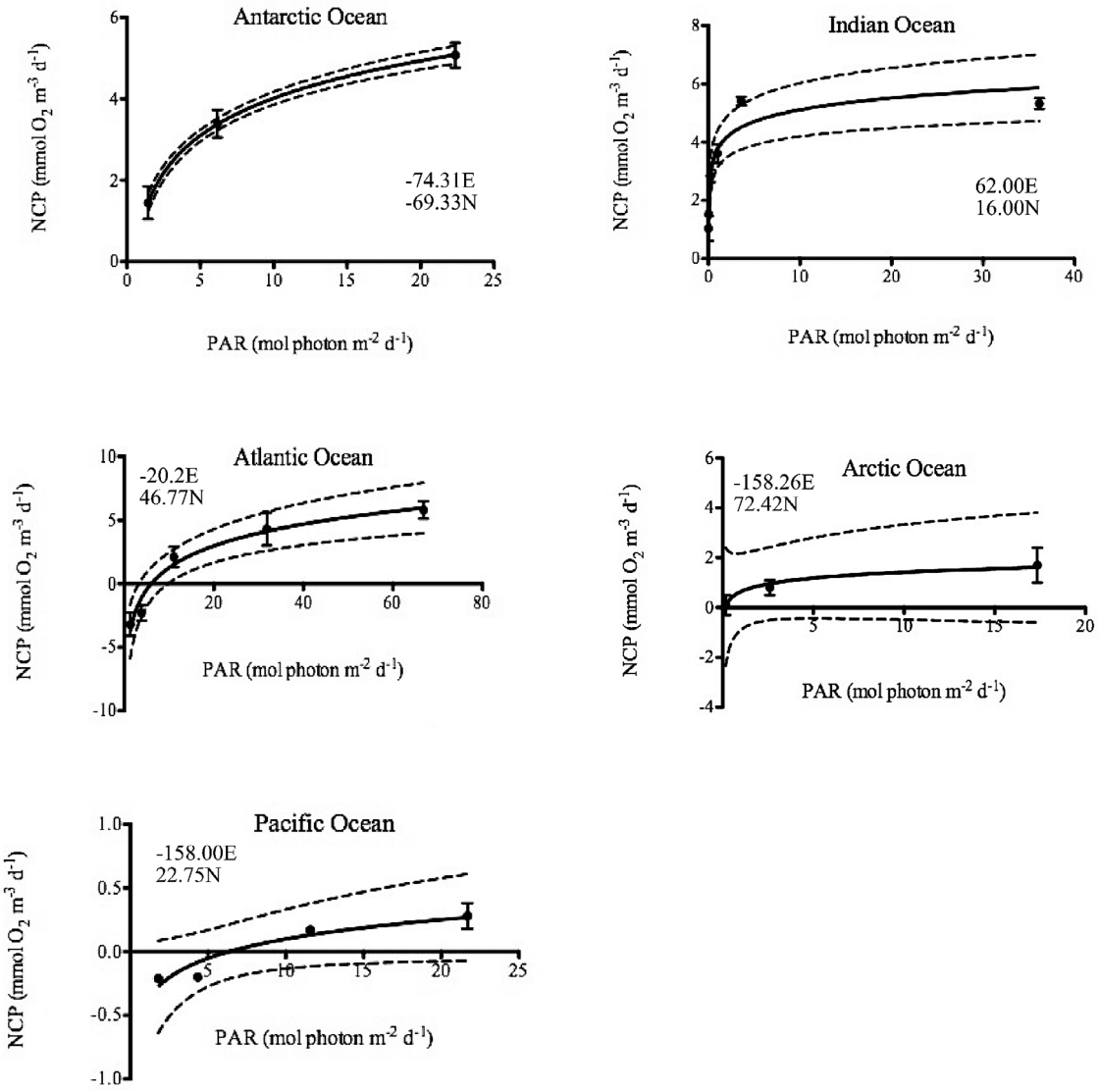

Figure 1. Examples of the exponential relationships between NCP (mmol O_2 m^{-3} d^{-1}) and in situ irradiance (mol PAR quanta m^{-2} d^{-1}) for stations in the Atlantic Ocean [*Kiddon et al.*, 1995], Pacific Ocean [*Williams et al.*, 2004], Indian Ocean [*Dickson et al.*, 2001], Arctic Ocean [*Cottrell et al.*, 2006], and Antarctic Ocean (this study) (Table 1). The compensation irradiance for metabolic balance (E_{com}) of the communities is determined as the intercept on the y axis (i.e., irradiance at NCP = 0) of the fitted regression line. Error bars show the SE of the mean NCP values, and the dashed lines show the 95% confidence intervals for the fitted regression line.

The compensation depth (Z_{com}) for metabolic balance can be estimated from E_{com} and the light extinction coefficient, k, using the following equation [*Sverdrup*, 1953]:

$$E_{com} = E_0 \times \exp^{(-k_{PAR} \times Z_{com})}, \quad (3)$$

$$Z_{com} = \frac{\ln\left(\frac{E_{com}}{E_0}\right)}{-k_{PAR}},$$

where E_0 is the surface PAR irradiance (mol quanta m^{-2} d^{-1}), k_{PAR} is the extinction coefficient for the downwelling PAR (m^{-1}), and Z_{com} is the compensation depth for metabolic balance (m).

[10] The compensation irradiance is undefined for heterotrophic communities, where the net community metabolism remains negative even at the highest incident irradiance, as there is no irradiance at which NCP equals 0. Hence, estimates of the compensation irradiance and depth for community metabolism can only be derived for stations supporting autotrophic communities within the euphotic layer.

[11] In addition to the estimates of the compensation irradiance and depth for community metabolism derived

