Limnol. Oceanogr., 50(1), 2005, 299–310
© 2005, by the American Society of Limnology and Oceanography, Inc.

Phytoplankton growth rates in the Atlantic subtropical gyres

Emilio Marañón[1]
Departamento de Ecología y Biología Animal, Universidad de Vigo, 36200 Vigo, Spain

Abstract

Reported estimates of phytoplankton growth rate (μ) in the subtropical gyres range widely from 0.1–0.2 to 1–2 d^{-1}. Dividing chlorophyll *a* (Chl *a*)–normalized photosynthesis (P^B) by the phytoplankton carbon (C) to Chl *a* ratio (C : Chl *a*) yields an estimate of phytoplankton μ. To reduce the current uncertainty regarding phytoplankton μ in the subtropical gyres, I have reviewed >230 determinations of Chl *a*–normalized photosynthesis (P^B) and >40 determinations of phytoplankton C : Chl *a* obtained in surface waters of the eastern North Atlantic Subtropical Gyre (NAST-E), the western NAST (NAST-W), and the South Atlantic Tropical Gyre (SATL). Means (95% confidence intervals) of μ were 0.26 (0.19–0.36), 0.51 (0.42–0.62), and 0.17 (0.13–0.22) d^{-1} at NAST-E, NAST-W, and SATL, respectively. These values are all significantly lower than the expected maximum μ for phytoplankton living in the warm, surface waters of the subtropical ocean. Thus, phytoplankton growth rates, and not only their biomass, seem to be nutrient-limited in the oligotrophic ocean. A low phytoplankton μ in the open ocean is consistent with our knowledge of the relationship between elemental composition of the cells and their physiological state and agrees with other ecological and biogeochemical observations in the subtropical gyres.

The oligotrophic subtropical gyres contribute significantly to global marine primary production and carbon (C) export from the euphotic zone (Longhurst et al. 1995; Emerson et al. 1997) and therefore play a role in regulating the exchange of CO_2 between the oceans and the atmosphere. Although our conceptual understanding of the functioning of the planktonic community in these regions has greatly advanced over the last decades, there is still considerable uncertainty regarding the quantification of the different biomass components and, more importantly, the fluxes of matter and energy through the microbial food web. In particular, the growth rate (μ) of phytoplankton must be known because this rate sets an upper limit to the heterotrophic biomass that can be sustained by a given amount of photoautotrophic biomass (Cho and Azam 1990). Depending on whether phytoplankton μ is closer to 0.1–0.2 d^{-1} or to 1–2 d^{-1}, totally different views are possible on the functioning of microbial communities and the variability of primary production in the oligotrophic ocean (e.g., Goldman et al. 1979; Marañón et al. 2000). Moreover, determining whether phytoplankton are growing at rates proximal to their theoretical maximum is critical to predict the responses of the planktonic ecosystem to potential changes in nutrient supply to the upper oligotrophic ocean. In his review of phytoplankton growth rates in the open ocean, Eppley (1980) concluded that at least an order of magnitude uncertainty existed in the rates of primary production in these regions. He ended by asking: ''Are specific rates of phytoplankton photosynthesis equivalent to 0.1–0.2 or to 1–2 doublings per day of phytoplankton carbon?'' (p. 240).

A brief review of the estimates of phytoplankton μ in surface waters of the oligotrophic gyres published during the last two decades suggests that no straight answer can be given to this question yet (Table 1). Reported rates range from average values of ~0.2–0.3 d^{-1} (Goericke and Welshmeyer 1998; Marañón et al. 2000) to average values near (Malone et al.1993; Quevedo and Anadón 2001) or well above 1 d^{-1} (Laws et al. 1987). Techniques used to obtain these estimates vary: ^{14}C-based primary production rates combined with phytoplankton C calculated from flow cytometry and microscopy cell counts, microzooplankton grazing experiments with the dilution method, and the labeling of chlorophyll *a* (Chl *a*) with ^{14}C, among others. However, there is no obvious association between each particular technique and the type of values obtained. Although this wide range of estimates reflects, at least partially, the intrinsic variability of phytoplankton dynamics in the central gyres (e.g., Karl 1999; Marañón et al. 2003), it should still be possible to obtain an indication of the average phytoplankton μ with a narrower confidence interval. This requires that a sufficiently high number of observations is available for large expanses of the oligotrophic ocean. However, determining phytoplankton growth rates in the sea is a difficult task, and most studies report on just a few measurements conducted at particular geographic areas, thus making generalizations difficult.

Phytoplankton μ can be estimated simply by dividing the rate of photosynthesis normalized to Chl *a* (P^B) by the carbon to Chl *a* ratio (C : Chl *a*) of phytoplankton (Eppley 1972; Cullen et al. 1992). In the Atlantic Ocean, P^B has been de-

[1] Corresponding author (em@uvigo.es).

Acknowledgments

I thank Luisa M. Lorenzo, Natalia González, and Emilio Fernández for providing access to their primary production data, as well as Mike Zubkov and Derek Harbour for supplying the data on phytoplankton biomass. Comments by Francisco G. Figueiras, Natalia González, and two anonymous reviewers greatly helped in improving an earlier version of the manuscript. Special thanks go to Bernardino G. Castro for his advice on the use of bootstrap statistical methods.

Most of the data used in this study were obtained within the framework of the Atlantic Meridional Transect (AMT) consortium, funded by the U.K. Natural Environment Research Council (grant NER/O/S/2001/00680). Some data were collected during the CANIGO project, funded by the European Union (contract MAS3CT960060). The Bermuda Biological Station for Research and the U.S. National Science Foundation are also acknowledged for provision of data from the Bermuda Atlantic Time-series (BATS) station. This is AMT contribution 96.

Table 1. Review of post-1980 estimates of phytoplankton growth rates (μ, d^{-1}) in surface waters of the subtropical gyres in the Pacific Ocean and the Atlantic Ocean. The mean and range of reported values are given.

Reference	Method	Region*	μ (d^{-1})
Laws et al. 1987	Pigment labeling with ^{14}C	NPTG	1.2(1.0–1.5)
Malone et al. 1993	^{14}C uptake and phytoplankton C	NAST-W	0.7(0.6–0.9)
Jones et a. 1996	Pigment labeling with ^{14}C	NPTG	0.7
Goericke and Welschmeyer 1998	Pigment labeling with ^{14}C	NAST-W	0.3(0.1–0.5)
Lessard and Murrell 1998	Dilution technique	NAST-E	0.3(0.1–0.7)
Stelfox-Widdicombe et al. 2000	Dilution technique	NAST-E	0.6(0.4–0.8)
Quevedo and Anadón 2001	Dilution technique	NAST-E	0.7(0.5–1.3)

* NPTG, North Pacific Tropical Gyre; NAST-E, eastern North Atlantic Subtropical Gyre; NAST-W, western North Atlantic Subtropical Gyre.

termined over very large spatial scales in different tropical and subtropical regions during the last decade (e.g., Hood 1995; Marañón and Holligan 1999; Lorenzo et al. 2004), which means that the existing dataset is representative of the vast areas of the central gyres. In addition, the Bermuda Atlantic Time-study Series (BATS) program has provided an excellent coverage of the seasonal variability of P^B in the northwestern Sargasso Sea since 1989 (Steinberg et al. 2001).

Several improvements also have taken place during the last years concerning both the in situ determination of C : Chl *a* (Buck et al. 1996; Goericke and Welschmeyer 1998; Veldhuis and Kraay 2004) and the understanding of the physiological basis for its variability (Geider et al. 1998; MacIntyre et al. 2002). Flow cytometry enables a more accurate determination of the abundance of the picophytoplankton, which are the dominant component of total photoautotrophic biomass in the oligotrophic open ocean (Campbell et al. 1994; Buck et al. 1996). The combination of flow cytometry and light microscopy has been used successfully in several surveys of the subtropical gyres, yielding consistent estimates of C : Chl *a* (Campbell et al. 1994; Buck et al. 1996; Marañón et al. 2000). The ^{14}C labeling of Chl *a*, another technique allowing the estimation of C : Chl *a* (Redalje and Laws 1981), has produced estimates of this variable that are comparable to those obtained with flow cytometry and microscopy (e.g., Goericke and Welschmeyer 1998). Mechanistic models of phytoplankton physiology, on the basis of knowledge of photoacclimation processes (Geider et al. 1998), have proven able to reproduce both the temporal (Lefèvre et al. 2003) and the latitudinal (Taylor et al. 1997) changes in C : Chl *a*. Finally, laboratory cultures of the dominant picophytoplankton species occurring in the central gyres, such as *Synechococcus* spp. and *Prochlorococcus* spp., can be used to test the accuracy of C : Chl *a* estimates obtained in situ (Moore et al. 1995; Liu et al. 1999, Bertilsson et al. 2003).

