Extraction of photosynthesis-irradiance parameters from phytoplankton production data: demonstration in various aquatic systems

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A method is presented for extraction of the photosynthesis-response parameters from profiles of phytoplankton production. The procedure, previously proposed but not tested, is implemented here in various types of aquatic system and a protocol is established for its use. Values of daily primary production integrated over the photic zone were estimated from in situ or simulated in situ incubations in four coastal and open-ocean marine systems, and from photosynthesis-irradiance (P–E) curves in the afore-mentioned marine systems, as well as in two freshwater systems. The slope of the measured daily water-column production (normalised to water-column chlorophyll a biomass) plotted against the daily incident irradiance was variable from system to system (0.09 to 0.60), showing a broader range than previously reported values. Using an iterative procedure, we estimated the photosynthetic parameters from this linear relationship. Generally, estimated values lie within the 95% confidence interval of the photosynthetic parameters obtained from the P–E curves, showing that the estimates agree well with measurements. The new method, based on the photosynthetic properties of the phytoplankton community, provides a way to enhance our ability to compute primary production from remote sensing of ocean colour.

INTRODUCTION

Primary production by phytoplankton, the base of the food web in aquatic systems, regulates energy availability to higher trophic levels as well as carbon and oxygen fluxes between the ocean and the atmosphere. Remote sensing of ocean colour has proven to be a valuable tool to provide synoptic fields of primary production (Longhurst et al., 1995; Antoine et al., 1996; Behrenfeld and Falkowski, 1997), from which it has been deduced that, globally, oceanic primary production fixes 36.5–50 gigatonnes of carbon every year, which is equivalent in magnitude to global terrestrial primary production (Longhurst et al., 1995; Behrenfeld et al., 2001; Cramer et al., 2001). To quantify primary production on synoptic scales in this manner, remotely sensed estimates of chlorophyll a concentration, daily irradiance and attenuation coefficients have to be combined with the characteristics of pigment-biomass profiles and photosynthetic response (Platt and Sathyendranath, 1988; Sathyendranath and Platt, 1993). Under the simplified assumption of vertical homogeneity, only the photosynthetic parameters are required as auxiliary data (Platt and Sathyendranath, 1993).

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Photosynthetic parameters are extracted from production-irradiance curves (P–E curves) in which production $P$ is normalised to chlorophyll $a$ concentration which is taken as a surrogate for biomass, $B$ ($P_B$) (Fig. 1). The two parameters required to describe the $P$–$E$ relationship are $\alpha_B$, the initial slope of the relationship, and $P_m^B$, the light-saturated production plateau. The projection on the abscissa of the intersection of $\alpha_B$ and $P_m^B$ provides the photoacclimation parameter $E_K$.

These parameters are derived from experiments made under light-controlled conditions in a light-gradient incubation box. Good estimates of phytoplankton production can be obtained by combining photosynthetic parameters with the underwater irradiance field and biomass concentration (see for example Côté and Platt, 1984; Platt and Sathyendranath, 1988; Kyewalyanga et al., 1997). However, the problem of under-sampling $P$–$E$ parameters, especially in some biogeochemical provinces in the southern hemisphere, has been pointed out as a circumstance that limits the applicability of the procedure at the global scale (Longhurst et al., 1995). At the same time, substantial existing databases provide data on water-column primary production from in situ or simulated in situ incubation (O’Reilly et al., 1987; see also Table III in Campbell et al., 2002). Thus, if one could extract the required photosynthetic parameters from in situ or simulated in situ primary production measurements, an important contribution would be made to satellite-based primary-production measurements.

One approach to this problem that has been suggested earlier (Behrenfeld and Falkowski, 1997) is through the study of measured, vertical biomass-specific profiles of primary production from which a set of productivity parameters, $P_{opt}^B$ and $E_{max}^B$ are extracted. However, these parameters are different from those derived from production-irradiance curves, and cannot be easily extrapolated to other conditions since they are, in principle, influenced by daily variations in irradiance at the time of the incubation. Moreover, field measurements of $P_m^B$ are usually unavailable for comparison with estimates of $P_{opt}^B$, production datasets generally being composed of either in situ water-column production or P–E experiments.

Here we explore and refine a new method for retrieving the photosynthetic parameters, $\alpha_B$ and $P_m^B$, from a series of in situ and simulated in situ primary production measurements from different regions and seasons (Platt and Sathyendranath, 1993). We show how the method can be implemented to extract the photosynthetic parameters of two freshwater systems. We then apply the method to measurements of both in situ and simulated in situ water-column primary production in marine systems and find a generalisation that will simplify the retrieval of the photosynthetic parameters. Finally, we verify the method on an independent data set, from the Canadian Arctic waters.