here, we searched the published literature and public data sources for data allowing calculation of additional estimates. The majority of the reports used the same method to derive net community metabolism as used here, but most failed to report the light extinction coefficient, precluding calculation of the compensation depth. Only five different published reports [*Kiddon et al.*, 1995; *Bender et al.*, 1999; *Dickson et al.*, 2001; *Williams et al.*, 2004; *Cottrell et al.*, 2006] (Table 1) provided sufficient data to derive the compensation irradiance for planktonic community metabolism.

[12] The error involved in calculations of individual estimates of the compensation irradiance was estimated using bootstrapping techniques to propagate the error across the various components of the estimates, namely, the error about the irradiance just below the surface and the error about the light extinction coefficient yielding the error in the irradiance at depth, and the error about individual net community production estimates and the error in fitting the regression equation. Values for each of these components were derived by sampling random values from normal distributions with the observed mean and standard deviation for each component and an E_{com} estimate derived by fitting regression analysis as described above. This procedure was derived multiple times to retrieve a frequency distribution for E_{com} estimates. We could only complete this exercise for our own data, for which we had all necessary components. This exercise was conducted for all stations for which sufficient information was provided (24 of 61 stations). The mean E_{com} value, and its error standard for data of which this exercise was done, was 0.77 ± 0.07 mol quanta m^{-2} d^{-1}, which provides an indication of the magnitude of the uncertainty associated with individual E_{com} estimates. To evaluate the accuracy of the estimate, the mean deviation of the E_{com} was calculated. The mean absolute deviation between the bootstrapped average E_{com} and the experimental one was 0.183 mol quanta m^{-2} d^{-1}. No significant difference was observed between the bootstrapped and the experimental average E_{com}, indicating that the experimental values were unbiased (Wilcoxon test, $p > 0.05$).