To estimate phytoplankton growth rates in the oligotrophic ocean, I present here a review of P^B and C : Chl *a* measurements collected in surface waters of three biogeographic provinces in the Atlantic Ocean: the eastern North Atlantic Subtropical Gyre (NAST-E), the western NAST (NAST-W), and the South Atlantic Tropical Gyre (SATL). I concentrate on surface (e.g., 0–20 m, where irradiance (E_z) is higher than 0.5 × incident irradiance (E_0) rather than water column values for a number of practical and conceptual reasons. More P^B and C : Chl *a* measurements are available for the surface than for any other depth. During simulated in situ ^{14}C experiments, in situ temperature is always correctly reproduced for the surface samples, because the incubator is easily refrigerated with water pumped from the surface. Cell photodamage as a result of exposure to bright light is less likely when manipulating samples collected from the surface. Using only surface values makes comparison between studies easier because it avoids the nonlinear effects of photoacclimation irradiance on C : Chl *a*. Finally, the highest values of phytoplankton μ are typically measured in the upper few meters (0–20 m; e.g., Laws et al. 1987; Jones et al. 1996; Goericke and Welschmeyer 1998). My goal here is to reduce the current uncertainty regarding phytoplankton μ in the oligotrophic ocean and to see whether the available measurements of P^B and C : Chl *a* can help answer Eppley's original question: Are phytoplankton growing at rates near 0.1–0.2 or 1–2 d^{-1}?

Methods

Approach—An estimate of μ (d^{-1}) attainable by a phytoplankton assemblage can be calculated as

$$\mu = P^B/\text{C : Chl } a, \tag{1}$$

where P^B is the photosynthesis rate per unit Chl *a* (mg C [mg Chl *a*]$^{-1}$ d^{-1}) and C : Chl *a* is the carbon to Chl *a* ratio (mg C [mg Chl *a*]$^{-1}$). In the equation above, I follow the recommendations of Kirchman (2002), who showed that the most appropriate approach to calculating microbial growth rates is simply dividing the production rate by the biomass. A variation of Eq. 1 is to use the light-saturated, chlorophyll-normalized photosynthesis rate (P^B_m, mg C [mg Chl *a*]$^{-1}$ h^{-1}) instead of P^B, thus obtaining an estimate of the maximum potential growth rate (μ_m) attainable by a phytoplankton assemblage:

$$\mu_m = D \times P^B_m/\text{C : Chl } a. \tag{2}$$

P^B_m is usually measured in short-term (1–2 h) experiments during which natural phytoplankton samples are incubated with ^{14}C under an irradiance gradient. P^B_m is the asymptote of the photosynthesis–irradiance (P-E) curve, whereas the initial slope of the curve (α) represents the light-limited photosynthetic efficiency. In Eq. 2, P^B_m is multiplied by the duration of the photoperiod (D) to convert hourly productivity rates into daily rates. The short duration of P-E experiments minimizes the effects of ^{14}C respiration, bottle confinement,

and trophic losses such as microzooplankton grazing, thus rendering estimates of C fixation that approach gross photosynthesis. In addition, P-E experiments are typically conducted at noon or near the central hours of the day and therefore give estimates of P^B_m that are close to its daily maximum (Behrenfeld et al. 1998). Equation 2 seems then appropriate to estimate the maximum potential growth rate of a phytoplankton assemblage and thus is likely to overestimate the realized, actual growth rates.

Note that common determinations of P^B or P^B_m do not include the production of dissolved organic carbon (DOC), which represents a substantial fraction of total primary production in oligotrophic environments and has profound implications for the microbial ecology and the biogeochemistry of the open ocean (Nagata 2000). However, insofar as DOC production does not contribute to an increase in algal biomass, it can be ignored for the purpose of determining the effective growth rate of phytoplankton. Other approaches used to determine phytoplankton μ in the ocean do not consider DOC production either, so the results presented here will be fully comparable with those reported in the literature.

Data collection—To estimate μ and μ_m, my approach was to collect recent (post-1990) published and unpublished data of P^B, P^B_m, and C : Chl *a* measured in surface waters (0–20 m) of three oligotrophic provinces in the Atlantic Ocean: NAST-E, NAST-W, and SATL. Measurements of surface P^B and P^B_m were based on ^{14}C uptake experiments described before (Marañón and Holligan 1999; Steinberg et al. 2001; Lorenzo et al. 2004). All P^B data were obtained from long (8–12 h) ^{14}C incubations that (1) started at dawn or early in the morning, (2) ended at dusk, and (3) were conducted under natural irradiance. Primary production experiments in the NAST-W province were conducted in situ (Steinberg et al. 2001), whereas those carried out in NAST-E and SATL were conducted on deck with a set of incubators that reproduced the irradiance and temperature conditions at the sampling depth (Marañón et al. 2003). It has been found previously that no significant differences exist between the production estimates obtained from in situ incubations and those obtained from on-deck incubations (Joint et al. 1993). P^B_m was always determined in P-E experiments that lasted for ~2 h, were conducted near midday, and were carried out inside linear, temperature-controlled incubators.

Most of the P^B and P^B_m data from NAST-E and SATL have been obtained within the framework of the U.K. Atlantic Meridional Transect and European Union Canary Islands-Azores-Gibraltar Observations (CANIGO) programs (e.g., Marañón and Holligan 1999; Marañón et al. 2000; Lorenzo et al. 2004), whereas P^B data from NAST-W are monthly measurements taken at the BATS station (NW Sargasso Sea) from 1990 to 2000. In total, 234 measurements of P^B and P^B_m were used. Two points are worth mentioning in relation to these productivity experiments with surface seawater. First, the risk of cell photodamage during sample manipulation was avoided because phytoplankton living in the upper 10–20 m of the subtropical gyres typically experience irradiances above 60–70% of E_0, and protecting the samples from direct sunlight is normal practice during the preparation of ^{14}C experiments. Second, contamination of the samples by toxic substances was unlikely because modern protocols of primary production include the use of acid-clean, nontoxic sampling and incubation bottles.

It is important to emphasize that P^B and P^B_m measurements in NAST-E and SATL were conducted at different times of the year (April–May and September–October) over large spatial scales, in most cases spanning several thousand miles. For its part, the BATS P^B data used here adequately reflect the seasonal variability of primary production in the western Sargasso Sea. It is therefore reasonable to assume that the present dataset of surface P^B and P^B_m is representative of the variability of phytoplankton photosynthesis in the subtropical waters of the Atlantic Ocean. As explained below, my approach to calculate μ (or μ_m) from data of P^B (or P^B_m) and C : Chl *a* requires the use of the original data points for each variable. Although individual P^B data from station ALOHA in the North Pacific subtropical gyre are abundant and easily accessible, I have been unable to obtain original C : Chl *a* data from that station. For this reason, estimates of phytoplankton μ in oligotrophic waters of the North Pacific subtropical gyre are not attempted here.

For C : Chl *a*, I used a total of 43 measurements obtained in surface waters of the NAST-E, SATL, and NAST-W provinces. In the case of NAST-E and SATL data, phytoplankton C was estimated from cell abundances determined with a combination of light microscopy, epifluorescence microscopy, and flow cytometry during cruises AMT-3 and AMT-4 (Zubkov et al. 1998; Marañón et al. 2000). Cell numbers and biovolume data were converted into phytoplankton C with conversion factors and cell volume–C relationships. The average size of *Prochlorococcus* spp. and *Synechococcus* spp. was estimated by size fractionation through 0.2-, 0.4-, 0.6-, 0.8-, and 1.0-μm pore-size Nuclepore filters, as explained in detail by Zubkov et al. (1998). Then, C biomass was calculated by applying a carbon density factor of 0.35 pg C μm^{-3} (Bjørnsen 1986). The average biovolume of the picoeukaryotes was measured with an image analysis system connected to an epifluorescence microscope. Picoeukaryote C biomass was calculated with the conversion factor 0.22 pg C μm^{-3} (Booth 1988). For nano- and microphytoplankton, estimates of cellular C content for each species were obtained by determining cell volumes according to Kovala and Larrance (1966) and applying the cell volume–C relationship of Eppley et al. (1970). C : Chl *a* was then calculated simply by dividing phytoplankton C by the Chl *a* concentration, which was measured fluorometrically.

In the case of NAST-W, I used the monthly C : Chl *a* data measured by Goericke and Welschmeyer (1998) during an annual cycle at the Ocean Flux program station, which lies 8 km north of the BATS station (Steinberg et al. 2001). Goericke and Welschmeyer (1998) estimated phytoplankton C with the Chl labeling method (Redalje and Laws 1981). In this method, a sample is incubated with ^{14}C and the incorporation of the isotope into both particulate organic carbon (POC) and Chl *a* is determined. Assuming balanced growth over the incubation period, the quotient between ^{14}C in POC and ^{14}C in Chl *a* at the end of the experiment is equal to the phytoplankton C : Chl *a*.

All measurements of C : Chl *a* used in this analysis were collected either in repeated monthly samplings at a particular

location during a full annual cycle (e.g., NAST-W data) or during surveys over large spatial scales conducted at different times of the year (NAST-E and SATL data). This means that the resulting C : Chl *a* dataset should be representative of the variability in cellular Chl *a* content of surface phytoplankton in the Atlantic subtropical gyres.