### Theoretical considerations

Along with phytoplankton biomass, light is a major limiting factor for primary production. Thus, understanding the relationship between daily water-column primary production ($P_{ZT}$) and daily irradiance ($E_T$) is a fundamental step towards the computation of water-column primary production (Fig. 2a). By calculating $P_{ZT}$ from a hypothetical population at different times of the year, Ryther showed for the first time the curvilinear relationship between the daily relative water-column production ($R_0$) and the available light at the surface of the ocean (Ryther, 1956). Many other authors have studied the relationship between $P_{ZT}$ and $E_T$ (Ryther and Yentsch, 1957; Talling, 1957; Rodhe, 1965; Platt et al., 1990), and a canonical form has been found (Platt et al., 1990; Platt and Sathyendranath, 1993) for this relationship:

$$P_{ZT} = \frac{BDP_m^B}{K} f\left(\frac{E_a^m}{E_a^*}\right),$$

where $B$ is the chlorophyll $a$ concentration, $D$ is day-length, $K$ is the attenuation coefficient for downwelling irradiance and $f\left(\frac{E_a^m}{E_a^*}\right)$ is a function of $E_a^*$ (dimensionless irradiance computed as surface irradiance at noon, $E_0^*$, normalised to $E_K$) (Fig. 2b), whose particular form depends on the equation selected to represent the photosynthesis-irradiance curve. The first part of the right-hand side of the equation, $BDP_m^B/K$, is a scale factor, whereas the second half, $f\left(\frac{E_a^m}{E_a^*}\right)$, provides the
curvilinear shape of the relationship with a steep slope at low light levels, and a much lower slope at high irradiance.

The relationship between the daily water-column production normalised to chlorophyll a concentration in the euphotic zone \( (\Lambda = P_{ZT}/B) \) and daily irradiance \( (E_t) \) has been studied for many years (Malone, 1976; Morel, 1978; Falkowski, 1981; Jordan and Joint, 1984; Platt, 1986; Platt et al., 1988). In many respects, this relationship is similar to that of the \( P-E \) curves, but deals with the production not only of a single water sample but of an entire ecosystem, often on a seasonal time-scale. The normalised production measured at low light is forced mainly by the light-limited properties of the phytoplankton community \( (\alpha^h) \), whereas normalised production measured at high light is related more to light-saturated properties of the phytoplankton community \( (P^B_m) \). However, describing an accurate curvilinear relationship with light-limited and light-saturated parameters is much more difficult for an entire ecosystem than for \( P-E \) experiments, due to the limited range of daily surface irradiance encountered. Many authors (Malone, 1976; Morel, 1978; Falkowski, 1981; Jordan and Joint, 1984; Platt, 1986; Platt et al., 1988) have proposed to represent this relationship using a linear approximation with a slope \( \Psi \) (Fig. 2a). The slope \( \Psi \) is referred to as the water-column light utilisation index (Falkowski, 1981), and it has been pointed out (Platt et al., 1988) that \( \Psi \) varies by only a factor of 2 in all the studies reviewed in their paper [0.29–0.52 g C (g Chl a)\(^{-1}\) m\(^{-2}\) (mol quanta\(^{-1}\)]). It has been proposed that the linear approximation to the relationship between \( \Lambda \) and \( E_t \) carries information on the photosynthetic parameters (Platt and Sathyendranath, 1993). However, the proposition has not yet been tested.

Suppose that, over a given range of \( E^m \), the linear approximation of \( f(E^m) \) is represented by

\[
f (E^m) = c + bE^m,
\]

with slope \( b \) and intercept \( c \) (Fig. 2b). It has been shown that equations (1) and (2) can be combined and rewritten as a function of the photosynthetic parameters:

\[
\Lambda = \frac{cD}{4.6} P^B_m + \frac{b\pi}{9.2} \alpha^B E_T,
\]

where the intercept contains \( P^B_m \) and the slope contains \( \alpha^B \) (Platt and Sathyendranath, 1993). Since \( b \) and \( c \) are unknown, the parameters \( \alpha^B \) and \( P^B_m \) cannot be estimated directly from equation (3), unless an iterative procedure is established. Here we develop and test such a method.

The procedure could be substantially simplified if a typical range of \( E^m \) were defined, such that values of \( b \) and \( c \) could be estimated from linear approximation of \( f(E^m) \). It has been pointed out that a small range of \( E^m \) (from 5 to 8) might cover many situations in temperate latitudes (Platt and Sathyendranath, 1993). Here we examine this suggestion using several data sets of primary production to determine the range of \( E^m \) they represent, and then calculate the corresponding values of \( b \) and \( c \) for each set. Next, we generalise the results and validate the resultant simplified approach using an independent data set.

**METHOD**

**Study sites**

To test the above method and its applicability, six different datasets were used. The systems studied encompass
Incubation times ranged from 6 to 24 h. Third, simulated in situ primary production was measured using a similar approach, with the exception that the bottles were incubated on deck in temperature-controlled chambers, shaded to mimic the different optical depths (100, 50, 30, 15, 5, 1 and 0.2% of surface PAR). Incubation time ranged from 8–10 h. The water-column integrated production from in situ and simulated in situ incubations was computed as the sum of production $P_i$ in each of the $n$ layers where production was measured

$$\int P(z)dz = \sum_{i=1}^{n} P_i H_i,$$  

where $i$ represents the layer and $H_i$ is the thickness of the $i$th layer (Platt and Irwin, 1968). When incubation time was less than the daylength, the computed production was scaled to obtain daily, water-column production by multiplying by $E_T$ and dividing by the total irradiance during the period of incubation. Similarly, mean chlorophyll $a$ in the euphotic zone was computed as $\sum_{i=1}^{n} B_i H_i / z_p$ where $B_i$ is the measured chlorophyll concentration in the $i$th layer and the integration is carried out over the euphotic depth $z_p$ where light is reduced to 1% of its value at the surface.