[13] The upper depth of the nitracline was determined from vertical profiles of nitrate concentration at the stations, when available, as the mean depth where nitrate concentration start to present a sharp gradient (Table 1). The uncertainty about the nitracline depth depends on the vertical resolution of the profiles and was represented as half the vertical distance, in meters, between the two shallower depths within which nitrate concentrations first increased sharply. The mixed layer depth was determined using the criteria proposed by *de Boyer Montégut et al.* [2004] for the global ocean of *Kara et al.* [2000],

$$\Delta T = 0.5^{\circ}\mathrm{C} \text{ and } \Delta\rho_0 = \rho_0(T + \Delta T, S) - \rho_0(T, S), \quad \text{with } \Delta T = 0.8^{\circ}\mathrm{C}, \tag{4}$$

where T is the temperature, ρ_0 is the potential density, S is the salinity, and ΔT and $\Delta\rho_0$ are the variation of temperature and potential density relative to the surface at a reference depth (Z_{ref}; here 10 m).

[14] All of the estimates derived from our own studies and RODA II, ATOS-Arctic, and ATOS-Antarctic cruises. Samples for nutrient (nitrate + nitrite, silicate, and phosphate) analyses were collected at each depth and kept frozen until analyzed in a Bran Luebe AA3 autoanalyzer using standard methods [*Hansen and Koroleff*, 1999].

3. Results

[15] The data set compiled (Table 1 and Figure 2) included our own experimental assessment and the literature reports for different areas of the ocean. The compensation irradiance of the pelagic planktonic communities examined here averaged 1.1 ± 0.4 mol quanta m^{-2} d^{-1} and ranged fourfold from 0 (1–3.3 mol quanta m^{-2} d^{-1}). E_{com} was lower in the communities examined in the Antarctic Ocean than that in communities studied elsewhere, significantly different from E_{com} from the Atlantic, Pacific, and Antarctic Oceans (t test, $p < 0.05$); and the highest E_{com} was observed in the Pacific Ocean, significantly different from E_{com} from the Indian and Antarctic Oceans (t test, $p < 0.05$) (Table 1). There was no significant relationship between E_{com} and the rates of respiration ($p > 0.05$), but there was a significant negative ($p < 0.05$) correlation between E_{com} and NCP and GPP (Figure 3), indicating that productive planktonic communities tend to have lower E_{com} than unproductive ones. No significant relationship was observed between E_{com} and chlorophyll *a* or nutrient concentration for the cruises where we determined E_{com} experimentally, where data on chlorophyll *a* and nutrient concentration were available.

[16] The compensation depth for pelagic metabolism (Z_{com}, meters) averaged 36 ± 9 m and ranged from 21 to 95 m for the communities investigated, with the deeper and shallower Z_{com} observed in the Pacific Ocean and the Arctic Ocean, respectively. A strong correlation was observed, as expected, between the compensation depth (Z_{com}) and the extinction coefficient (Figure 4). The nitracline depth was closely correlated ($r^2 = 0.47$, $p < 0.05$) with Z_{com} for the stations where Z_{com} has been resolved. However, Z_{com} tended to be shallower than the nitracline depth (Wilcoxon signed, paired test, $p < 0.05$) (Figure 5).

4. Discussion

[17] The values provided here provide, however, useful indications of the compensation irradiance for plankton communities, which help assess irradiance-derived constraints to net community production in oceanic plankton communities. The results observed here of compensation irradiance and depth of the planktonic communities are derived from a limited set of communities, which provide an insufficient basis to represent the global ocean or any one of its basins (Figure 2). Indeed, the communities examined here do not represent a random sample of the global ocean or any of its basins, so that direct extrapolation of the results derived here to other areas involves uncertainties.

