

Flux of particulate organic material from the euphotic zone of oceans: Estimation from phytoplankton biomass

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Abstract. A major objective of modern biological oceanography is to quantify, model, and predict the downward flux of biogenic carbon. Previous papers have documented an empirical relationship between the sinking flux of particulate organic material from the euphotic zone (S) and phytoplankton biomass (B), in oceans, and suggested that S could be estimated directly from B . The present paper investigates, using a mathematical model and data from the literature, the relationship between S and B . Calculations show that S is determined mostly by B and also by p (instantaneous coefficient of net phytoplankton production minus euphotic zone heterotrophic community respiration and incorporation in the pelagic food web). The regression $S = f(B)$ accounts for 90% of the variation in S . In remote sensing, B is derived from ocean color, phytoplankton production (P) is derived from B , and S is derived from P . Within that context, the biomass approach could be used as an additional means to constrain the estimates of S .

1. Introduction

It is debated whether the oceans are a significant sink for anthropogenic CO_2 . Within that context, a major objective of modern biological oceanography is to quantify, model, and predict the flux of particulate and dissolved organic carbon to depth. The downward dissolved flux may be significant in some cases [e.g., Carlson *et al.*, 1994; Michaels *et al.*, 1994] but, since it has not been quantified in most situations, this flux is not considered here. High sinking of particulate organic material (POM) from the euphotic zone often occurs following blooms of large-sized phytoplankton, at which time the downward POM flux mostly consists of aggregated cells and fecal pellets from herbivorous mesozooplankton grazing on large phytoplankton [Legendre, 1990, and references therein]. High sinking has also been reported during nonbloom conditions, at which time the downward POM flux was dominated by pellets from omnivorous mesozooplankton efficiently grazing on the microbial food web [Rivkin *et al.*, 1996]. Because the latter situation is of transient nature, there generally is, as reported below, good correspondence between euphotic zone phytoplankton and sinking POM, when measurements are integrated over reasonably long periods (for example, a few weeks; see equations (1) and (2) below). The present paper focuses on using phytoplankton to estimate the sinking POM flux from the euphotic zone (S).

A direct approach to measuring S is to use sediment traps located close to the bottom of the euphotic zone. An indirect approach consists in deriving S from estimates of phytoplankton production in the euphotic zone (P); the dimensions of S and P are [$\text{mass area}^{-1} \text{ time}^{-1}$]. This indirect approach proceeds in at least two steps. (1) Phytoplankton production may be estimated directly from shipboard measurements (for example, maps in the work by Berger [1989]), or indirectly from

remotely sensed images. The latter involves derivation of chlorophyll *a* concentration (*Chl*) from ocean color images [e.g., Lewis *et al.*, 1983; Balch *et al.*, 1989; Morel and Berthon, 1989], followed by computation of P by combining *Chl* maps with information on solar radiation and shipboard estimates of phytoplankton photosynthetic characteristics [e.g., Platt and Sathyendranath, 1993; Sathyendranath and Platt, 1993; Longhurst *et al.*, 1995]. (2) Phytoplankton production is converted into sinking flux using empirical equations relating S to P , where S are sediment trap estimates, that is, $S = f(P)$ [e.g., Eppeley and Peterson, 1979; Wassmann, 1990]; $S(z) = f(P, z)$ (where z is depth in the water column [e.g., Betzer *et al.*, 1984; Pace *et al.*, 1987]); $S = P \times f\text{-ratio} = P_{\text{new}}$ [Eppeley and Peterson, 1979; Platt and Sathyendranath, 1988], where P_{new} is new phytoplankton production, that is, the part of P which is fueled by allochthonous (called new) nutrients (generally assumed to be mostly nitrate [Dugdale and Goering, 1967]), so that $f\text{-ratio} = \text{uptake of } \text{NO}_3 / \text{uptake of total N nutrients}$ (generally, $\text{NO}_3 + \text{NH}_4 + \text{sometimes urea}$). The $f\text{-ratio}$ approach assumes that phytoplankton biomass in the euphotic zone (B) is in steady state over large spatiotemporal scales [e.g., Eppeley and Peterson, 1979; Platt *et al.*, 1989]. On the Scotian Shelf (NW Atlantic), for example, Dauchez *et al.* [1996] proposed that the relevant timescale is 6 months or more. The $f\text{-ratio}$ can be estimated directly from shipboard measurements of N uptake rates [e.g., Dugdale and Goering, 1967; Dugdale and Wilkerson, 1986], or derived from empirical relationships between the $f\text{-ratio}$ and other, more readily available variables. These variables include P [e.g., Eppeley and Peterson, 1979], size-fractionated P or *Chl* [Tremblay *et al.*, 1997], and ambient NO_3 concentrations [e.g., Harrison *et al.*, 1987; Sathyendranath *et al.*, 1991]. Because there often is a local inverse relationship between NO_3 concentration and temperature [e.g., Kamykowski and Zentara, 1986; Babin *et al.*, 1991], it may be possible to derive $f\text{-values}$ from remotely sensed sea surface temperature [e.g., Dugdale *et al.*, 1989; Sathyendranath *et al.*, 1991].