**Iterative procedure**

For an initial test of the method, daily production estimated from photosynthetic parameters using Fee’s model (Fee, 1990) in two freshwater systems was used. This model consists of a numerical integration over depth and time and implies homogeneity of the water column, which corresponds to the premise of the Platt

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**Table I: Description of the aquatic systems under study and of the types of production measurements ($N =$ number of observations) included in the analyses**

<table>
<thead>
<tr>
<th>Systems</th>
<th>Lat., Long.</th>
<th>Type</th>
<th>Season</th>
<th>Production estimation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lac Croche*</td>
<td>45°59’N, 74°01’W</td>
<td>Lacustrine</td>
<td>Summer</td>
<td>P–E curve (N = 23)</td>
</tr>
<tr>
<td>St Lawrence River*</td>
<td>45°16’N, 74°06’W</td>
<td>Fluvial</td>
<td>Summer</td>
<td>P–E curve (N = 16)</td>
</tr>
<tr>
<td>Canary Current#</td>
<td>31°04’N, 10°50’W</td>
<td>Coastal</td>
<td>Autumn</td>
<td>In situ and P–E curve (N = 7)</td>
</tr>
<tr>
<td>Sargasso Sea*</td>
<td>37°30’N, 40°00’W</td>
<td>Open Ocean</td>
<td>Spring</td>
<td>In situ and P–E curve (N = 8)</td>
</tr>
<tr>
<td>NW Atlantic shelf#</td>
<td>43°53’N, 57°56’W</td>
<td>Open Ocean</td>
<td>Spring</td>
<td>In situ (simulated) and P–E curve (N = 9)</td>
</tr>
<tr>
<td>Canadian Arctic#</td>
<td>74°52’N, 80°02’W</td>
<td>Open Ocean</td>
<td>Summer</td>
<td>In situ and P–E curve (N = 5)</td>
</tr>
</tbody>
</table>

#Platt (1986).
*Irwin et al. (1988).
^Kyewalyanga et al. (1997).
#Kyewalyanga et al. (1992).
'Unpublished data.
^Irwin et al. (1989).

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a broad range of biogeochemical properties (Table I), varying from lacustrine, fluvial and coastal to open ocean systems. These systems were sampled at different times of the year and presented mixing conditions from well mixed to fully stratified water column. All of the systems studied are within eastern Canada and the Northwest Atlantic, with the exception of the Canary Current coastal province, which is located in the Northeast Atlantic Ocean. The Northwest Atlantic Shelf refers to a Lagrangian study (C-SOLAS) of the decline of a spring bloom. During this study, a water mass containing the bloom was sampled at eight occasions from 25 April to 2 May 2003 (d1 to d8), where d8 falls outside the studied water mass. The Lagrangian study site was also sampled on 14 May 2003 (referred as d20).

**Primary production measurements**

Primary production was measured using three different techniques. First, P–E experiments were performed by incubating samples for 3–4 h in a light-gradient incubator, either using $^{14}$C uptake (Irwin et al., 1985) or the oxygen evolution (high precision Winkler method, Carignan et al., 1998). A photosynthetic quotient of 1.25 was used to transform oxygen production in carbon units (Williams and Robertson, 1991). The photosynthetic parameters were obtained by fitting the equation of Platt et al. (Platt et al., 1980) to the observations. Attenuation coefficients of photosynthetically active radiation in the water column were also measured.

Second, in situ primary production was measured using the $^{14}$C technique (Irwin et al., 1985). Water samples were collected from different depths, bottled and returned to their specific depth for incubation.
and Sathyendranath’s model (Platt and Sathyendranath, 1993). To start the iterative procedure, initial estimates of photosynthetic parameters were used to obtain initial values for $E^*$. Then $f(E^*)$ was computed (see Table A1 of Platt and Sathyendranath, 1993) for each observation, and a linear approximation [equation (2)] was fitted to the values. This yielded initial values of $b$ and $c$, which were then substituted into equation (3) to obtain new values for $a^B$ and $P^B_m$ from the slope ($\Psi = b\pi a^B/9.2$) and the intercept ($\xi = D B P^B_m/4.6$) of the linear equation fitted to $\Lambda$ as a function of $E_T$. Then, through successive iterations, a final set of photosynthetic parameters should be retrieved by convergence. We found here that trial fits to both parameters at the same time did not lead to convergence, perhaps because the results were sensitive to initial guesses, as had been suggested earlier (Platt and Sathyendranath, 1993). Therefore, Equation (3) was applied separately in each of two ranges of daily irradiance determined arbitrarily: $<15$ mol photons m$^{-2}$ day$^{-1}$ to retrieve $a^B$ and $>50$ mol photons m$^{-2}$ day$^{-1}$ to retrieve $P^B_m$. This procedure led to successful convergence for the parameters. The same technique was then applied to the four sets of data with in situ or simulated in situ water-column incubations. When the observed irradiance range did not offer any data points in either of the two ranges, the two points each from the lowest and highest irradiance levels were used for the estimation. This compromise had to be made in three of the six studied systems: the Canary Current coastal province, the Sargasso Sea and the Northwest Atlantic Shelf. For all of these systems, the photosynthetic parameters estimated from the iteration procedure were compared with the measurements from the $P-E$ curves.