[18] The results presented here demonstrate that net autotrophic planktonic communities in the studied oceanic regions meet their respiratory requirements at irradiances at about 1.1 ± 0.4 mol quanta m^{-2} d^{-1} and tend to be auto-

Table 1. Average (±SE) of Sampling Stations for Oceanic Planktonic Communities Examined Experimentally (This Study) and Calculated From Data Reported in Published Reports Derived From Different Regions of the Ocean[a]

Location	References	Studied Location	Number of Stations	E_{com}[b] (mol quanta m^{-2} d^{-1})	% I_0	Z_{com} (m)	E_0 (mol quanta m^{-2} d^{-1})	k_{PAR} (m^{-1})	Chl a (mg m^{-2})	Z_{nit} (m)	ΔNO^{3-} (mmol m^{-4})	Z_{MLD} (m)
Atlantic Ocean	*Kiddon et al.* [1995]	Northeastern Atlantic	10	1.8 ± 0.2	3%	36 ± 2	60.2 ± 8.0	0.10 ± 0.01	33.2 ± 2.2 (23.6 − 42.3)	n.d.[c]	n.d.	n.d.
	This study (cruise 1)[d]	North subtropical Atlantic	2	1.2 ± 0.3	2%	32[e]	94.4[e]	0.12[e]	32.5 ± 4.3 (11.7 − 44.2)	110 ± 19	0.06 ± 0.03	115 ± 11
Mean				1.5 ± 0.2	3%	36 ± 9	66.4 ± 8.0	0.10 ± 0.01	32.9 ± 2.1	110 ± 19	0.06 ± 0.03	115 ± 11
Pacific Ocean	*Bender et al.* [1999]	Equatorial Pacific	1	0.1 e	0.2%	95[e]	28.9[e]	0.06[e]	n.d.	n.d.	n.d.	n.d.
	Williams et al. [2004]	North subtropical Pacific	3	3.3 ± 1.1 (71m − 77m)	4%	85 ± 10	88.7 ± 0.7	0.04 ± 0.01	n.d.	n.d.	n.d.	n.d.
	Duarte et al. (unpublished)	Southeastern Pacific	2	0.8e	3%	27[e]	33.4[e]	0.13[e]	18.7[e]	n.d.	n.d.	n.d.
Mean				1.9 ± 0.9	3%	67 ± 15	60.3 ± 14.6	0.08 ± 0.02	n.d.	n.d.	n.d.	n.d.
Indian Ocean	*Dickson et al.* [2001]	Arabian Sea	11	0.4 ± 0.2 (23 m − 35 m)	3%	29 ± 3	39.9 ± 2.2	0.31 ± 0.06	n.d.	n.d.	n.d.	n.d.
Arctic Ocean	*Cottrell et al.* [2006]	Western Arctic	4	1.0 ± 0.8	4%	37 ± 18	20.5 ± 4.2	0.56 ± 0.52	n.d.	n.d.	n.d.	n.d.
	This study (cruise 2)	Eastern Arctic	8	1.3 ± 0.4 (20 m − 24 m)	4%	22 ± 2	50.5 ± 16.9	0.19 ± 0.04	54.1 ± 9.8 (34.0 − 89.8)	38 ± 7	0.22 ± 0.04	16 ± 3
Mean				1.2 ± 0.4	4%	27 ± 6	40.5 ± 11.7	0.31 ± 0.16	54.1 ± 9.8	38 ± 7	0.22 ± 0.04	16 ± 3
Antarctic Ocean	This study (cruise 3)	Antarctic Peninsula	15	0.3 ± 0.1 (21 m − 22 m)	2%	21 ± 3	30.2 ± 5.9	0.30 ± 0.05	91.0 ± 47.3 (7.9 − 560.9)	24 ± 9	0.84 ± 0.58	27 ± 7
Overall means			56	1.1 ± 0.4	3%	36 ± 9	47.5 ± 7.6	0.22 ± 0.05	56.0 ± 16.5	66 ± 12	0.23 ± 0.08	61 ± 13

[a]Data show the compensation irradiance for metabolic balance (E_{com}) and its depth uncertainties (Min − Max), the corresponding percentage of incident irradiance for metabolic balance (% I_0), the compensation depth for metabolic balance (Z_{com}), the incident irradiance at the surface (E_0), the light extinction coefficient (k_{PAR}), the depth-integrated chlorophyll *a* concentration (Chl a) and its range (Min − Max), the upper depth of nitracline (Z_{nit}), the nitrate gradient within the upper layer of the nitracline, and the mixed layer depth (Z_{MLD}).