Although Chl *a* concentrations used to calculate C : Chl *a* was measured with a Turner fluorometer in NAST-E and SATL, in the case of the NAST-W province, it was measured by high-performance liquid chromatography (HPLC; Goericke and Welschmeyer 1998). It was then necessary to check whether the two types of measurements agreed, thus allowing the comparison of C : Chl *a* data from different provinces. For a large dataset from the BATS station for the period 1990–2001, I found a good agreement between Chl *a* concentration measured with the Turner fluorometer (Turner Chl) and Chl *a* concentration measured with HPLC (HPLC Chl), as indicated by the model II linear regression between the two variables: (Turner Chl) = 0.98 × (HPLC Chl) − 0.0013, $r^2 = 0.78$, $n = 1{,}786$).

Statistical analyses—Given that the distributions of P^B, P^B_m, and C : Chl *a* were all nonnormal, I used bootstrap methods (Manly 1997) to calculate the mean and its 95% confidence interval for each variable in each province. For each group of *n* measurements of a particular variable in a particular province, I used random resampling with replacement to obtain 2,000 bootstrap samples of size *n*. Then I calculated the mean of each bootstrap sample and constructed the frequency distribution of the 2,000 means. The mean of this bootstrap distribution is an estimator of the true mean of the population, whereas the 2.5 and 97.5 percentiles of the bootstrap distribution give the limits of the 95% confidence interval of the mean (Efron 1979). Two thousand randomizations proved sufficient to obtain smooth frequency histograms, and increasing the number of bootstrap samples to 3,000 did not affect the values of the obtained estimates.

To estimate the mean and 95% confidence interval of μ, 100 means were randomly selected from the bootstrap distributions of P^B and C : Chl *a* (each comprising 2,000 bootstrap means). By dividing 100 means of P^B by 100 means of C : Chl *a*, an empirical distribution of 10,000 μ values was obtained. The mean and the 2.5 and 97.5 percentiles of this distribution are estimates of the mean of μ and its 95% confidence interval. The same procedure was used for μ_m, but in this case, with the use of P^B_m instead of P^B.

I checked the validity of this approach to estimate the distribution of μ from the bootstrap distributions of independent measurements of P^B and C : Chl *a* by comparing its results with direct determinations of phytoplankton growth rate obtained from simultaneous measurements of P^B and C : Chl *a* on the same samples. To do this, I used a set of 12 measurements from the SATL province where it was possible to determine simultaneously both P^B and phytoplankton C : Chl *a* on the same samples. By dividing P^B by phytoplankton C : Chl *a* for each sample, a direct calculation was possible of phytoplankton growth rates in SATL. The mean and 95% confidence interval of this distribution of 12 direct measurements of μ was 0.33 (0.27–0.40) d^{-1}. In addition, I combined all 12 determinations of each variable into a pooled sample, which I then used to obtain bootstrap distributions of 2,000 means of P^B and C : Chl *a*, as explained above. Then from each bootstrap distribution I sampled randomly 100 means of P^B and 100 means of C : Chl *a*. By dividing 100 means of P^B by 100 means of C : Chl *a*, I obtained an empirical distribution of 10,000 μ values. The mean and the limits of the 95% confidence interval of this simulated distribution of μ was 0.32 (0.25–0.40), thus closely matching the values obtained when direct measurements of P^B and C : Chl *a* on the same samples were used.

Results and discussion

Variability of P^B *and* P^B_m—Chl *a*–normalized photosynthesis (P^B) at the surface varied widely between biogeographic provinces (Fig. 1A). Means (95% confidence intervals) of surface P^B were 38.4 (29.3–49.5), 75.0 (67.4–83.2), and 19.7 (15.3–24.6) mg C (mg Chl *a*)$^{-1}$ d^{-1} for NAST-E, NAST-W, and SATL provinces, respectively (Fig. 2A; Table 2). The differences in P^B between paired provinces were in all cases statistically significant (Mann–Whitney test, $p < 0.001$). These differences in productivity agree with our knowledge of the phytoplankton biomass, degree of thermal stratification, and relative nutrient input to the euphotic layer in each province.

NAST-W, as observed at the BATS site, is characterized by relatively strong winter mixing (see Steinberg et al. 2001) and the frequent occurrence of mesoscale eddies (Siegel et al. 1999), all of which lead to nutrient injections to the euphotic layer and an enhancement of primary production. Similar nutrient enrichments are not usually observed in NAST-E. SATL is the most oligotrophic province in the Atlantic Ocean (Longhurst et al. 1995), as a result of the strong, persistent thermal stratification and the extremely low rate of nutrient supply to the photic layer. Compared to NAST-E, SATL typically shows warmer surface temperature and a deeper nitracline, which explains its lower productivity (Marañón et al. 2003). The light-saturated rate of chlorophyll-normalized photosynthesis (P^B_m) was also higher at NAST-E than at SATL (Figs. 1B, 3). P^B_m took a value of 4.4 (3.3–5.6) mg C (mg Chl *a*)$^{-1}$ h^{-1} at NAST-E, compared with 3.4 (2.6–4.3) mg C (mg Chl *a*)$^{-1}$ h^{-1} at SATL. These differences, however, were not statistically significant (Mann–Whitney test, $p > 0.4$).

It is interesting to compare these P^B values with those measured in another well-studied oligotrophic province such as the North Pacific Tropical Gyre. The average P^B measured at the surface of station ALOHA during 1990–2003 was 90.2 ± 34.8 mg C (mg Chl *a*)$^{-1}$ d^{-1}. This value is slightly higher than that measured at NAST-W (75.0 mg C [mg Chl *a*]$^{-1}$ d^{-1}) but much higher than those measured at NAST-E and SATL (38.4 and 19.7 mg C [mg Chl *a*]$^{-1}$ d^{-1}, respectively). This comparison highlights that significant differences in productivity exist between different subtropical provinces of the open ocean, even if they all can be broadly regarded as oligotrophic.

Variability of C : Chl a—Phytoplankton C : Chl *a* at the surface showed little variability between provinces (Fig. 1C).

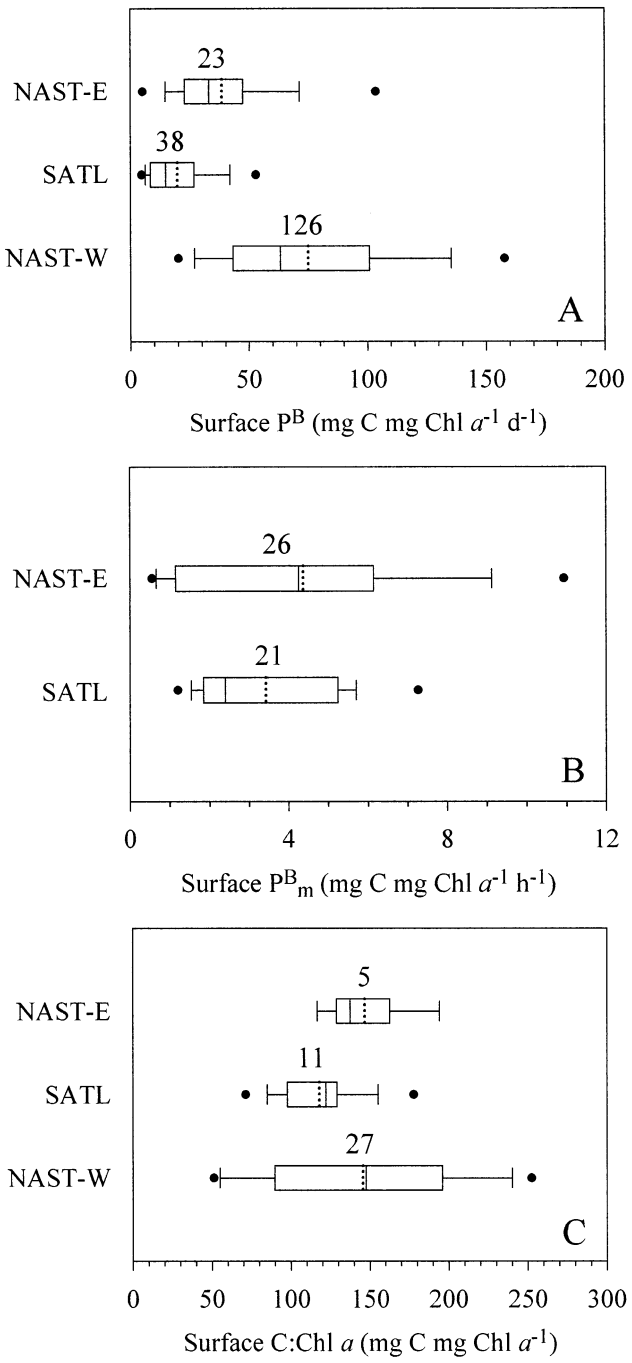

Fig. 1. Variability of (A) the photosynthesis to Chl *a* ratio, P^B; (B) the light-saturated, Chl *a*-specific rate of photosynthesis, P^B_m; and (C) the phytoplankton C : Chl *a* in surface waters of the eastern North Atlantic Subtropical Gyre (NAST-E), western NAST (NAST-W), and South Atlantic Tropical Gyre (SATL) biogeographic provinces. Circles indicate the 5th and 95th percentiles, bars indicate the 10th and 90th percentiles, boxes indicate the 25th and 75th percentiles, the central continuous line represents the median, and the central dashed line represents the mean. Numbers on top of the boxes indicate the total number of observations in each dataset. P^B_m data are not available for NAST-W.