The previous paragraph shows that estimating S from P often requires complex data sets and is generally based on a

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large number of assumptions. An alternative indirect approach would be to estimate S from B . This variable (generally $B = \text{Chl}$), whose dimensions are $[\text{mass area}^{-1}]$, is easily measured at sea or can be derived from remotely sensed color images (see previous paragraph). At least two papers have suggested that S could be estimated from Chl [Legendre, 1990; Baines *et al.*, 1994]. In the latter publication, the authors empirically derived the following relationship from a large set of S ($\text{mg C m}^{-2} \text{ d}^{-1}$) and average Chl in the euphotic zone (mg m^{-3}), representing a wide range of marine production regimes:

$$\log S = 2.09 + 0.81 \log \text{Chl} \quad (1)$$

S measurements were close to the bottom of the euphotic zone and sediment traps were deployed from 1 day to 5 months (most measurements lasted between 3–4 days and 1 month). The regression (ordinary least squares) accounts for $r^2 = 0.90$ of the variance in $\log S$ (\log stands for \log_{10}). No theoretical explanation was given for (1) so that despite the empirical evidence showing that S can be estimated from B , this straightforward approach is not used. The present paper investigates, with a mathematical model and data from the literature, the relationship between S and B . The aim is to provide a theoretical basis to the estimation of S from B .

2. Model

2.1. General Assumptions and Theoretical Bases

In oceans, the fluxes of biogenic carbon resulting from net (versus gross) particulate phytoplankton production (P) are remineralization in the euphotic zone (that is, heterotrophic community respiration; R), incorporation in the pelagic food web (F), and sinking of POM (S). Assuming that over appropriate timescales and space scales, all phytoplankton production is respired (R) or exported ($F + S$) and horizontal advection is negligible relative to the other fluxes, the above terms are related as follows:

$$P = R + F + S \quad (2)$$

All terms in (2) have dimensions $[\text{mass area}^{-1} \text{ time}^{-1}]$. As explained by Legendre and Rassoulzadegan [1996], each term on the right-hand side may result from the combination of several food web flows. For example, carbon respired within the euphotic zone which is fixed again by phytoplankton and ultimately sinks belongs to S and not R .

Equation (2) applies to timescales where there is no net change in B . When focusing on S , an appropriate timescale for (2) is the length of major phytoplankton blooms. During such blooms, B initially increases rapidly, after which it comes back to its initial value (or close). At short timescales (for example, during blooms), changes in phytoplankton biomass per unit time (t) are

$$dB/dt = (pe - s)B \quad (3)$$

where pe is the instantaneous coefficient $[\text{time}^{-1}]$ of net phytoplankton production minus euphotic zone heterotrophic community respiration and incorporation in the pelagic food web (pe corresponds to exportable phytoplankton production $PE = P - R - F$) and s is the coefficient of sinking (which

corresponds to S). PE cannot be estimated directly, but it can be computed as net phytoplankton production minus heterotrophic respiration and net heterotrophic production. Equation (3) is rewritten as

$$dB/B = (pe - s)dt \quad (4)$$

Integration of (4) gives

$$B(t_2) = B(t_1) \exp[(pe - s)(t_2 - t_1)] \quad (5)$$

Over time interval $\Delta t = [t - 1, t] = 1$ time unit, sinking is

$$S(t - 1, t) = PE(t - 1, t) - \Delta B(t - 1, t) \quad (6)$$

This equation provides a theoretical basis to the various indirect approaches described above for estimating S . Concerning the approach based on P , summing up all terms of (6) over time interval $[0, n]$ gives

$$\sum_{t=1}^n S(t-1, t) = \sum_{t=1}^n PE(t-1, t) - \sum_{t=1}^n \Delta B(t-1, t) \quad (7)$$