[b]The E_{com} means and their errors were calculated as the mean and SEs calculated from the series of individual E_{com} values derived or reported in each study cited.

[c]n.d., not determined.

[d]Cruise 1, RODA II cruise; cruise 2, ATOS-Arctic cruise; cruise 3, ATOS-Antarctic cruise.

[e]The number of data was insufficient to calculate the SE.

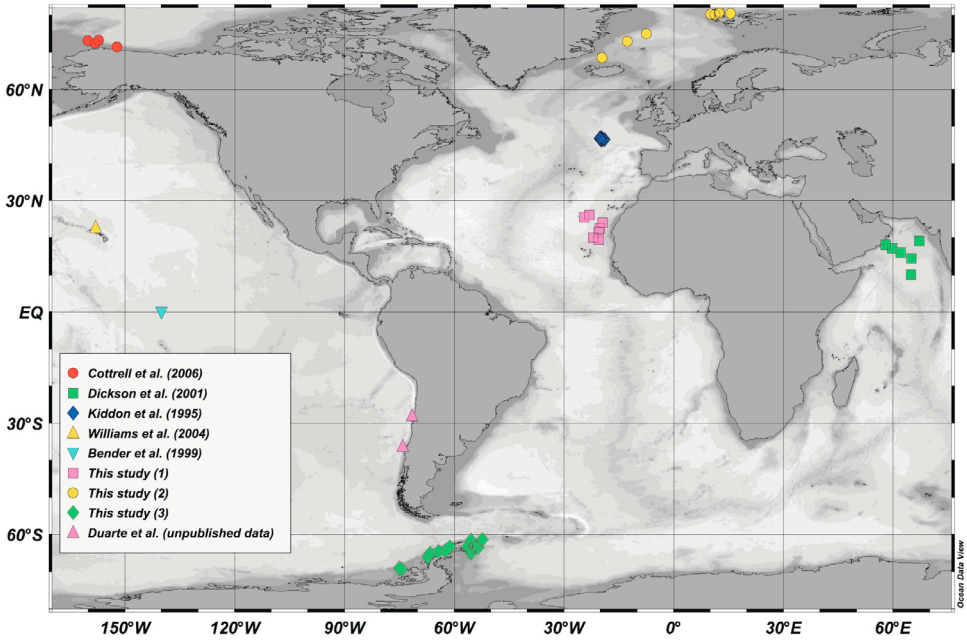

Figure 2. Geographic distribution of the stations included in the analysis of the compensation irradiance of plankton communities.

trophic above an average depth of 36 ± 9 m (Table 1). These properties varied by an order of magnitude across communities and twofold across communities studied in different ocean basins (Table 1). The communities studied in the Pacific Ocean had the highest compensation irradiance for metabolic balance, whereas the communities studied in the Arctic and Antarctic Oceans had, respectively, the lowest Z_{com} and E_{com}. The balance between photosynthesis and respiration for the planktonic communities studied in the Pacific Ocean seemed to occur deeper into the water column than that for the communities studied in polar oceans. Whereas our data set is too limited to be representative of ocean basins, these observations suggest that the light requirements for metabolic balance may vary with latitude. Indeed, the compensation irradiance for studied pelagic metabolism tends to be lower for strongly autotrophic communities (Figure 3), which shows that productive communities in this study are more tolerant to a light reduction in the water column. As the planktonic respiration rate increases relative to photosynthesis in oceanic communities, the compensation irradiance increases, and the depth for metabolic compensation of the communities approaches the surface. In heterotrophic communities, where respiration exceeds production, the compensation irradiance and the compensation depth for pelagic metabolism are undefined. These heterotrophic communities have been typically found in the most oligotrophic areas of the ocean [*Duarte and Agustí*, 1998; *Duarte and Prairie*, 2005], those with the highest light requirements for metabolic balance. The E_{com} values derived here (Table 1) are much higher than the values derived, on the basis of phytoplankton respiration losses alone [*Sverdrup*, 1953], of 0.25–0.5 mol quanta m^{-2} d^{-1} [*Sverdrup*, 1953; *Nelson and Smith*, 1991]. As a consequence, the compensation depths derived here are much shallower than the critical depth values Sverdrup calculated for other studies [*Sverdrup*, 1953; *Nelson and Smith*, 1991].