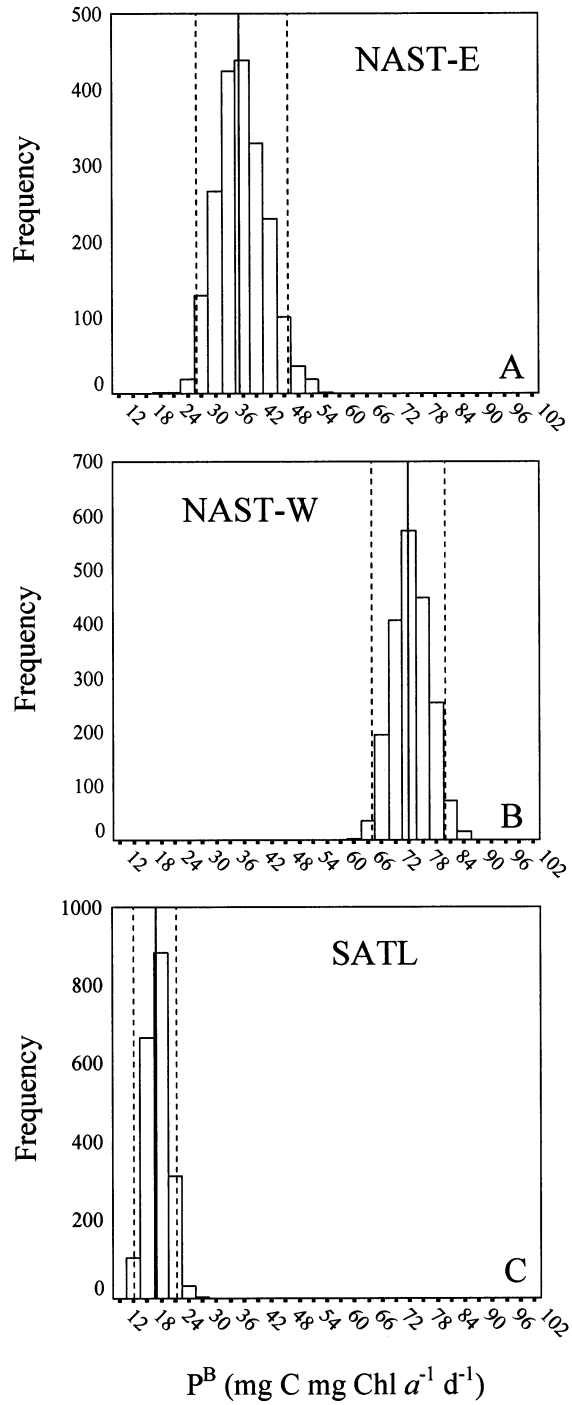

Fig. 2. Frequency distributions of 2,000 bootstrap means of P^B, as obtained from original measurements in surface waters of (A) NAST-E, (B) NAST-W, and (C) SATL biogeographic provinces. Vertical dashed lines indicate the limits of the 95% confidence intervals, and vertical continuous lines indicate the mean.

Means (95% confidence intervals) of surface C : Chl *a* were 147.0 (127.2–171.5), 145.9 (120.7–171.0), and 118.0 (102.9–134.2) mg C (mg Chl *a*)$^{-1}$ for NAST-E, NAST-W, and SATL provinces, respectively (Fig. 4; Table 2). No significant differences in C : Chl *a* existed between provinces (Kruskal–Wallis test, $p > 0.3$). These C : Chl *a* values agree

Table 2. Mean (95% confidence intervals) of the photosynthesis to Chl *a* ratio (P^B), the light-saturated, Chl *a*–specific photosynthesis (P^B_m), and the phytoplankton carbon to Chl *a* ratio (C : Chl *a*) measured in surface waters of the eastern North Atlantic Subtropical Gyre (NAST-E), the western NAST (NAST-W), and the South Atlantic Tropical Gyre (SATL) biogeographic provinces. Confidence intervals were computed by applying bootstrap methods to the original measurements. *n* indicates the number of observations in each original data set. See Methods for details on data sources and calculations.

	Biogeographic province		
	NAST-E	NAST-W	SATL
P^B (mg C [mg Chl *a*]$^{-1}$ d^{-1})	38.4(29.3–49.5) $n = 23$	75.0(67.4–83.2) $n = 126$	19.7(15.3–24.6) $n = 38$
P^B_m (mg C [mg Chl *a*]$^{-1}$ h^{-1})	4.4(3.3–5.6) $n = 26$	—	3.4(2.6–4.3) $n = 21$
C : Chl *a* (mg C [mg Chl *a*]$^{-1}$)	147.0(127.2–171.5) $n = 5$	145.9(120.7–171.0) $n = 27$	118.0(102.9–134.2) $n = 11$

well with previous estimates reported for surface, oligotrophic waters of the subtropical gyres in both the Atlantic and the Pacific Oceans (Table 3). It is remarkable that the variability between the different estimates shown on Table 3 is relatively small, particularly in view of the fact that different techniques and conversion factors were used on each study to estimate C : Chl *a*. The consistency of the C : Chl *a* values obtained in a wide range of studies suggests that the reported estimates are accurate.

High C : Chl *a* values were to be expected because it is well established from physiological studies that this ratio tends to increase under conditions of high irradiance and low nutrient concentration (Geider et al. 1998; MacIntyre et al. 2002). In tropical and subtropical regions of the open ocean, an inverse relationship exists between phytoplankton abundance and C : Chl *a* (Buck et al. 1996), illustrating the physiological response of decreasing relative Chl *a* content in the cells with increasing degree of oligotrophy. In addition, different models of phytoplankton physiology and water column dynamics predict C : Chl *a* values between 100 and 160 for the upper mixed layer of the open ocean at low latitudes (Taylor et al. 1997; Lefèvre et al. 2003). However, a more rigorous test of the validity of the C : Chl *a* values reported here comes from the comparison with C : Chl *a* measured in the laboratory, virtually without experimental error, on cultures of those species that dominate the photoautotrophic biomass in the oligotrophic ocean, namely *Prochlorococcus* spp. and *Synechococcus* spp. Several studies have shown that the contribution of these two cyanobacteria to total photoautotrophic biomass in the upper layer of the subtropical gyres is typically >50–60% (Buck et al. 1996; Marañón et al. 2000), reaching in some cases values >70–80% (Campbell et al. 1994; Veldhuis and Kraay 2004). If the C : Chl *a* determined in situ are accurate, they should coincide with the C : Chl *a* measured on *Prochlorococcus* and *Synechococcus* cultures, at least when growth conditions are similar to those typical of the upper oligotrophic ocean (e.g., high irradiance and low nutrient concentration). Unfortunately, a similar type of comparison is not possible for the eukaryotic pico- and nanophytoplankton living in the tropical ocean because their taxonomic composition at the species level is not well resolved yet (e.g., Veldhuis and Kraay 2004).

Several reports are available in the literature that can help constrain the variability in the C : Chl *a* of *Prochlorococcus* and *Synechococcus*. The Chl *a* cell content of *Prochlorococcus* experiencing high irradiances (e.g., >400 μmol quanta m^{-2} s^{-1}) is around 0.5 fg cell^{-1} (Moore et al. 1995; Claustre et al. 2002). Combining this figure with the C content typically measured in *Prochlorococcus* (40–80 fg C cell^{-1}, see Bertilsson et al. 2003 and references therein) gives a C : Chl *a* in the range of 80–160. For *Synechococcus*, Liu et al. (1999) have provided a comprehensive study on the physiological characteristics of continuous cultures growing under a range of nitrate supply rates. These authors found that cellular Chl *a* concentration varied between 1 and 2 fg cell^{-1}. Given that the C content of *Synechococcus* is frequently within the range of 200–300 fg C cell^{-1} (Kana and Glibert 1987; Bertilsson et al. 2003 and references therein), the resulting C : Chl *a* is then 100–300. Despite this considerable degree of variability, which reflects the physiological plasticity of the cells in response to variations in growth conditions, it seems clear that the C : Chl *a* tends to take relatively high values (i.e., >100) in these two species of cyanobacteria. Thus, the average C : Chl *a* in surface samples of the subtropical gyres, measured by many different workers and different experimental procedures, is also consistent with our knowledge of the physiology of the dominant photoautotrophs in these regions. This agreement, reinforced by the consistency between in situ observations and model predictions, supports the use of the C : Chl *a* to estimate the variability of phytoplankton growth rates in the subtropical gyres.