As mentioned for (2), it is generally assumed that over an appropriate time interval $[0, n]$, all produced biomass is respired or exported. Hence

$$\Delta B(0, n) = 0 \quad (8)$$

Because of (8), equation (7) becomes

$$\sum_{t=1}^n S(t-1, t) = \sum_{t=1}^n PE(t-1, t) \quad (9)$$

Equation (9) shows that, over time interval $[0, n]$, S is equivalent to new phytoplankton production (by definition, $PE = P_{\text{new}}$ [Eppley and Peterson, 1979]). Hence, if P_{new} can be derived from P (this assumption will be discussed later), the latter or P_{new} can be used to estimate S .

In order to examine the approach based on B , expressions are derived for the two terms on the right-hand side of (6). Over time interval $[t - 1, t]$, exportable phytoplankton production is (equation (5))

$$PE(t - 1, t) = B(t - 1) [\exp(pe) - 1] \quad (10)$$

and the change in B is

$$\Delta B(t - 1, t) = B(t) - B(t - 1) \quad (11)$$

Using these two expressions, (6) is rewritten as follows:

$$S(t - 1, t) = B(t - 1) \exp(pe) - B(t) \quad (12)$$

Summing up all terms of (12) over time interval $[0, n]$ gives

$$\sum_{t=1}^n S(t-1, t) = \sum_{t=1}^n B(t-1) \exp(pe) - \sum_{t=1}^n B(t) \quad (13)$$

Equation (13) shows that over time interval $[0, n]$, S can be derived from B and pe . If the range of variation of $[\exp(pe)]$ is

small relative to that of B (this assumption will be discussed later), then S can be estimated from B only. Using (9) or (13) for estimating S depends on the availability of either P or B data and whether the underlying assumptions are satisfied or not (see below).

If s was always equal to pe , there would never be any change in B . The condition for an increase in B to occur is a time lag between enhanced pe (for example, upon vertical stabilization of a previously deeply mixed water column, or input of limiting nutrient) and enhanced s . This well-known phenomenon (bloom [Legendre, 1990, and references therein]) can be simply modeled as an initial period $[0, x]$ without POM sinking out of the euphotic zone ($s = 0$), followed by a period $[x, n]$ with sinking ($s > 0$), where n is the duration of the period over which (2) is satisfied. If the aim of the study was to model the development of natural phytoplankton, it would be better to progressively increase s , from a small value before $t = x$ to its maximum value after. Since the objective here is instead to understand the relationship between S and B , using a progressively changing s would unduly complicate the exercise without improving the understanding. Consequently, $s = 0$ up to $t = x$ and $s > 0$ after.

2.2. Equations

Phytoplankton blooms are generally characterized by an initial period of exponential growth $[0, x]$, after which phytoplankton experience increasingly limiting nutrient conditions and are subjected to increasing grazing pressure. Hence, after $t = x$, pe progressively decreases. The simplest way to model this is to take pe as constant (that is, $pe = p$) during period $[0, x]$, and linearly decreasing from p down to zero afterward. The corresponding equation for period $[x, n]$ is

$$pe = p(n - t) / (n - x) \quad (14)$$

Using (14), equation (4) is rewritten as follows, for period $[x, n]$:

$$dB/B = (pe - s) dt = \{[p(n - t)/(n - x)] - s\} dt \quad (15)$$

Integration of (15) gives

$$B(t_2) = B(t_1) \exp \left\{ \left[p / (n - x) \right] \left[n(t_2 - t_1) - 0.5(t_2^2 - t_1^2) \right] - \int s dt \right\} \quad (16)$$

During the period without sinking ($t = 1, x$), pe is constant ($pe = p$) and $s = 0$, so that $B(t)$ is calculated as follows (equation (5)):

$$B(t) = B(0) \exp(p t) \quad (17)$$

During the period with sinking ($t = x + 1, n$), pe varies continuously and $s > 0$. In order to obtain the expression for $B(t)$, (8) is first rewritten as follows:

$$B(n) = B(0) \quad (18)$$

Using (16), $B(n)$ is computed as

$$B(n) = B(x) \exp \{ [p / (n - x)] [n(n - x) - 0.5(n^2 - x^2)] - \int s dt \} \quad (19)$$