RESULTS

Prior to evaluating the results of the iterative procedure, estimates and measurements of water-column primary production were compared to establish whether the models used were capable of reproducing the observations well (Fig. 3). Estimates of water-column primary production from the two different models (Fee, 1990; Platt et al., 1990) showed good agreement, with values tightly distributed around the one-to-one line, with a small but consistent over-estimation of primary production by the model of Platt et al. compared to that of Fee. In situ and simulated in situ measurements showed higher variability when compared with modelled production (Platt et al., 1990). Primary production in the Bedford Basin measured over a 24 h incubation was much lower than measurements from 6 h incubations, and from estimates using the model of Platt et al. (Platt et al., 1990). Since measurements using $^{14}$C did not account for planktonic respiration, such divergence between short and long incubations was expected: short incubations yield estimates closer to gross primary production, whereas long incubations represent net primary production. Production estimates from the Canary Current coastal province and the Sargasso Sea were often higher than values computed using the model of Platt et al. (Platt et al., 1990). However, results remained well distributed around the one-to-one line.

The iterative procedure was based on the relationship between normalised production ($\Lambda$) and daily irradiance ($E_T$) (Fig. 4). For all of the systems under study, the magnitudes of $\Lambda$ were similar, except for the Northwest Atlantic Shelf which showed remarkably low $\Lambda$ values. Highest values were found in the two freshwater systems and the Sargasso Sea. To account for differences in duration of incubation, the daily production from longer in situ incubations (Bedford Basin, 24 h incubation and Northwest Atlantic Shelf, 8–10 h incubation) was corrected for respiration to match estimates from short (4 hour or less) $P-E$ incubations: we used the empirical relationship of Smith and Kemp (Smith and Kemp, 1995) between volumetric respiration and temperature. This relationship accounts only for temperature, which is a strong predictor of respiration in Chesapeake Bay (Sampou and Kemp, 1994; Smith and Kemp, 1995), although others (Del Giorgio and Peters, 1994; Carignan et al., 2000) have shown that biomass (chlorophyll a concentration) is also an important factor regulating planktonic respiration. Corrected data yielded a positive linear relationship between $\Lambda$ and $E_T$ for all of the systems, with the exception of the two open-ocean systems (Sargasso Sea and Northwest Atlantic Shelf). For the Sargasso Sea dataset, daily irradiance showed consistently high values, and the low range of $E_T$ limited any further analysis of light-dependent changes in production. In the Northwest Atlantic Shelf, the apparent decrease of $\Lambda$ with light was counter-intuitive, which prompted further examination.

The Northwest Atlantic Lagrangian time series (Fig 5a) showed a decline in the average chlorophyll a concentration integrated over the euphotic depth from d1 to d8. Observations from satellite images (C. Fuentes-Yaco, personal communication) showed that our field measurements covered only the decline of the spring bloom and that peak biomass occurred during the previous week. Total primary production integrated over the euphotic depth was fairly high on d1 and d2 but dropped markedly on d3 after which it remained relatively constant until the end of the Lagrangian study and increased slightly on d20 (Fig. 5b). Normalised
Fig. 3. Relationship between water-column primary production estimated from models of Fee (1990) and Platt et al. (1990) where $y = 0.94x - 14.1; r^2 = 0.97$ (left) and relationship between water-column primary production measured from in situ incubation and that estimated from the model of Platt et al. (1990) where $y = 1.19x - 32.7; r^2 = 0.71$ (right). Units of production are mg C m$^{-2}$ day$^{-1}$. In both graphs, the dashed line is the 1 to 1 line and the solid line represents the linear regression.

Fig. 4. Relationship between the normalised daily water-column production $A [P_{ZT}/B_2]$ and daily irradiance ($E_{ZT}$) for the six systems studied. For Bedford Basin, the 6 h (filled circles) and 24 h (grey circles) incubations are presented, as well as the 24 h incubation corrected for planktonic respiration (blank squares). For the Northwest Atlantic Shelf, the net production (grey circles) and the gross production (blank squares) are presented. The parameters and $r^2$ of the regression lines are presented in Table II.
Fig. 5. Lagrangian time-series carried out on the Northwest Atlantic Shelf from 24 April 2003 to 14 May 2003. (A) mean chlorophyll a concentration integrated over the photic zone and mean temperature of the photic zone; (B) daily water-column primary production; (C) daily water-column primary production normalised to the water-column chlorophyll biomass; (D) photosynthetic parameters $a^B$ and $P^B_{m}$. In panel c, the time-series has been divided into three groups according to $\Lambda (P_{ZT}/B_{Z})$.

Table II: Measurements of photosynthetic parameters (average ± standard deviation) and ecosystem productivity parameters, where $\Psi$ is the slope of the relationship between normalised production $\Lambda (P_{ZT}/B_{Z})$ and $E_{T}$ whereas $\xi$ is the intercept. The values of the slope $\Psi$ and intercept $\xi$ refer to Figs. 4 and 6; $r^2$ values are also presented. Sargasso sea data are excluded from the analyses due to the low range of daily irradiance.