Phytoplankton growth rates—The distribution of the estimated phytoplankton μ in each biogeographic province reflected the differences in P^B that were described above (Fig. 5). Phytoplankton μ was 0.26 (0.19–0.36), 0.51 (0.42–0.62), and 0.17 (0.13–0.22) d^{-1} at NAST-E, NAST-W, and SATL, respectively (Table 4). These values are all smaller than the maximum theoretical growth rates (~1.5 d^{-1}) calculated by Eppley (1972) for unicellular algae growing at the warm temperatures (22–26°C) typical of surface waters in the subtropical gyres. It could be argued that the low growth rates estimated here are the result of the underestimation of C fixation in ^{14}C uptake experiments that involve relatively long (8–12 h) bottle incubations. If this were the case, we would have expected μ_m (on the basis of P^B_m measurements from 2-h incubations) to take much higher values than μ and

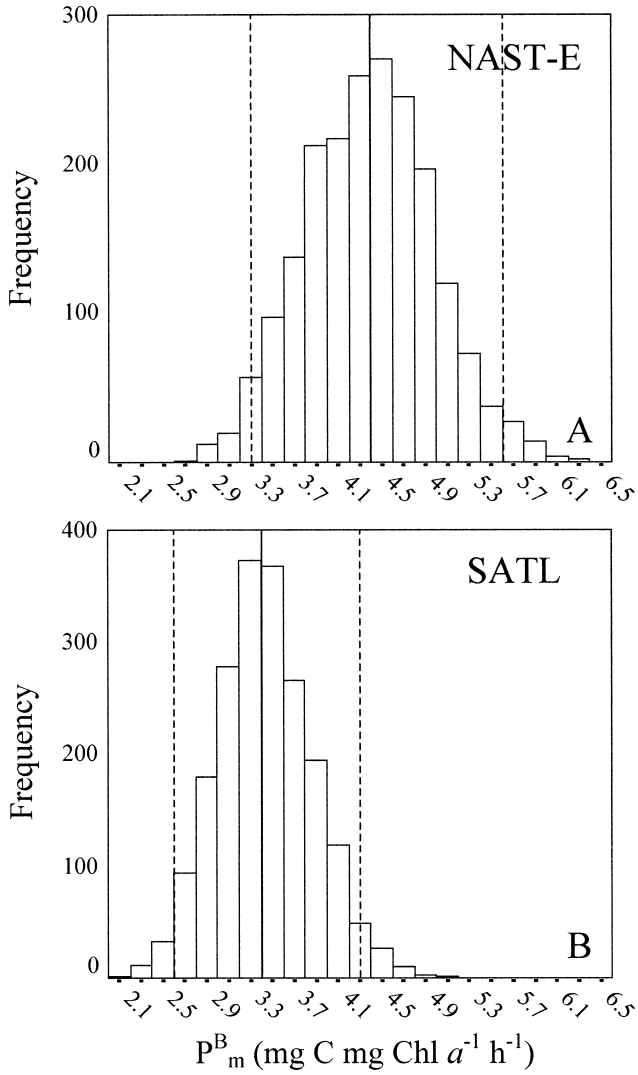

Fig. 3. Same as Fig. 2 but for P^B_m, as obtained from original measurements in surface waters of (A) NAST-E, and (B) SATL biogeographic provinces.

Table 4. Means (95% confidence intervals) for phytoplankton growth rate (μ) and maximum growth rate (μ_m) in surface waters of the eastern North Atlantic Subtropical Gyre (NAST-E), the western NAST (NAST-W), and the South Atlantic Tropical Gyre (SATL) biogeographic provinces. μ and μ_m were calculated as P^B/C : Chl *a* and $D \times P^B_m$/C : Chl *a*, respectively, where *D* is the duration of the photoperiod (h) and P^B is the photosynthesis to Chl *a* ratio. See Methods for further details on calculations.

	Biogeographic province		
	NAST-E	NAST-W	SATL
μ (d^{-1})	0.26(0.19–0.36)	0.51(0.42–0.62)	0.17(0.13–0.22)
μ_m (d^{-1})	0.35(0.24–0.47)	—	0.35(0.26–0.46)

approach the maximum theoretical growth rates. For the reasons explained before (*see Methods*), μ_m is an indicator of the maximum potential of a phytoplankton assemblage to increase its biomass and is likely to overestimate the actual growth rate. However, μ_m took values that, although somewhat higher than μ, were still low (range 0.2–0.5 d^{-1}; Fig. 6; Table 4) and well below maximum theoretical growth rates. The data presented here thus strongly suggest that not only the standing stocks of phytoplankton but their growth rates as well are limited in the surface layer of the subtropical gyres, most likely as a result of the low supply of nutrients. Similarly low estimates of phytoplankton μ have been reported before for the subtropical gyres (see Table 1). Unlike previous studies, though, the present analysis is based on numerous measurements that were obtained by different techniques over wide temporal and spatial scales. In addition, bootstrap techniques allowed to quantify the variability in μ, and the resulting confidence intervals were all relatively narrow. These facts make the present estimates of phytoplankton μ particularly robust and broadly representative of the Atlantic subtropical gyres.

Knowledge of C : Chl *a* alone already suggests that phytoplankton inhabiting the surface waters of the subtropical gyres must grow at rates well below 1 d^{-1}. With C : Chl *a* in the range of 120–150 mg C (mg Chl *a*)$^{-1}$, P^B and P^B_m would have to be >120–150 mg C (mg Chl *a*)$^{-1}$ d^{-1} and 10–12 mg C (mg Chl *a*)$^{-1}$ h^{-1}, respectively, for μ or μ_m to approach 1 d^{-1}. Such high assimilation numbers are rare in

Table 3. Review of measurements of phytoplankton carbon to chlorophyll *a* ratio (C : Chl *a*) in surface oligotrophic waters of the subtropical gyres in the Pacific Ocean and the Atlantic Ocean. The mean and, where available, the range of the reported values are given. *n* indicates the number of observations in each original data set.

Reference	Region*	C : Chl *a*	*n*
Furuya 1990	NPTG	108	10
Campbell et al. 1994	NAST-W	128	23
Caron et al. 1995	NAST-W	98(40–193)	10
Buck et al. 1996	NAST-E	180	12
Jones et al. 1996	NPTG	156	—
Goericke and Welschmeyer 1998	NAST-W	146(45–266)	27
Veldhuis and Kraay 2004	NAST-E, NATR	165(97–194)	5
This study	NAST-E	147(117–194)	5
This study	SATL	118(70–180)	11

* NATR, North Atlantic Tropical Gyre; NPTG, North Pacific Tropical Gyre; NAST-W, western North Atlantic Subtropical Gyre; NAST-E, eastern NAST; SATL, South Atlantic Tropical Gyre.

the subtropical gyres of the Atlantic Ocean. At the BATS station, surface P^B values >120 mg C (mg Chl a)$^{-1}$ d^{-1} were measured in <15% of the ~130 visits made during the period 1990–2000 (Fig. 1A). During two 13,000-km latitudinal transects in the Atlantic Ocean, in which 150 P-E experiments were conducted, Marañón and Holligan (1999) found $P^B_m > 10$ mg C (mg Chl a)$^{-1}$ h^{-1} only in temperate waters and in the upwelling region off Mauritania. Behrenfeld and Falkowski (1997) plotted >1,000 determinations of the maximum chlorophyll-specific C fixation rate (P^B_{opt}), which is an analogue of P^B_m, as a function of sea surface temperature. They found that, across a sea surface temperature range from −1°C to 28°C, the highest median values of P^B_{opt} were 6–7 mg C (mg Chl a)$^{-1}$ h^{-1} and occurred at temperatures <20°C. Moreover, Cullen et al. (1992), in their review of the relationship between photosynthetic parameters and relative growth rate in phytoplankton cultures, found that the highest measured values of P^B_m were 6–8 mg C (mg Chl a)$^{-1}$ h^{-1}. With these laboratory and field results in mind, it does not seem plausible to expect that phytoplankton in the oligotrophic gyres normally have photosynthetic efficiencies sufficiently high to sustain growth rates near 1 d^{-1}. However, different literature reviews show that μ estimates well above 2 d^{-1} have been reported frequently for the open ocean (Eppley 1972; Goldman et al. 1979; Gasol et al. 1997). Are these high turnover rates possible in surface waters of the subtropical gyres? Even if the C : Chl a takes a value of around 100–120 (i.e., the lower bound of the 95% confidence intervals in Fig. 4), a μ of 2.5 d^{-1} implies a $P^B > 25$ mg C (mg Chl a)$^{-1}$ h^{-1}, which is the theoretical maximum for light-saturated photosynthesis (Falkowski 1981) and is rarely measured either in optimal laboratory conditions (Glover 1980) or nutrient-rich coastal waters (Hood et al. 1991). Furthermore, the confidence intervals shown on Fig. 5 indicate that phytoplankton growth rates >0.6 d^{-1} must be infrequent in surface waters of the oligotrophic ocean. When reviewing the literature for estimates of μ in the open ocean, these confidence intervals might serve as a guide to assess the validity of extreme values, especially if they are consistently yielded by particular experimental approaches or persistently obtained in specific surveys. Similarly, the mean and range of μ shown on Fig. 5 can be useful to constrain phytoplankton-mediated fluxes in biogeochemical budgets of the open ocean, given that measured rates must be compatible with the available estimates of algal standing stocks and biomass turnover rates.