$B(x)$ is obtained from (17):

$$B(x) = B(0) \exp(p x)$$

Combination of this expression with (19) gives

$$B(n) = B(0) \exp[0.5 p(n + x) - \int s dt]$$

Using this last relationship, it can be shown that in order to satisfy the assumption of (18),

$$\int s dt = 0.5 p(n + x) \quad (20)$$

Computation of $B(t)$ requires one to consider the equation for $B(n)$, which is derived from (19) and (20):

$$\begin{aligned} B(n) &= B(x) \exp \{ [p / (n - x)] [n(n - x) - 0.5(n^2 - x^2)] - 0.5 p(n + x) \} \\ B(n) &= B(x) \exp \{ [p / (n - x)] [-x(n - x)] \} \end{aligned}$$

Hence

$$B(t) = B(t - 1) \exp[-p x / (n - x)]$$

or, using (17),

$$\begin{aligned} B(t) &= B(0) \exp(p x) \exp \{ [-p x / (n - x)] (t - x) \} \\ B(t) &= B(0) \exp[p x(n - t) / (n - x)] \quad (21) \end{aligned}$$

In order to compute $S(t - 1, t)$, which occurs during period ($t = x + 1, n$) only, the expression for $PE(t - 1, t)$ is first derived from (16), with $s = 0$, $t_2 = t$, and $t_1 = (t - 1)$:

$$\begin{aligned} PE(t - 1, t) &= B'(t) - B(t - 1) \\ &= B(t - 1) \{ \exp[p(n - t + 0.5) / (n - x)] - 1 \} \quad (22) \end{aligned}$$

where $B'(t)$ would be phytoplankton biomass at time t in absence of sinking. Given (10),

$$B(t - 1) \exp(pe) = PE(t - 1, t) + B(t - 1)$$

equation (22) provides the first right-hand term of (12):

$$B(t - 1) \exp(pe) = B(t - 1) \exp[p(n - t + 0.5) / (n - x)] \quad (23)$$

The second right-hand term of (12), $B(t)$, is given by (21). Hence

$$\begin{aligned} S(t - 1, t) &= B(0) \{ \exp[p(n x + x + n + 0.5 - x t - t) / (n - x)] \\ &\quad - \exp[p x(n - t) / (n - x)] \} \quad (24) \end{aligned}$$

Mean phytoplankton biomass at sea is generally estimated by averaging instantaneous measurements (shipboard or derived from satellite images) over the period of interest. This is simulated here by computing the average biomass in the euphotic zone over period ($t = 1, n$), that is, summing up values $B(t)$ (equations (17) and (21)) and dividing the result by the number of data n :

$$B = (1/n) \left[\sum_{t=1}^x B(t) + \sum_{t=x+1}^n B(t) \right] \quad (25)$$

It can be shown that the first term in the brackets corresponds to a geometric progression with the following first term (A), common ratio (C), and number of terms (N):

$$A = B(0) \exp(p)$$

$$C = \exp(p)$$

$$N = x$$

so that the sum of the N terms is

$$\sum_{t=1}^x B(t) = A [\exp(px) - 1] / [\exp(p) - 1] \quad (26)$$

Similarly, the second term in the brackets in (25) corresponds to a geometric progression with

$$A = B(0) \exp[p x (n - x - 1) / (n - x)]$$

$$C = \exp[-p x / (n - x)]$$

$$N = n - x$$

so that

$$\sum_{t=x+1}^n B(t) = A [\exp(-px) - 1] / \{\exp[-p x / (n - x)] - 1\} \quad (27)$$