<table>
<thead>
<tr>
<th>Systems</th>
<th>$\alpha^B$ (g C g Chl a$^{-1}$ (W m$^{-2}$ h$^{-1}$))</th>
<th>$P^B_{m}$ (g C g Chl a$^{-1}$ h$^{-1}$)</th>
<th>$\psi$ (g C g Chl a$^{-1}$ (mol photons m$^{-2}$ h$^{-1}$))</th>
<th>$\xi$ (g C g Chl a$^{-1}$ day$^{-1}$)</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lac Croche</td>
<td>0.143 ± 0.036</td>
<td>4.07 ± 0.88</td>
<td>0.47</td>
<td>5.17</td>
<td>0.62</td>
</tr>
<tr>
<td>St Lawrence R.</td>
<td>0.149 ± 0.037</td>
<td>6.72 ± 1.53</td>
<td>0.60</td>
<td>8.10</td>
<td>0.80</td>
</tr>
<tr>
<td>Bedford Basin (6 h)</td>
<td>0.084 ± 0.018</td>
<td>3.37 ± 1.01</td>
<td>0.32</td>
<td>3.64</td>
<td>0.67</td>
</tr>
<tr>
<td>Canary Current</td>
<td>0.072 ± 0.013</td>
<td>4.97 ± 0.78</td>
<td>0.31</td>
<td>6.93</td>
<td>0.38</td>
</tr>
<tr>
<td>Sargasso Sea</td>
<td>0.097 ± 0.024</td>
<td>7.41 ± 2.09</td>
<td>-1.16</td>
<td>81.93</td>
<td>0.21</td>
</tr>
<tr>
<td>NW Atlantic Shelf</td>
<td>0.014 ± 0.004</td>
<td>0.84 ± 0.15</td>
<td>0.09</td>
<td>2.31</td>
<td>0.51</td>
</tr>
</tbody>
</table>
production ($\Lambda$) on d1 and d2 presented higher values as on d8 and d20, but estimates for d3 to d7 were significantly lower ($t$-test, $P < 0.01$). The time-series of water-column normalised production (Fig. 5c) along with its relationship with $E_T$ (Fig. 6) allowed us to identify three groups of samples. In situ observations revealed that samples from group I were characteristic of a diatom bloom, which declined in samples from group II, followed in group III by a mixed phytoplankton population (M. Lizotte, personal communication).

For the photosynthetic parameters (Fig. 5d), groups I and III presented higher average values of the photosynthetic parameters [mean ± standard deviation; group I: $\alpha^B = 0.024 \pm 0.014 \text{ mg C mg chl}^{-1} \text{ (W m}^{-2})^{-1} \text{ h}^{-1}$; $P_m^B = 1.04 \pm 0.43 \text{ mg C mg chl}^{-1} \text{ h}^{-1}$; group III: $\alpha^B = 0.024 \pm 0.0057 \text{ mg C mg chl}^{-1} \text{ (W m}^{-2})^{-1} \text{ h}^{-1}$; $P_m^B = 1.92 \pm 0.17 \text{ mg C mg chl}^{-1} \text{ h}^{-1}$] than the second group [$\alpha^B = 0.014 \pm 0.0035 \text{ mg C mg chl}^{-1} \text{ (W m}^{-2})^{-1} \text{ h}^{-1}$; $P_m^B = 0.84 \pm 0.15 \text{ mg C mg chl}^{-1} \text{ h}^{-1}$].

A positive linear relationship was observed between $\Lambda$ (corrected for respiration) and $E_T$ (Fig. 6) for group II ($r^2 = 0.51$, $N = 5$); groups I and III were too small ($N = 2$ for both groups) to obtain statistical analyses. Group II regression was used to retrieve the photosynthetic parameters by iterative procedure for the Northwest Atlantic Lagrangian study for a decaying population of diatoms.

The photosynthetic parameters estimated from the iteration procedure were fairly close to the photosynthetic parameters measured from the $P–E$ experiments (Fig. 7) usually falling within the 95% confidence interval for all the systems studied. The only important discrepancy between estimated and measured photosynthetic parameters occurred in the Bedford Basin data, for which the samples were incubated in situ for a period of 24 h and in the Northwest Atlantic Shelf (8–10 h incubations). After correction for planktonic respiration, the estimated photosynthetic parameters were much closer to the measured values from the $P–E$ experiments. As explained earlier, respiration rates were estimated taking only temperature into account. Refining the estimation of planktonic respiration would probably have resulted in a better agreement between estimated and measured photosynthetic parameters. A similar correction should be applied to all $^{14}$C in situ primary production measurements, when $in situ$ incubation exceeds 6 h. The implementation of the model requires that observations of production be made over a range of irradiance values to allow retrieval of parameters for light-limited and light-saturated conditions. Furthermore, the model assumes that the parameters remain stable throughout the experiments. When these conditions are satisfied, the retrieval technique yields good estimates of the parameters (Fig. 7).
Table III: Photosynthetic parameters retrieved by iterative procedure and linear approximation of the relationship between $f(E_{aa}^w)$ and $E_{aa}^w$ as estimated from $b$ and $c$ values for each ecosystem

<table>
<thead>
<tr>
<th>System</th>
<th>$a^B$ (g C g Chl$^{-1}$ (W m$^{-2}$) h$^{-1}$)</th>
<th>$P_{aa}^B$ (g C g Chl$^{-1}$ h$^{-1}$)</th>
<th>$b$ Dimensionless</th>
<th>$c$ Dimensionless</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lac Croche</td>
<td>0.144</td>
<td>4.14</td>
<td>0.164</td>
<td>0.382</td>
</tr>
<tr>
<td>St Lawrence R.</td>
<td>0.133</td>
<td>9.26</td>
<td>0.226</td>
<td>0.272</td>
</tr>
<tr>
<td>Bedford Basin</td>
<td>0.058</td>
<td>3.92</td>
<td>0.279</td>
<td>0.314</td>
</tr>
<tr>
<td>Canary Current</td>
<td>0.063</td>
<td>6.57</td>
<td>0.248</td>
<td>0.415</td>
</tr>
<tr>
<td>NW Atlantic Shelf</td>
<td>0.023</td>
<td>0.89</td>
<td>0.214</td>
<td>0.526</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
<td>0.23</td>
<td>0.38</td>
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</tbody>
</table>