The results of the present analysis contradict the frequently held view that phytoplankton μ in the oligotrophic ocean is high (≥1 d^{-1}) and, furthermore, that it is not limited by nutrient availability (e.g., Harris 1984; Gasol et al. 1997). The conceptual basis for this view comes, ultimately, from the work of Goldman and collaborators (Goldman et al. 1979; Goldman 1980). These authors discovered, through a series of elegant experiments with continuous cultures of different species of eukaryotic phytoplankton, that the Redfield proportions for cellular C, N, and P are attained only when cells grow at a rate close to maximum μ and nutrient sufficiency is approached. In those cultures growing at rates <20% of their maximum μ, typical molar C : N were as high as 15–20 (Goldman 1980). The common observation that the molar C : N of particulate organic matter (POM) in the open ocean takes values in the range 6–7 (e.g., Sterner and Elser 2002 and references therein) has led to the conclusion that phytoplankton grow at a rate close to their maximum

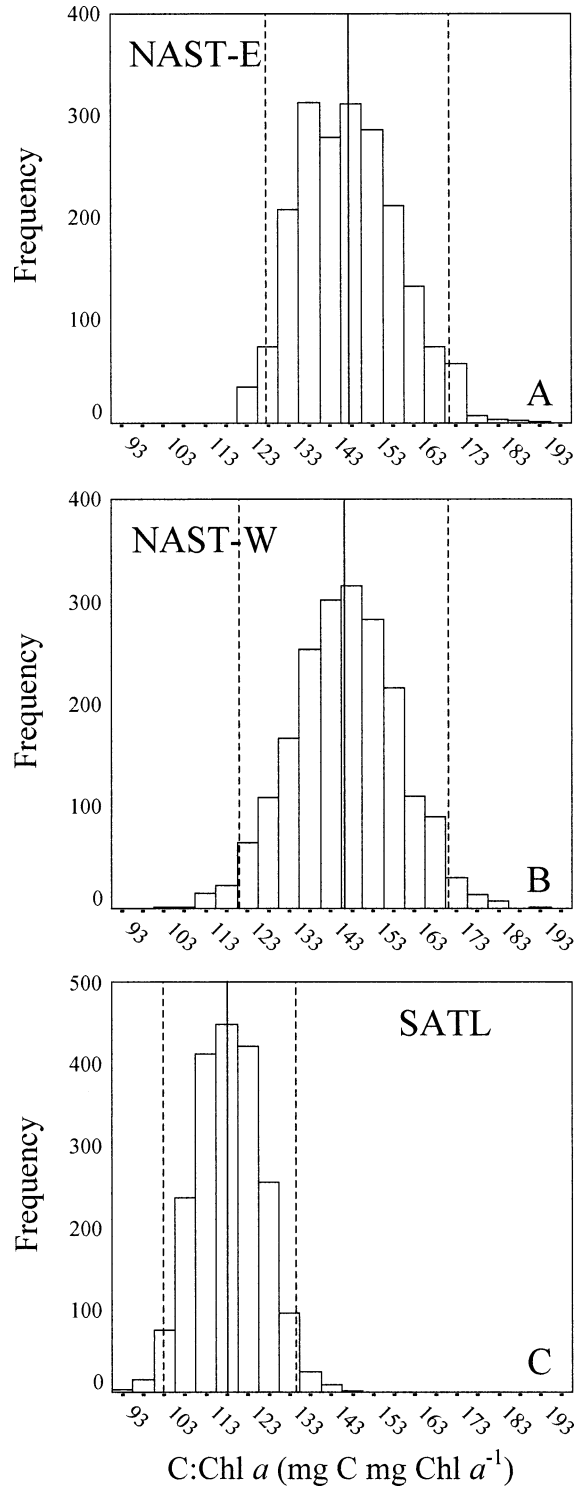

Fig. 4. Same as Fig. 2 but for the C : Chl a, as obtained from original measurements in surface waters of (A) NAST-E, (B) NAST-W, and (C) SATL biogeographic provinces.

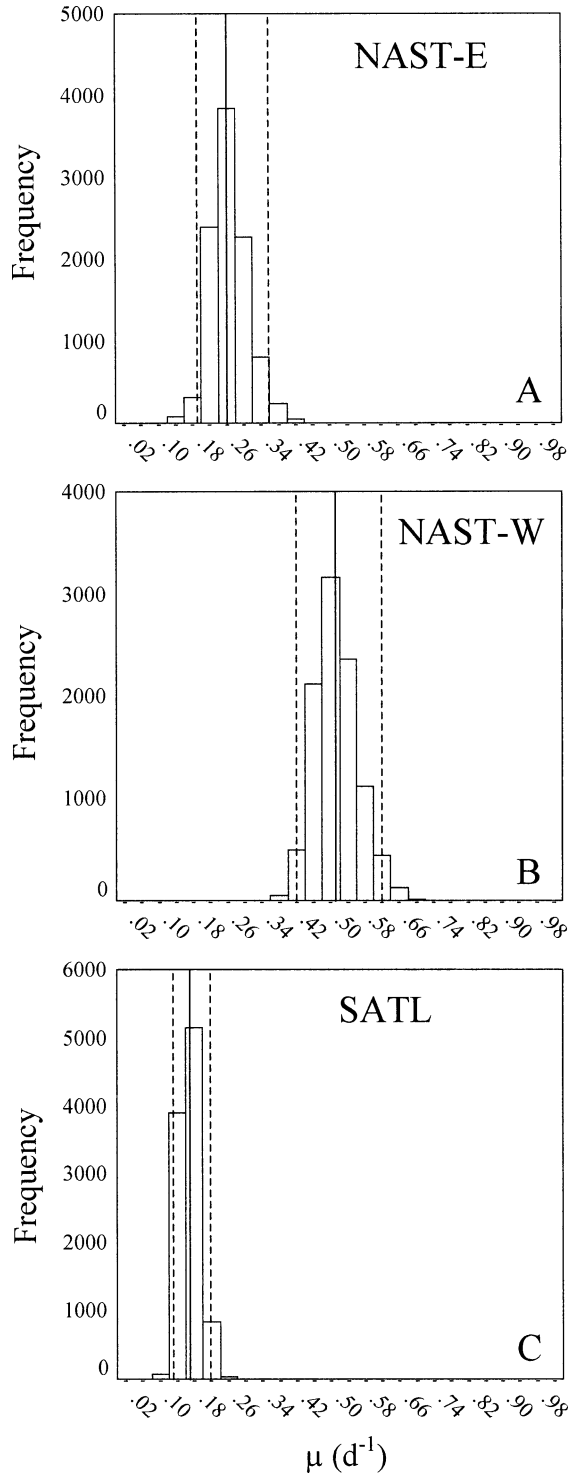

Fig. 5. Frequency distributions of 10,000 values of the mean phytoplankton growth rate, μ, calculated by dividing 100 randomly selected bootstrap means of P^B by 100 randomly selected bootstrap means of C : Chl *a* for (A) NAST-E, (B) NAST-W, and (C) SATL biogeographic provinces.

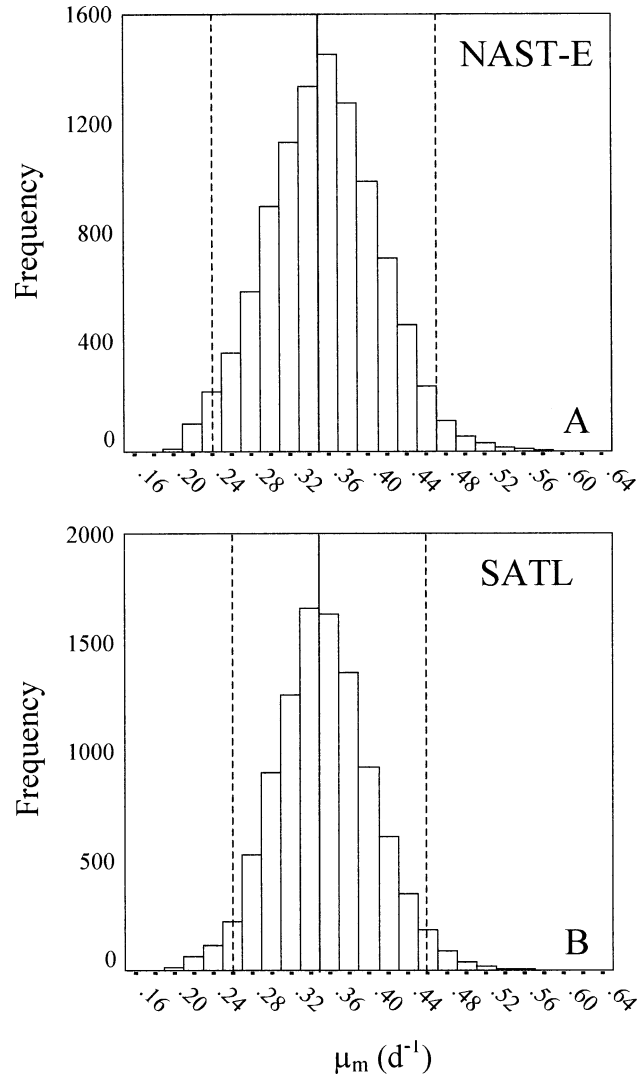

Fig. 6. Same as Fig. 5 but for the maximum phytoplankton growth rate, μ_m, calculated by dividing 100 randomly selected bootstrap means of P_m^B by 100 randomly selected bootstrap means of C : Chl *a* for (A) NAST-E and (B) SATL biogeographic provinces.

growth rates, which would imply absolute values of $\mu > 1\ d^{-1}$.