The sinking flux is generally measured at sea using sediment traps, which are deployed over the period of interest. In order to get S per unit time, total POM collected in a trap is divided by the duration of deployment. This is simulated here by summing up values $S(t-1, t)$ (equation (24)) and dividing the result by the duration of period ($t=1, n$), that is, n :

$$S = (1/n) \sum_{t=x+1}^n S(t-1, t) \quad (28)$$

given that

$$\sum_{t=1}^x S(t-1, t) = 0$$

The sum in (28) is a combination of two geometric progressions (equation (24)):

$$S = I - II \quad (29)$$

For part the first of (24),

$$A = B(0) \exp[p(n x + n - 0.5 - x^2 - x) / (n - x)]$$

$$C = \exp[-p(x+1)/(n-x)]$$

$$N = n - x$$

so that

$$I = A \{\exp[-p(x+1)] - 1\} / \{\exp[-p(x+1)/(n-x)] - 1\} \quad (30)$$

For the second part of (24),

$$A = B(0) \exp[p x (n - x - 1) / (n - x)]$$

$$C = \exp[-p x / (n - x)]$$

$$N = n - x$$

so that

$$II = A [\exp(-p x) - 1] / \{\exp[-p x / (n - x)] - 1\} \quad (31)$$

3. Simulations

Figure 1 illustrates temporal changes in pe , $B(t)$, and $S(t-1, t)$ over a period of $n = 50$ days, computed with the model and using parameters $x = 6$ and 12 days and $p = 0.158 \text{ d}^{-1}$ (doubling time of the exportable biomass = $\log_e 2 / 0.158 \text{ d}^{-1} = 4.4$ days). The figure shows that time lag x deeply influences $B(t)$ and $S(t-1, t)$ and, hence, B and S .

Table 1 gives values of B and S computed with the model over a period of $n = 50$ days, for a range of values of parameters x and p . Variables B and S increase with increasing x and p . Table 2 gives similar values computed for a range of values of parameter n , with $x = 6$ and 12 days and $p = 0.158 \text{ d}^{-1}$. Large changes in n cause only small changes in B and S .

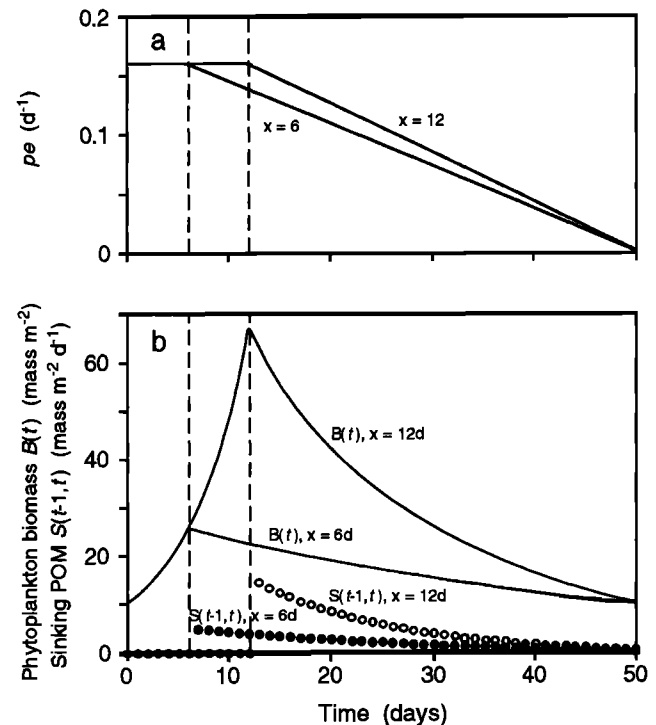


Figure 1. Model: (a) instantaneous coefficient pe of exportable phytoplankton production and (b) phytoplankton biomass in the euphotic zone $B(t)$ and POM sinking from the euphotic zone $S(t-1, t)$, as a function of time t (days). Time lags x between enhanced production and sinking are 6 and 12 days; $B(0) = 10 \text{ mass units m}^{-2}$. Dashed lines are for visual reference.

Table 1. Values Generated by the Model: Average Phytoplankton Biomass in the Euphotic Zone (B) and Average Sinking POM (S) as a Function of the Time Lag (x) Between Enhanced Production and Sinking and of the Initial Value (p) of the Instantaneous Coefficient of Exportable Phytoplankton Production (pe)

x , days	p , d ⁻¹	B , mass m ⁻²	S , mass m ⁻² d ⁻¹
3	0.005	10.08	0.03
3	0.016	10.24	0.09
3	0.050	10.79	0.30
3	0.158	12.80	1.21
3	0.500	23.24	9.04
6	0.005	10.15	0.03
6	0.016	10.49	0.09
6	0.050	11.66	0.34
6	0.158	16.68	1.75
6	0.500	63.80	29.43
9	0.005	10.23	0.03
9	0.016	10.75	0.10
9	0.050	12.63	0.40
9	0.158	22.14	2.53
9	0.500	198.72	101.77
12	0.005	10.31	0.03
12	0.016	11.01	0.11
12	0.050	13.70	0.46
12	0.158	29.89	3.67
12	0.500	675.11	368.74
15	0.005	10.38	0.03
15	0.016	11.29	0.12
15	0.050	14.89	0.52
15	0.158	41.00	5.34
15	0.500	2430.83	1383.72

Total period $n = 50$ days; $B(0) = 10$ mass units m⁻².