We have shown that the application of the method proposed by Platt and Sathyendranath (Platt and Sathyendranath, 1993) can be implemented to yield useful estimates of photosynthetic parameters for vastly different aquatic systems. The question then arises, what generalisation could be made by combining results from all areas? Using the photosynthetic parameters estimated from the iterative procedure, we estimated $b$ and $c$ (equation 3) from the linear fit between $A$ and $E_T$ for five of the six systems (Table III); values of $b$ and $c$ could not be estimated for the Sargasso Sea system because this data set did not span a sufficient irradiance range. The values of $b$ and $c$ varied about 2-fold and were thus more stable than the photosynthetic parameters themselves which varied about 5-fold over the range of aquatic systems. As shown in Fig. 2b, values of $b$ and $c$ are expected to vary according to the range of $E_{aa}^w$ observed for each system.

Values of $b$ and $c$ can also be derived from the slope and the intercept of the regression of $A$ on $E_T$ in each system, given independent estimates of $a^B$ and $P_{aa}^B$, respectively. Note that such estimates would be based on direct measurements of in situ production and of $P–E$ parameters, and therefore would be completely independent of the iteration method developed in this paper. We can derive $c$ from the intercept of equation (3) if daylength $D$ and $P_{aa}^B$ are known, and $b$ from the slope, if $a^B$ is known. From Fig. 8, we found that the slope $\Psi$ varied linearly with $a^B$ and the intercept $\xi$ with $P_{aa}^B$, suggesting that $b$ and $c$ were fairly stable among systems. Therefore, the best estimates of $b$ and $c$ were obtained using linear fits passing through the origin and the average daylength for all sampling days (14.1 h). These fits yielded values of 0.19 for $b$ and 0.41 for $c$ (dimensionless units), which were very close to those obtained by averaging the $b$ and $c$ values for each aquatic system (Table III, $b = 0.23$, $c = 0.38$). Plotting the linear approximation derived from these values of $b$ and $c$ superimposed on the full theoretical solution (curvilinear relationship between $f(E_{aa}^w)$ and $E_{aa}^w$) showed that our approximation held true over a range of $E_{aa}^w$ between 0 and 11 (Fig. 9).

Using the above values of $b$ and $c$ established for aquatic systems in the North Atlantic (marine) and the Eastern Canada (freshwater), values of photosynthetic parameters were estimated using equation (3) for an independent dataset, the Arctic Waters, for which both in situ production and $P–E$ parameters were available (Tables IV and V). The $E_{aa}^w$ values for the Arctic data set ranged from 1.1 to 1.6, which was at the lower end of the general $E_{aa}^w$ range observed for the systems described earlier (Fig. 9). The photosynthetic parameters estimated...
from equation (3) using fixed values of $b$ and $c$ were close to the measured values from $P–E$ experiments, with the $P_m^b$ value falling within the 95% confidence interval.

**DISCUSSION**

Primary production can be calculated using many different models, and ultimately estimated from satellite images of ocean colour to obtain global coverage of the global ocean. Following the approach of Longhurst (Longhurst, 1998), the ocean can be divided into a suite of biogeochemical provinces, each one having its own specific physical, chemical and biological properties. Furthermore, these properties vary seasonally. Here, we have developed a method for estimating the photosynthetic parameters from *in situ* measurements of primary production that can be successfully applied across a wide range of marine and freshwater systems.

**Inter-system variations**

In temperate regions, seasonal changes in temperature and wind conditions induce the alternance of stratified and mixed (other seasons) water columns in lacustrine as well as oceanic systems. Our use of data sets derived from widely different aquatic systems allowed us to examine the effects of seasonal stratification (or lack thereof) on water-column primary production estimates. Both the model of Platt and Sathyendranath (Platt and Sathyendranath, 1993) used in the iteration procedure and the Fee’s model (Fee, 1990) assume a vertically homogeneous water column. This shared assumption partly explains the surprisingly good agreement between production estimates derived from those two models, which performed equally well when applied to a stratified (lacustrine) or a well-mixed (riverine) system (Fig. 3a). In contrast, oceanic production estimates derived from Platt’s model (Platt et al., 1990) should differ most markedly from in situ measurements for samples from early autumn and summer due to water column stratification. In spite of seasonal differences in stratification, the agreement between in situ measurements and modelled primary production was high (Fig. 3, right).