The validity of this conclusion depends critically on the extent to which the C : N of POM in the oligotrophic ocean really reflects the C : N of living phytoplankton. It is now well established that photoautotrophic biomass is a relatively minor component of POM in unproductive marine waters, being frequently outweighed by detrital and bacterial biomass (e.g., Cho and Azam 1990; Caron et al. 1995; Veldhuis and Kraay 2004). This is illustrated, for instance, in the northwest Sargasso Sea by both the high average POC : Chl *a* (434 ± 32 mg C [mg Chl *a*]$^{-1}$) and the lack of correlation between Chl *a* and POC concentrations ($r = 0.12$, $p > 0.15$, $n = 127$) observed at the BATS station during the period 1990–1999. Given that heterotrophic bacteria are characterized by low C : N (~4–5; e.g., Nagata 1986; Fagerbakke et al. 1996), their biomass contribution could well mask the elemental composition of phytoplankton and lead to a total POM C : N near 7.

For example, simple calculations show that if the C biomass of bacteria having a C : N = 4.5 is the same as the C biomass of phytoplankton having a C : N = 16 (indicative of strong nutrient limitation of μ), the C : N of total microbial biomass will still be 7. The contribution of detrital matter, which might represent >50% of total POC in oligotrophic waters (Cho and Azam 1990; Caron et al. 1995; Veldhuis and Kraay 2004) can push the total POM C : N toward even lower values, if the low C : N (<6) measured in detrital particles of the oligotrophic Mediterranean Sea (Mostajir et al. 1998) are widespread in the open ocean. Ironically, the original experiments of Goldman and coworkers yielded also a result that, when considering the present review of C : Chl *a*, supports the concept of slow phytoplankton growth in the oligotrophic ocean. These authors showed that the C : Chl *a* was inversely related to μ, so that cultures growing at rates below 0.2–0.3 d^{-1} typically had C : Chl $a > 120$ (Goldman 1980). This is precisely the kind of C : Chl *a* values that have been measured in the subtropical gyres.

It must be emphasized that the present analysis does not imply that phytoplankton μ in the oligotrophic gyres is always slow. There is abundant evidence to support the existence of events of nutrient enrichment in the open ocean that lead to enhanced rates of primary production and, presumably, phytoplankton growth rates as well. These events can be caused by several mechanisms, including eddy- or internal wave–induced nutrient pumping and atmospheric deposition of nutrients, among others. What the present analysis does suggest is that in a ''normal'' state of affairs, phytoplankton growth in the oligotrophic ocean is slow, so that photoautotrophic biomass turns over no faster than approximately once every 3–4 d. The limitation of growth rates by nutrient supply is consistent with the observation of enhanced physiological condition in phytoplankton following experimental nutrient additions to surface waters in the subtropical gyres (Graziano et al. 1996; Mills et al. 2004).

The present review of P^B, P^B_m, and C : Chl *a* measured in surface waters of three biogeographic provinces in the subtropical Atlantic Ocean strongly suggests that phytoplankton grow at rates well below maximum growth rates. Slow growth rates ($\leq$0.5 d^{-1}) in the oligotrophic ocean are consistent with the existing knowledge on the relationship between elemental composition and physiological state in phytoplankton. Embracing the concept of slow-growing phytoplankton in the oligotrophic ocean is the only way to reconcile the concurrent observations of both high C : Chl *a* and low assimilation numbers. It also fits with measurements of low turnover rates (<0.2 d^{-1}) of heterotrophic biomass in the oligotrophic ocean (Zubkov et al. 2000). Furthermore, the view that photoautotrophic biomass in the open ocean is characterized by high C : N agrees with the recurrent biogeochemical observation of higher rates of C consumption than could be expected on the basis of N supply rates and the Redfield ratio (e.g., Sambrotto et al. 1993). The relative constancy of the POM C : N from coastal to open ocean regions would thus reflect, rather than a permanently high phytoplankton turnover rate, the increasing trend in the contribution of nonphotosynthetic material to total biomass as the productivity of the system declines (Buck et al. 1996; Gasol et al. 1997). This trend, it can be hypothesized, would be coupled to increasing phytoplankton C : N, in turn indicative of progressively slower, nutrient-limited growth rates.

References

BEHRENFELD, M. J., AND P. G. FALKOWSKI. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnol. Oceanogr. **42:** 1–20.

———, O. PRASIL, Z. S. KOLBER, M. BABIN, AND P. G. FALKOWSKI. 1998. Compensatory changes in photosystem II electron turnover rates protect photosynthesis from photoinhibition. Photo. Res. **58:** 259–268.

BERTILSSON, S., O. BERGLUND, D. M. KARL, AND S. W. CHISHOLM. 2003. Elemental composition of marine *Prochlorococcus* and *Synechococcus*: Implications for the ecological stoichiometry of the sea. Limnol. Oceanogr. **48:** 1721–1731.

BJØRNSEN, P. K. 1986. Automatic determination of bacterioplankton biomass by means of image analysis. Appl. Environ. Microbiol. **51:** 1199–1204.

BOOTH, B. C. 1988. Size classes and major taxonomic groups of phytoplankton at two locations in the subarctic Pacific Ocean in May and August, 1984. Mar. Biol. **97:** 275–286.

BUCK, K. R., F. P. CHAVEZ, AND L. CAMPBELL. 1996. Basin-wide distribution of living carbon components and the inverted trophic pyramid of the central gyre of the North Atlantic Ocean, summer 1993. Mar. Ecol. Prog. Ser. **10:** 283–298.

CAMPBELL, L., H. A. NOLLA, AND D. VAULOT. 1994. The importance of *Prochlorococcus* to community structure in the central North Pacific Ocean. Limnol. Oceanogr. **39:** 954–961.

CARON, D. A., AND OTHERS. 1995. The contribution of microorganisms to particulate carbon and nitrogen in surface waters of the Sargasso Sea near Bermuda. Deep-Sea Res. I **42:** 943–972.

CHO, B. C., AND F. AZAM. 1990. Biogeochemical significance of bacterial biomass in the ocean's euphotic zone. Mar. Ecol. Prog. Ser. **63:** 253–259.

CLAUSTRE, H., AND OTHERS. 2002. Diel variations in *Prochlorococcus* optical properties. Limnol. Oceanogr. **47:** 1637–1647.

CULLEN, J. J., X. YANG, AND H. L. MACINTYRE. 1992. Nutrient limitation and marine photosynthesis, p. 69–88. *In* P. G. Falkowski and A. D. Woodhead [eds.], Primary productivity and biogeochemical cycles in the sea. Plenum.

EFFRON, B. 1979. Bootstrap methods: Another look at the jacknife. Ann. Stat. **7:** 1–26.

EMERSON, S., P. QUAY, D. M. KARL, C. WINN, L. TUPAS, AND M. R. LANDRY. 1997. Experimental determination of the organic carbon flux from open ocean surface waters. Nature **389:** 951–954.

EPPLEY, R. W. 1980. Estimating phytoplankton growth rates in the central oligotrophic gyres, p. 231–242. *In* P. G. Falkowski [ed.], Primary production in the sea. Plenum.

———. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. **70:** 1063–1085.

———, F. M. H. REID, AND J. D. H. STRICKLAND. 1970. Estimates of phytoplankton crop size, growth rate and primary production. Bull. Scripps Inst. Oceanogr. **17:** 33–42.

FAGERBAKKE, K. M., M. HELDAL, AND S. NORLAND. 1996. Content of carbon, nitrogen, oxygen, sulfur and phosphorus in native and cultured aquatic bacteria. Aquat. Microb. Ecol. **10:** 15–27.

FALKOWSKI, P. G. 1981. Light–shade adaptation and assimilation numbers. J. Plankton Res. **3:** 203–216.

FURUYA, K. 1990. Subsurface chlorophyll maximum in the tropical and subtropical western Pacific Ocean: Vertical profiles of phytoplankton biomass and its relationship with chlorophyll *a* and particulate organic carbon. Mar. Biol. **107:** 529–539.

GASOL, J. M., P. A. DEL GIORGIO, AND C. M. DUARTE. 1997. Bio-

mass distribution in marine planktonic communities. Limnol. Oceanogr. **42:** 1353–1363.

GEIDER, R. J., H. L. MACINTYRE, AND T. M. KANA. 1998. A dynamic regulatory model of phytoplankton acclimation to light, nutrients and temperature. Limnol. Oceanogr. **43:** 679–694.

GLOVER, H. E. 1980. Assimilation numbers in cultures of marine phytoplankton. J. Plankton Res. **2:** 69–79.

GOERICKE, R., AND N. A. WELSCHMEYER. 1998. Response of Sargasso Sea phytoplankton biomass, growth rates and primary production to seasonally varying physical forcing. J. Plankton Res. **20:** 2223–2249.