Reduced major axis regressions of model generated values are

$$S = -7.86 + 0.58 B \quad (r^2 = \text{approximately } 1.00 \text{ (Figure 2a)}) \quad (32)$$

$$\log S = -2.99 + 2.14 \log B \quad (r^2 = 0.84 \text{ (Figure 2b)}) \quad (33)$$

Reduced major axis regressions are used here because the calculations aim at describing functional relationships between S and B , not obtaining expressions to compute S from B . The high r^2 value for (32) does not mean that all estimates of S are the same as the observed values, but it instead reflects the fact that the regression, which indeed provides good estimates of S , is mostly determined a few large B values. Thus, B accounts for most of the variation in S and $\log B$ accounts for >80% of the variation in $\log S$.

The reduced major axis regression of S/B on $[\exp(p) - 1]$ is

$$S/B = -0.01 + 0.80 [\exp(p) - 1] \quad (r^2 = 0.97) \quad (34)$$

Hence, variations in S/B are largely determined by changes in $[\exp(p) - 1]$.

4. Discussion

Equation (34) shows that the ratio of sinking to biomass (S/B) is determined by p , so that B and p set the value of S . Equations (26) and (27) and Table 1 indicate that parameters x and p strongly influence B . Consequently, the reduced major

Table 2. Values Generated by the Model: Average Phytoplankton Biomass in the Euphotic Zone (B) and Average Sinking POM (S) as a Function of the Length of the Period Considered (n) and the Time Lag (x) Between Enhanced Production and Sinking

n , days	x , days	B , mass m ⁻²	S , mass m ⁻² d ⁻¹
20	6	16.69	1.96
20	12	29.97	4.29
35	6	16.69	1.81
35	12	29.91	3.85
50	6	16.68	1.75
50	12	29.89	3.67

Initial value of the instantaneous coefficient of exportable phytoplankton production (pe) is $p = 0.158$ d⁻¹; $B(0) = 10$ mass units m⁻².

axis regression of B on x and p (based on the 75 B values in Figure 2) accounts for most of the variation in B :

$$B = 18.91 + 1.38 \exp(x p) \quad (r^2 = \text{approximately } 1.00) \quad (35)$$

Hence, time lag x and coefficient p strongly influence the average biomass B (equation (35)), whereas the latter and p determine the average sinking flux S (equation (34)). Hence, x influences S through its effect on B .