The relationship between daily water-column production (normalised to chlorophyll $a$ concentration) and daily irradiance has been studied for many years (Malone, 1976; Morel, 1978; Falkowski, 1981; Jordan and Joint, 1984; Platt, 1986; Platt et al., 1988). In this study (Fig. 4), the range of slope $\Psi$ obtained (Table II: 0.09–0.60 g C (g chl $a$)$^{-1}$ mol photons$^{-1}$ m$^2$) was much wider than that reported earlier (Platt et al., 1988: 0.29–0.52 g C (g chl $a$)$^{-1}$ mol photons$^{-1}$ m$^2$). The main difference comes from the Northwest Atlantic Lagrangian Study, which yielded a $\Psi$ of 0.09 g C (g chl $a$)$^{-1}$ mol photons$^{-1}$ m$^2$. Due to the declining status of its phytoplankton flora, the mixed layer of the Lagrangian study site presented nutrient-limited conditions (J. Pommier, personal communication). On the other hand, the St. Lawrence River, a freshwater system, exhibited the steepest slope ($\Psi = 0.60$ g C (g chl $a$)$^{-1}$ mol photons$^{-1}$ m$^2$) indicative of eutrophic conditions. Given that the aquatic systems covered here included inland freshwater, coastal and open ocean systems, such a broad range in the ecosystem productivity parameters is not surprising.

![Fig. 9](https://example.com/fig9.png)

**Table IV:** Photosynthetic parameters from Arctic water samples measured from $P–E$ experiments (values ± 95% confidence interval) and from equation (3) using fixed values of $b$ and $c$ from the common range of $E_m^a$ for aquatic systems in the North Atlantic and Eastern Canada. The range of $E_m^a$ is also provided (min–max values)

<table>
<thead>
<tr>
<th>Methods</th>
<th>$a^b$ (g C g Chla$^{-1}$ W$^{-1}$ m$^2$ h$^{-1}$)</th>
<th>$P_h^c$ (g C g Chla$^{-1}$ h$^{-1}$)</th>
<th>$E_m^a$ Dimensionless</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P–E$ curves</td>
<td>0.090 ± 0.008</td>
<td>1.40 ± 0.035</td>
<td>1.11 – 1.63</td>
</tr>
<tr>
<td>Equation (3)</td>
<td>0.103</td>
<td>1.73</td>
<td>0 – 11</td>
</tr>
</tbody>
</table>

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and emphasizes the importance of a small number of common forcing variables on phytoplankton.

Extraction of photosynthetic parameters

The photosynthetic parameters derived from \textit{in situ} experiments were fairly close to those measured in \( P-E \) experiments (Fig. 7). Sometimes, \( \alpha^P \) was slightly underestimated whereas \( P_B^m \) was overestimated. The problem originated in the underestimation of the initial slope of the \( \lambda - E_T \) relationship, resulting in an overestimation of \( P_B^m \). The underestimation of the initial slope arose from two possible causes: insufficient data points at low light level (Canary Current coastal province and Northwest Atlantic Shelf), or an underestimation of the water-column primary production from long \textit{in situ} experiments and short (3–4 h) incubations. The limited ranges of \( b \) and \( c \) values for each system (Table IV). However, these values of \( b \) and \( c \) were also sensitive to errors in the estimation of the photosynthetic parameters from the iterative procedure. To avoid this source of error, \( b \) and \( c \) values were also estimated from the relationship of \( \Psi \) with \( \alpha^P \) and \( \xi \) with \( P_B^m \) (Fig. 8), using equation (3) \( (b = 0.19; c = 0.41 \text{ in dimensionless units}) \). The result would be applicable to a range of \( E_T^m \) from 0 to 11, which is broader than the restricted range of 5–8 previously proposed, as being the usual range of \( E_T^m \) for marine ecosystems at temperate latitudes (Platt and Sathyendranath, 1993). Photosynthetic parameters can thus be estimated.