GOLDMAN, J. C. 1980. Physiological processes, nutrient availability, and the concept of relative growth rate in marine phytoplankton ecology, p. 179–197. *In* P. G. Falkowski [ed.], Primary production in the sea. Plenum.

———, J. J. MCCARTHY, AND D. G. PEAVEY. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature **279:** 210–215.

GRAZIANO, L. M., R. J. GEIDER, W. K. W. LI, AND M. OLAIZOLA. 1996. Nitrogen limitation of North Atlantic phytoplankton: Analysis of physiological condition in nutrient enrichment experiments. Aquat. Microb. Ecol. **11:** 53–64.

HARRIS, G. P. 1984. Phytoplankton productivity and growth measurements: Past, present and future. J. Plankton Res. **6:** 219–237.

HOOD, R. R. 1995. Light response of phytoplankton in the South Atlantic Ocean: Interpretation of observations and application to remote sensing. J. Geophys. Res. **100:** 10,927–10,942.

———, M. R. ABBOTT, AND A. HUYER. 1991. Phytoplankton and photosynthetic light response in the coastal transition zone of northern California in June 1987. J. Geophys. Res. **96:** 14,769–14,780.

JOINT, I., A. POMROY, G. SAVIDGE, AND P. BOYD. 1993. Size fractionated primary production in the North East Atlantic in early summer 1989. Deep-Sea Res. **40:** 423–440.

JONES, D. R., D. M. KARL, AND E. A. LAWS. 1996. Growth rates and production of heterotrophic bacteria and phytoplankton in the North Pacific subtropical gyre. Deep-Sea Res. I **43:** 1567–1580.

KANA, T. M., AND P. M. GLIBERT. 1987. Effect of irradiances up to 2000 μE m^{-2} s^{-1} on marine *Synechococcus* WH7803-I. Growth, pigmentation, and cell composition. Deep-Sea Res. I **34:** 479–495.

KARL, D. M. 1999. A sea of change: Biogeochemical variability in the North Pacific subtropical gyre. Ecosystems **2:** 181–214.

KIRCHMAN, D. L. 2002. Calculating microbial growth rates from data on production and standing stocks. Mar. Ecol. Prog. Ser. **233:** 303–306.

KOVALA, P. E., AND J. D. LARRANCE. 1966. Computation of phytoplankton cell numbers, cell volume, cell surface and plasma volume per litre, from microscopical counts. University of Washington Department of Oceanography Special Report 38.

LAWS, E. A., G. R. DITULLIO, AND D. G. REDALJE. 1987. High phytoplankton growth and production rates in the North Pacific subtropical gyre. Limnol. Oceanogr. **32:** 905–918.

LEFÈVRE, N., A. H. TAYLOR, F. J. GLIBERT, AND R. J. GEIDER. 2003. Modeling carbon to nitrogen and carbon to chlorophyll *a* ratios in the ocean at low latitudes: Evaluation of the role of physiological plasticity. Limnol. Oceanogr. **48:** 1796–1807.

LESSARD, E. J., AND M. C. MURRELL. 1998. Microzooplankton herbivory and phytoplankton growth in the northwestern Sargasso Sea. Aquat. Microb. Ecol. **16:** 173–188.

LIU, H., R. R. BIDIGARE, E. A. LAWS, M. R. LANDRY, AND L. CAMPBELL. 1999. Cell cycle and physiological characteristics of *Synechococcus* (WH7803) in chemostat culture. Mar. Ecol. Prog. Ser. **189:** 17–25.

LONGHURST, A., S. SATHYENDRANATH, T. PLATT, AND C. CAVERHILL. 1995. An estimate of global primary production in the ocean from satellite radiometer data. J. Plankton Res. **17:** 1245–1271.

LORENZO, L. M., F. G. FIGUEIRAS, G. H. TILSTONE, B. ARBONES, AND I. MIRÓN. 2004. Photosynthesis and light regime in the Azores Front region during summer: Are light-saturated computations of primary production sufficient? Deep-Sea Res. I **51:** 1229–1244.

MACINTYRE, H. L., T. M. KANA, T. ANNING, AND R. J. GEIDER. 2002. Photoacclimation of photosynthesis irradiance response curves and photosynthetic pigments in microalgae and cyanobacteria. J. Phycol. **38:** 17–38.

MALONE, T. C., S. E. PIKE, AND D. J. CONLEY. 1993. Transient variations in phytoplankton productivity at the JGOFS Bermuda time series station. Deep-Sea Res. I **40:** 903–924.

MANLY, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology, 2nd ed. Chapman & Hall.

MARAÑÓN, E., M. J. BEHRENFELD, N. GONZÁLEZ, B. MOURIÑO, AND M. V. ZUBKOV. 2003. High variability of primary production in oligotrophic waters of the Atlantic Ocean: Uncoupling from phytoplankton biomass and size structure. Mar. Ecol. Prog. Ser. **257:** 1–11.

———, AND P. M. HOLLIGAN. 1999. Photosynthetic parameters of phytoplankton from 50°N to 50°S in the Atlantic Ocean. Mar. Ecol. Prog. Ser. **176:** 191–203.

———, ———, M. VARELA, B. MOURIÑO, AND A. J. BALE. 2000. Basin-scale variability of phytoplankton biomass, production and growth in the Atlantic Ocean. Deep-Sea Res. I **47:** 825–857.

MILLS, M. M., C. RIDAME, M. DAVEY, J. LA ROCHE, AND R. J. GEIDER. 2004. Iron and phosphorus co-limit nitrogen fixation in the eastern tropical North Atlantic. Nature **429:** 292–294.

MOORE, L. R., R. GOERICKE, AND S. W. CHISHOLM. 1995. Comparative physiology of *Synechococcus* and *Prochlorococcus*: Influence of light and temperature on growth, pigments, fluorescence and absorptive properties. Mar. Ecol. Prog. Ser. **116:** 259–275.

MOSTAJIR, B., K. M. FAGERBAKKE, M. HELDAL, T. F. THINGSTAD, AND F. RASSOULZADEGAN. 1998. Elemental composition of individual pico- and nano-sized marine detrital particles in the northwestern Mediterranean Sea. Oceanol. Acta **21:** 589–596.

NAGATA, T. 1986. Carbon and nitrogen content of natural planktonic bacteria. Appl. Environ. Microbiol. **52:** 28–32.

———. 2000. Production mechanisms of dissolved organic matter, p. 121–152 *In* D. L. Kirchman [ed.], Microbial ecology of the oceans. Wiley-Liss.

QUEVEDO, M., AND R. ANADÓN. 2001. Protist control of phytoplankton growth in the subtropical north-east Atlantic. Mar. Ecol. Prog. Ser. **221:** 29–38.

REDALJE, D. G., AND E. A. LAWS. 1981. A new method for estimating phytoplankton growth rates and carbon biomass. Mar. Biol. **62:** 73–79.

SAMBROTTO, R. N., AND OTHERS. 1993. Elevated consumption of carbon relative to nitrogen in the surface ocean. Nature **360:** 248–250.

SIEGEL, D. A., D. J. MCGILLICUDDY, AND E. A. FIELDS. 1999. Mesoscale eddies, satellite altimetry, and new production in the Sargasso Sea. J. Geophys. Res. **104:** 13,359–13,379.

STEINBERG, D. K., C. A. CARLSON, N. R. BATES, R. J. JOHNSON, A. F. MICHAELS, AND A. H. KNAP. 2001. Overview of the US JGOFS Bermuda Atlantic Time-series Study (BATS): A decade-scale look at ocean biology and biogeochemistry. Deep-Sea Res. II **48:** 1405–1447.

STELFOX-WIDDICOMBE, C. E., E. S. EDWARDS, P. H. BURKILL, AND M. A. SLEIGH. 2000. Microzooplankton grazing activity in the

temperate and sub-tropical NE Atlantic: Summer 1996. Mar. Ecol. Prog. Ser. **208:** 1–12.

STERNER, R. W., AND J. J. ELSER. 2002. Ecological stoichiometry. Princeton Univ. Press.

TAYLOR, A. H., R. J. GEIDER, AND F. J. H. GILBERT. 1997. Seasonal and latitudinal dependencies of phytoplankton carbon-to-chlorophyll ratios: Results of a modelling study. Mar. Ecol. Prog. Ser. **152:** 51–66.

VELDHUIS, M. J. W., AND G. W. KRAAY. 2004. Phytoplankton in the subtropical Atlantic Ocean: Towards a better assessment of biomass and composition. Deep-Sea Res. I **51:** 507–530.

ZUBKOV, M. V., M. A. SLEIGH, P. H. BURKILL, AND R. J. G. LEAKEY. 2000. Bacterial growth and loss in contrasting areas of North and South Atlantic. J. Plankton Res. **22:** 685–711.

———, ———, G. A. TARRAN, P. H. BURKILL, AND R. J. G. LEAKEY. 1998. Picoplanktonic community structure on an Atlantic transect from 50°N to 50°S. Deep-Sea Res. I **45:** 1339–1355.

Received: 16 July 2004
Amended: 20 September 2004
Accepted: 23 September 2004