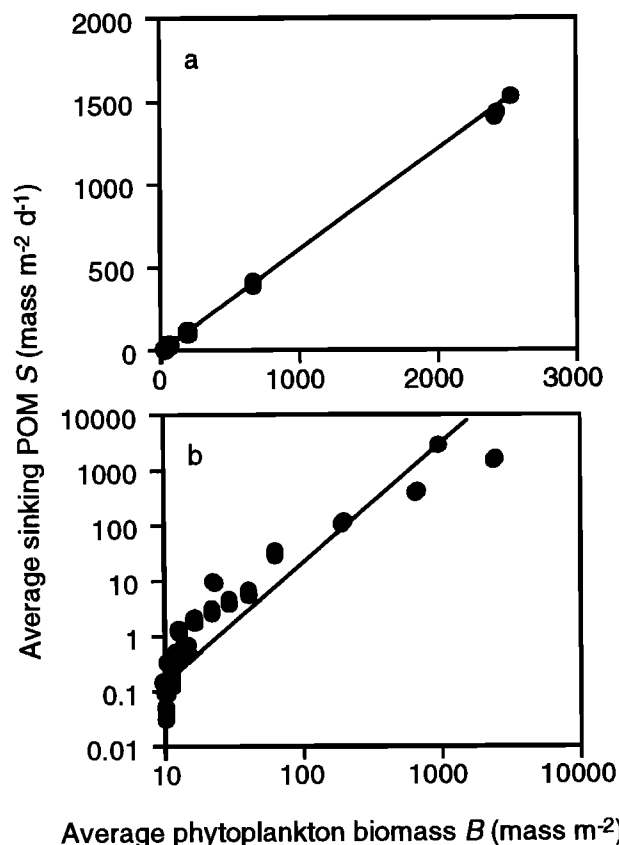


Figure 2. Values generated by the model: average POM sinking from the euphotic zone S as a function of average phytoplankton biomass in the euphotic zone B (75 pairs of values: $n = 20, 35$, and 50 days; $x = 3, 6, 9, 12$, and 15 days; $p = 0.005, 0.016, 0.050, 0.158$, and 0.500 d⁻¹). Major axis linear regressions (lines) are given for (a) nontransformed data (equation (32)) and (b) log-log transformed data (equation (33)).

In order to check how realistic the above theoretical approach is, data compiled by *Baines et al.* [1994] (see equation (1)) are used here to compute reduced major axis regressions. For comparison with values generated by the numerical models, B and S must share the same "currency". Consequently, $\text{Chl } a \text{ m}^{-3}$ were transformed into C m^{-2} , assuming a conversion factor of $50 \text{ mg C mg}^{-1} \text{ Chl } a$ and 40-m deep euphotic zone, that is, $\text{Chl } a$ concentrations were multiplied by 2000. The resulting regressions on nontransformed and log-log transformed values are

$$S = -0.06 + 0.05 B \quad (r^2 = 0.86 \text{ (Figure 3a)}) \quad (36)$$

$$\log S = -1.22 + 0.88 \log B \quad (r^2 = 0.90 \text{ (Figure 3b)}) \quad (37)$$

where S and B have units of $\text{g C m}^{-2} \text{ d}^{-1}$ and g C m^{-2} , respectively. It should be noted that data in (1) and (36) were log-log transformed not primarily to improve r^2 (90% for (1) and (37) versus 86% for (36)) but to account for the fact that in oceans, low S and B values are much more frequent than high values. Given that the intercept of (36) is not significantly

different from zero (its standard error is >0.1), it follows that on average in oceans

$$S/B = 0.05 \quad (38)$$

This equation is interpreted using model equation (34)

$$S/B = 0.8 [\exp(p) - 1] = 0.05 \quad (39)$$

It follows from (39) that $p = \log_e 1.06 = 0.06 \text{ d}^{-1}$. Given that p refers to exportable phytoplankton production (that is, production minus euphotic zone heterotrophic community respiration and incorporation into the pelagic food web), $p = 0.06 \text{ d}^{-1}$ is a realistic average value for oceans, where phytoplankton specific growth rates range between approximately 0.1 and 2.5 d^{-1} (from *Goldman et al.* [1979], where doubling rates range between <0.1 and 3.8 d^{-1} ; see also *Eppley* [1981]). This indicates that the model is consistent with the natural situation. Hence, realistic conclusions can be derived from the model (following paragraphs).

As already mentioned in relation to (9) and (13), S can be estimated from either P or B , depending on data available. The different approaches are based on different assumptions. (1) When S is estimated directly from P , equation (2) shows that R and F are assumed to be functions of P . Departure from this assumption may be responsible for residual variation in models $S = f(P)$, which account for 52–94% of the variance in S [*Wassmann*, 1990]. (2) Estimation of S from PE (or P_{new}) assumes that the latter can be realistically determined at sea. Recent reports that nitrate-based P largely overestimates S [e.g., *Miquel et al.*, 1994] suggest that it may be difficult to actually estimate P_{new} in oceans (that is, part of NO_3 -based P does not belong to P_{new} , as already found by *Ward et al.* [1989]) and, hence, use P_{new} for estimating S . (3) Estimation of S from B assumes that the range of variation of $[\exp(pe)]$ is small relative to that of B (equation (13)). In oceans, B values ($\text{mg Chl } a \text{ m}^{-3}$) vary by a factor of $37 / 0.1 = 370$ [*Baines et al.*, 1994, Table 3], whereas S/B values (units of S and B as in (36) and (37)), vary by a factor of $0.20 / 0.009 = 22$ (from the 79 pairs of S and Chl data used by *Baines et al.* [1994] for computing average values in their Table 3; data provided to us by S.B. Baines and M.L. Pace (1996)). Given that $[\exp(p)] = [1.25 (S/B) + 1]$ (from (34)), it follows that the range of variation of $[\exp(p)]$ is $1.25 / 1.01 = 1.2$. Hence, the range of variation of $[\exp(pe)]$ is very small relative to that of B , so that the assumption underlying (13) is realistic for oceans. A potential problem with the biomass approach may be seen in the variations in phytoplankton Chl:C ratios (values in the literature range between 8 and 250 [*Frenette et al.*, 1994, and references therein]). However, changes in concentrations of intracellular $\text{Chl } a$ cause changes in specific production rates, so that lower Chl:C should be accompanied by lower pe . Hence, Chl would be the appropriate estimator of B for computing S . The model $S = f(B)$ accounts for 90% of the variance in S , over a wide range of marine production regimes (equation (1)). Most of the residual variation is likely caused by differences in p among production regimes.