<table>
<thead>
<tr>
<th>Notation</th>
<th>Definition</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \alpha^P )</td>
<td>The initial slope of the production-irradiance relationship</td>
<td>mg C mg chla(^{-1}) (W m(^{-2}) h(^{-1}))</td>
</tr>
<tr>
<td>( \lambda )</td>
<td>Daily integrated water-column production normalised to water-column chlorophyll a ( (P_T^m P_B^m) )</td>
<td>mg C mg chla(^{-1}) day(^{-1})</td>
</tr>
<tr>
<td>( \xi )</td>
<td>The intercept of the linear relationship between ( P_B^m ) and ( E_T )</td>
<td>g C g chla(^{-1}) day(^{-1})</td>
</tr>
<tr>
<td>( \Psi )</td>
<td>Water-column light utilisation index, the slope of the linear relationship between ( P_B^m ) and ( E_T )</td>
<td>g C g chla(^{-1}) (mol photons m(^{-2}) h(^{-1}))</td>
</tr>
<tr>
<td>( b )</td>
<td>Slope of the linear relationship between ( f(E_T^m) ) and ( E_T^m )</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>( c )</td>
<td>Intercept of the linear relationship between ( f(E_T^m) ) and ( E_T^m )</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>( Z_p )</td>
<td>Euphotic depth, where light is reduced to 1% of its value at the surface</td>
<td>m</td>
</tr>
<tr>
<td>( B_a )</td>
<td>Chlorophyll a concentration integrated over the euphotic zone</td>
<td>mg chla m(^{-3})</td>
</tr>
<tr>
<td>( B_e )</td>
<td>Water-column chlorophyll a concentration</td>
<td>mg chla m(^{-2})</td>
</tr>
<tr>
<td>( D )</td>
<td>Daylength</td>
<td>h</td>
</tr>
<tr>
<td>( E_k )</td>
<td>The photo-acclimation parameter</td>
<td>W m(^{-2})</td>
</tr>
<tr>
<td>( E_{max} )</td>
<td>Daily PAR at the inflection point between light-limited and light-saturated production measured from \textit{in situ} incubations (Behrenfeld and Falkowski, 1997)</td>
<td>mole photons m(^{-2}) s(^{-1})</td>
</tr>
<tr>
<td>( E_T )</td>
<td>Daily irradiance (PAR)</td>
<td>mole photons m(^{-2}) day(^{-1})</td>
</tr>
<tr>
<td>( E_T^m )</td>
<td>Dimensionless irradiance computed as surface irradiance at noon normalised to ( E_T )</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>( f(E_T^m) )</td>
<td>Function of ( E_T^m )</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>( k )</td>
<td>Attenuation coefficient for downwelling irradiance (PAR)</td>
<td>m(^{-1})</td>
</tr>
<tr>
<td>( P_B^m )</td>
<td>Production normalised to chlorophyll a concentration</td>
<td>mg C mg chla(^{-1}) h(^{-1})</td>
</tr>
<tr>
<td>( P_L^m )</td>
<td>The assimilation number, the chlorophyll-specific production at light saturation</td>
<td>mg C mg chla(^{-1}) h(^{-1})</td>
</tr>
<tr>
<td>( P_{min} )</td>
<td>Maximum chlorophyll-specific carbon fixation measured from \textit{in situ} incubations (Behrenfeld and Falkowski, 1997)</td>
<td>mg C mg chla(^{-1}) h(^{-1})</td>
</tr>
<tr>
<td>( P )</td>
<td>Volumetric production</td>
<td>mg C m(^{-3}) day(^{-1})</td>
</tr>
<tr>
<td>( P_T^m )</td>
<td>Daily integrated water-column production</td>
<td>mg C m(^{-2}) day(^{-1})</td>
</tr>
<tr>
<td>( R_B )</td>
<td>Relative daily water-column production (Ryther, 1956)</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>( H )</td>
<td>The thickness of a layer</td>
<td>m</td>
</tr>
</tbody>
</table>
directly from the linear relationship between \( A \) and \( E_T \) using equation (3) and general values of \( b \) and \( c \), which eliminates the need for the iterative procedure. Obviously, if the aquatic system presented unusual \( E^n_p \) values, outside the range from 0 to 11 (Fig 9), this procedure would be inaccurate. The difficulty of course is that the values for \( E^n_p \) are unknown prior to the analyses. However, one could anticipate unusually high values of \( E^n_p \) if \( E_T \) values were unusually high. In such situations, the iterative approach would be preferred. Notwithstanding these potential limitations, the range established here for \( E^n_p \) (0 to 11) should include most cases encountered in the field. Therefore, the procedure we have developed should be of general applicability.

As an example, we have verified the applicability of this direct procedure using an independent data set collected in the Eastern Arctic (Table IV). Although this aquatic system was in a different biogeochemical province from those previously discussed, having unique underwater light conditions and photophysiological responses of the phytoplanktonic community with low values of \( E^n_p \) (range of 1.1–1.6), our new procedure performed very well, providing estimates of the photosynthetic parameters remarkably close to the measured values. This illustrates how the model could be used for global applications.

**Satellite application**

*In situ* or simulated *in situ* measurements of primary production provide information on the intensity of this process at a particular location, at a particular time. Extraction of \( P-E \) parameters from the data extends their use to answer the general question: what would be the production at that location if the biomass or light were different? A particular application of such information would be for satellite-based estimates of primary production. Note that the parameters, once estimated, can be used to estimate production in waters where the biomass shows vertical structure if an appropriate model is used, on condition that the parameters themselves do not show significant vertical structure.

The case of the Lagrangian site on the Northwest Atlantic shelf illustrates well the applicability of this method to satellite-based estimation of primary production. The sampling took place at the end of the spring bloom so the normalised production and the photosynthetic parameters were not constant, but rather decreased through the tail-end of the bloom, a sign of increase nutrient limitation as observed in the decline of other blooms (Platt et al., 1992). The question then arises ‘how do we treat ecosystem productivity parameters for such a system, if they change in time and space?’ Effectively, the physiological state of the phytoplankton population evolved with time and the species composition of the community changed in time and space, being diatom-dominated early during the Lagrangian time-series (groups I and II) and flagellate dominated in group III, outside the Lagrangian site (d8) and two weeks after the bloom (d20) (M. Lizotte, personal communication). Species composition was determined by microscopic analyses and confirmed by satellite imagery. Thus, spatial assignment of ecosystem productivity parameters could be made according to chlorophyll \( a \) concentration maps combined with diatom-occurrence maps (Sathyendranath et al. 2004).

Estimates of the photosynthetic parameters from both the iteration procedure and its approximation using a general range of \( E^n_p \) correspond to average values for a specific region. One could argue that this iterative procedure would not provide data with a high level of precision. However, because the estimation of primary production from satellite images is usually performed from composite images (bimonthly, monthly or seasonally), computation from average values for a specific region and time period is appropriate. In the context of operational remote-sensing estimates of primary production, photosynthetic parameters are usually assigned from a database according to the time of the year and to their spatial proximity to the available data (Platt and Sathyendranath, 1988). The method developed here to estimate photosynthetic parameters from *in situ* primary production provides the means to augment databases and enhance our ability to compute primary production from remotely sensed data on ocean colour.

**ACKNOWLEDGEMENTS**

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