[19] As observed by *Sverdrup* [1953], a strong relationship was observed between the Z_{com} and k_{PAR} (Figure 4). This relationship could be used to predict Z_{com} from estimates of light extinction coefficient of PAR, available at the global level [e.g., *Morel and Maritorena*, 2001]) and approach possibly allowing inference of Z_{com} for ocean waters not included in our study. In addition, the E_{com} values derived here are independent of chlorophyll *a* concentration (r^2 = 0.08, p = 0.204), so that the mean value of E_{com} presented here (Table 1) can be used, together with the estimated light extinction coefficient for PAR to approximate Z_{com} for ocean waters not included in this analysis, before direct estimates become available.

[20] The estimates reported here are, to the best of our knowledge, the first estimates of the compensation irradiance and compensation depth of autotrophic planktonic phytoplankton communities reported to date. The compensation irradiance for planktonic photosynthesis has been experimentally determined for individual species [*Falkowski and Owens*, 1978; *Langdon*, 1987], or communities [*Sverdrup*, 1953; *Riley*, 1957; *Siegel et al.*, 2002; *Marra*, 2004; *Gattuso et al.*, 2006], with values ranging from 0.3 to 3.5 mol quanta m^{-2} d^{-1}. These values are within the same range as the compensation irradiance for metabolic balance of planktonic communities determined here, which range from 0.1 to 3.3 mol quanta m^{-2} d^{-1} in the open ocean (Tables 1 and 2). Similarly, the compensation irradiance for photosynthesis is used to determine the depth of the euphotic layer of the ocean, with a convention that this corresponds to the irradiance receiving about 1% of the incident irradiance at the surface [*Banse*, 2004]. The compensation irradiance for planktonic