As already discussed, all indirect approaches for estimating S suffer from uncertainties. One strategy for constraining the estimates of S would be to combine different approaches. Remotely sensed information may prove ideal for this. As explained in section 1, three variables may be successively derived from ocean color images: B , P and, less frequently, P_{new} .

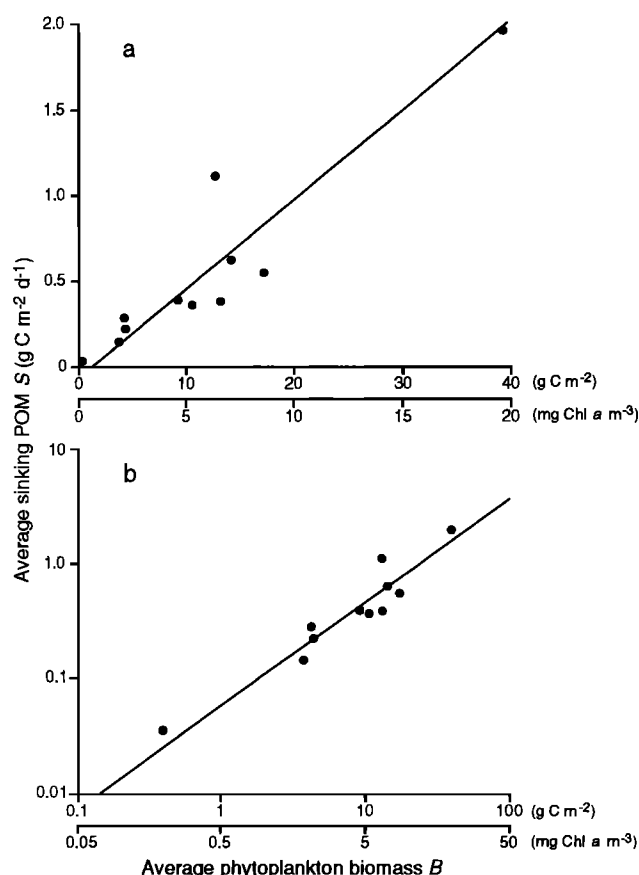


Figure 3. Average POM sinking from the euphotic zone (S) as a function of average phytoplankton biomass in the euphotic zone (B), for a wide range of marine production regimes. Data are from Table 3 of *Baines et al.* [1994], less a single value from the south California coast which they did not include in their calculation of (1). Major axis linear regressions (lines) are given for (a) nontransformed data (equation (36)) and (b) log-log transformed data (equation (37)). B is given in units of both $\text{mg Chl } a \text{ m}^{-3}$ (original data) and g C m^{-2} (see text). Points are 11 regional averages computed from 78 values.

Values of B could be used to obtain initial estimates of S (equation (1)). Additional estimates could be calculated from P , using empirical relationships $S = f(P)$. Finally, P_{new} values, when estimated, would provide further estimates. Comparison of several estimates could improve the values of S in oceans.

On the basis of empirical evidence (equation (1)), Baines *et al.* [1994] came to the conclusion that in oceans, S can generally be estimated from B . Simulations (Figure 2, equations (32) and (33)) support this empirical conclusion. The theoretical explanation is that in oceans, S is determined much more by B than by p . It follows that B is a robust estimator of S . Because the biomass approach rests on solid empirical and theoretical bases, it can be used as an additional means to constrain the estimates of S in oceans.

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