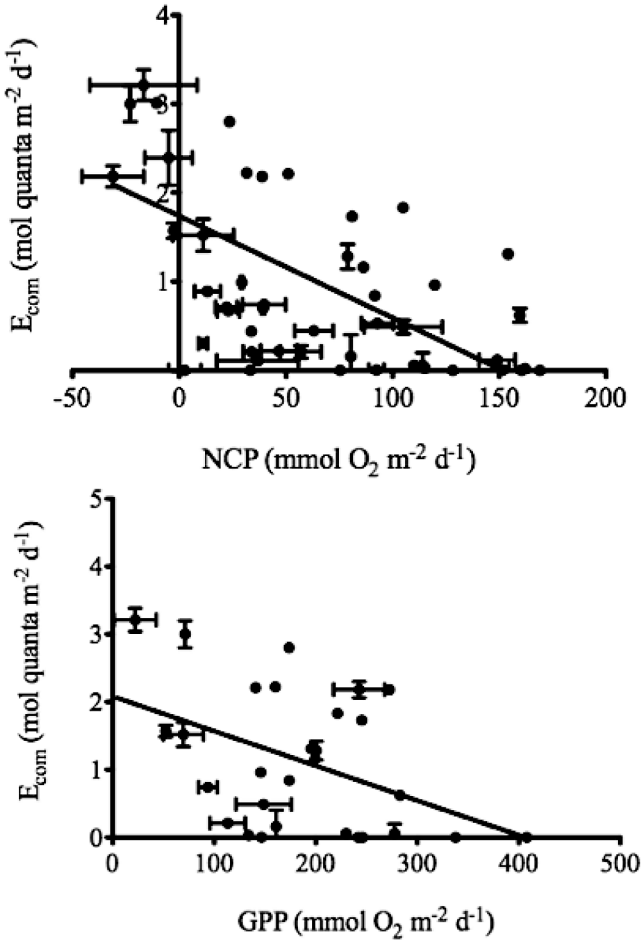

Figure 3. Relationship between the compensation irradiance for metabolic balance, E_{com} (mol quanta m^{-2} d^{-1}), and the integrated NCP (mmol O_2 m^{-2} d^{-1}) and GPP (mmol O_2 m^{-2} d^{-1}). The solid lines represent the model II regression equations: E_{com} = 1.74 (±0.20) − 0.01 (±0.002) NCP (r^2 = 0.32, $p < 0.0001$) and E_{com} = 2.08 (±0.38) − 0.01 (±0.002) GPP (r^2 = 0.21, p = 0.011), respectively. Bars show the SE for E_{com}, calculated by bootstrapping.

metabolic balance is slightly higher and corresponds, on average, to 3% of the incident irradiance (range of 0.2%–4%).

[21] The E_{com} determined here tends to be somewhat higher than that reported for microphytobenthos and comparable to that for macroalgal beds (Table 2). Hence, the metabolic balance of the planktonic communities studied is more sensitive to changes in irradiance or water transparency than that of microphytobenthic communities. Indeed, our results support the earlier suggestion that the high respiration rates of planktonic heterotrophs should lead to a higher E_{com} for the metabolic balance of pelagic communities compared to that of benthic communities [*Gattuso et al.*, 2006]. In addition, benthic primary production lives at fixed depths, offering better opportunities for photoadaptation than pelagic phytoplankton, which is mixing vertically in the water column.

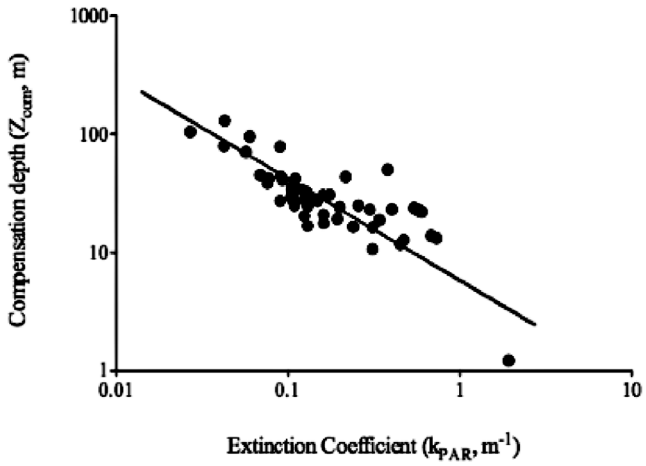

Figure 4. Relationship between the compensation depth (Z_{com}, m) and the extinction coefficient for PAR (k_{PAR}, m^{-1}). The solid line represents the model II regression: Log (Z_{com}) = 0.79 (±0.06) − 0.84 (±0.07) Log (k_{PAR}) (r^2 = 0.63, $p < 0.0001$).

[22] Whereas the compensation irradiance for photosynthesis is a key property for the dynamics of phytoplankton communities, the E_{com} for metabolic balance is a key property determining the role of planktonic communities in oceanic carbon budgets, biogeochemical cycles, and ecosystem dynamics. Communities receiving irradiances above the compensation irradiance or compensation depth are autotrophic and act as CO_2 sinks, whereas those at lower irradiances or located deeper in the water column act as CO_2 sources. Moreover, communities located above the com-

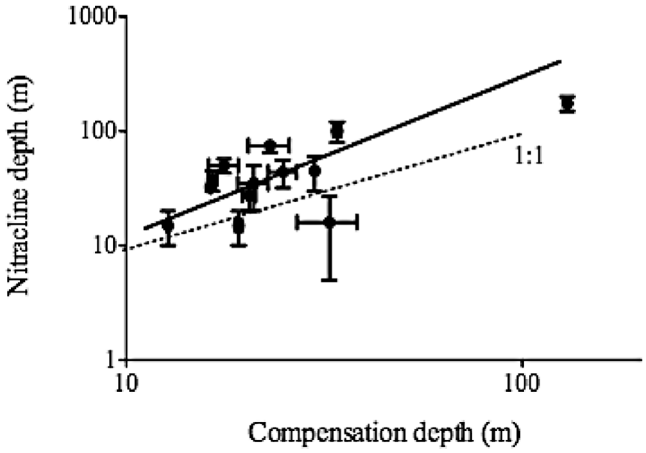

Figure 5. Relationship between the upper depth of the nitracline (m) and the compensation depth for net community metabolism (Z_{com}, m). The solid line represents the model II regression equation: Log (nitracline depth) = −0.18 (±0.40) + 1.27 (±0.28) Z_{com} (r^2 = 0.47, p = 0.0092). The dashed line represents the 1:1 line. The errors bars for the nitracline depth represent half the vertical distance, in meters, between the two depths within which nitrate concentrations increased sharply.

Table 2. Average Compensation Irradiance (E_{com}, mol quanta PAR m^{-2} d^{-1}) for the Metabolic Balance of Different Autotrophic Marine Communities

References	Community Type	E_{com} (mol quanta m^{-2} d^{-1})
This study	Oceanic plankton	1.1
Gattuso et al. [2006]	Microphytobenthos	0.2
	Macroalgal beds	1.6
	Seagrass beds	2.4
	Coral reefs	4.4

pensation depth for community metabolism act as sinks for inorganic nutrients, whereas those below act as sources for inorganic nutrients, as illustrated by the relationship between the depth of the upper nitracline and the compensation depth for community metabolism shown here. The observation that the compensation depth tends to be shallower than the nitracline depth is explained by the fact that the compensation depth is often encountered within the mixed layer, where a nitracline cannot develop. Hence, the nitracline depth is constrained by the mixed layer depth, but the compensation depth is not. Hence, the studied plankton communities become heterotrophic and act as nutrient sources toward the bottom of the mixed layer, but this can only be reflected in a nitracline below the mixed layer. The determination here that the studied pelagic oceanic communities tend to be autotrophic at depths above 36 m indicates that the studied communities extending from this depth to the bottom of the euphotic layer, roughly down to 100 m, tend to be heterotrophic, acting as CO_2 sources despite supporting measurable photosynthetic rates. The finding that the compensation irradiance for metabolic balance for the studied pelagic oceanic communities tend to be higher than that for microphytobenthos communities is indicative of the high rates of respiration in planktonic communities, associated with the high biomass [*Gasol et al.*, 1997] and metabolic activity [*del Giorgio and Duarte*, 2002] of the heterotrophic components of planktonic communities. As a result, autotrophic plankton communities tend to occupy a thin layer encompassing about 36 m of the studied ocean and yet affect, through their uptake of CO_2, the gaseous composition and climate of the planet.

[23] Increased ocean temperature is expected to have a greater impact in enhancing respiration rates than it does for photosynthetic rates [*López-Urrutia et al.*, 2006]. Accordingly, ocean warming should lead to an increase in the prevalence of heterotrophic plankton communities. Furthermore, increased inputs of organic carbon, from, for instance, enhanced deposition of dust and volatile organic carbon emitted to the atmosphere [*Dachs et al.*, 2005], would lead to even shallower layers of autotrophy in the ocean. Both these processes should weaken the capacity of plankton communities to regulate atmospheric CO_2 and therefore climate. Detecting such changes in the E_{com} and Z_{com} of plankton communities requires, however, extensive observational sets that are not yet available. The results presented here should prompt efforts to improve these estimates and assess the variability and controls of compensation irradiance for plankton metabolism in the ocean. While these data become available, the results and relationships presented here may help address this important property of the functioning of plankton communities in ocean ecosystem models.

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