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Limnol. Oceanogr., 34(1), 1989, 188–198
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Computation of aquatic primary production: Extended formalism to include effect of angular and spectral distribution of light

Abstract—With a new spectral model of the underwater light field and an extended formalism for the light-saturation curve, it is shown that the angular distribution of underwater light has to be considered to account correctly for light absorption and utilization by algal cells. Neglecting the effect of angular distribution on the light absorbed by phytoplankton can lead to underestimation of primary production. For the stations studied as examples, the minimum correction required is 5–13% for daily, column-integrated production. For instantaneous primary production, the error is greater when the solar zenith angle is larger (higher latitudes, early morning, and late afternoon). In the extended formalism, models of photosynthesis based on light absorbed are shown to have a more rigorous foundation than those based on light available.

For modeling the response of phytoplankton assemblages to available light, the formalism of the light-saturation curve, with its associated parameters, is well established (Platt and Jassby 1976; Platt et al. 1977, 1982; Platt and Gallegos 1980; Gallegos and Platt 1981). The utility of the approach as a tool for estimating primary production from chlorophyll and light has been demonstrated in various recent studies (Côté and Platt 1984; Harrison et al. 1985; Herman and Platt 1986). The same formalism can be applied to the development of algorithms for extracting information on primary production from remotely sensed data (Platt 1986; Lewis et al. 1986; Platt et al. 1988).

Acknowledgments

This work was supported by a grant-in-aid from the Department of Ocean Development (New Delhi) to NIO (Goa). The necessary collaboration was greatly facilitated by the award of an NSERC (Canada) International Scientific Exchange Fellowship to S.S. Further NSERC support through an operating grant to T.P. is gratefully acknowledged.

We thank Carla Caverhill for help with computations and John Raven for advice.

In estimating primary production from chlorophyll and light, the angular distribution of the incident light has usually been suppressed, not least because of the lack of a simple mathematical model of the irradiance field suitable for applications in biological oceanography. Such a model, containing both angular and spectral dependence, is now available (Sathyendranath and Platt 1988), and we can evaluate the significance of the angular and spectral structure of the irradiance field for the estimation of primary production for a given chlorophyll profile.

We show here that the angular effect is not trivial. It pertains to both the direct and diffuse components of irradiance. It is greater when the direct component subtends larger zenith angles and when the chlorophyll profile is highly structured. Finally, it exposes a fundamental difference between descriptions of photosynthesis in terms of light available and those in terms of light absorbed by the cells. We illustrate the theory with examples calculated from field data representative of various oceanographic regimes.

Consider first the *conventional light-saturation formalism*. In a suspension of phytoplankton cells, the dependence of photosynthesis, P^B , on *available* light, I , can be written in the general form

$$P^B = f(I; \text{parameters}) \quad (1)$$

where the superscript indicates normalization to the chlorophyll biomass B . A variety of functional forms has been used for the function f , which is known as the light-saturation curve (Platt et al. 1977). If for simplicity we exclude consideration of photo-inhibition, exactly two parameters are required to specify the light-saturation curve.

Some latitude exists for their selection, but the following have become standard:

$$\alpha^B = \left. \frac{\partial P^B}{\partial I} \right|_{I=0} \quad (2a)$$

(the initial slope),

and

$$P_m^B = \lim_{I \rightarrow \infty} P^B(I) \quad (2b)$$

(the assimilation number).

The so-called photoadaptation parameter, I_k , important in the subsequent development, is not an independent parameter but can be derived as the ratio of the other two:

$$I_k = P_m^B / \alpha^B. \quad (3)$$

All of the published formulations of the light-saturation curve can be reparameterized in terms of α^B and P_m^B and shown to be equivalent (Platt et al. 1977). Equation 1 can then be restated as

$$P^B = f(I; \alpha^B, P_m^B). \quad (4)$$

The *spectral irradiance model*, presented by Sathyendranath and Platt (1988) can briefly be summarized here. For a given depth z , and wavelength λ , the total downwelling irradiance, $I(z, \lambda)$, is partitioned into a direct component, I_d , and a diffuse component (sky light), I_s :

$$I(z, \lambda) = I_d(z, \lambda) + I_s(z, \lambda). \quad (5)$$

(In the optical literature, irradiance is usually represented by the symbol E . For the present purpose, however, we retain the symbol I for consistency with usage in the primary production literature.)

We assume that irradiance at the sea surface, $I(0, \lambda)$, is given by the clear-sky model of Bird (1984). The vertical attenuation coefficients for the direct and diffuse components of irradiance, $K_d(z, \lambda)$ and $K_s(z, \lambda)$, are given by

$$K_d(z, \lambda) = \frac{a(z, \lambda) + b_b(z, \lambda)}{\cos \theta_d} \quad (6a)$$

and

$$K_s(z, \lambda) = \frac{a(z, \lambda) + b_b(z, \lambda)}{\langle \cos \theta_s \rangle} \quad (6b)$$

where $a(z, \lambda)$ is the volume absorption coefficient at wavelength λ and depth z , $b_b(z, \lambda)$

the corresponding backscattering coefficient, θ_d the sun zenith angle in water, and $\langle \cos \theta_s \rangle$ the mean cosine of the zenith angles of the diffuse light (θ_s) after refraction at the sea surface. In computing $a(z, \lambda)$, the contribution from phytoplankton pigments, $a_c(z, \lambda)$, is expressed as

$$a_c(z, \lambda) = a_c^*(\lambda)C(z) \quad (7)$$

where $a_c^*(\lambda)$ is the specific absorption coefficient for the pigments and $C(z)$ the local pigment concentration (expressed as sum of the concentrations of chlorophyll a and pheopigments).

We now extend the light-saturation formalism to encompass those phenomena arising from the dependence of I on θ and λ .

Consider first a *collimated light source at normal incidence*. Equation 4 can be restated as

$$P^B(z) = \int f[I(z, \lambda); \alpha^B(z, \lambda), P_m^B(z)] d\lambda \quad (8)$$

where the integral is taken over the photosynthetically active spectrum ($400 \leq \lambda \leq 700$ nm) and where we have assumed, in the absence of information to the contrary, that P_m^B is *spectrally neutral* (Pickett and Myers 1966). The wavelength-dependent initial slope $\alpha^B(z, \lambda)$ is that measured in monochromatic light, as by Duysens (1970). Examples of suitable data from natural assemblages of algae are given by Lewis et al. (1985a,b, 1986). Interactions between wavelengths, such as the Emerson enhancement effect, are ignored (cf. Sathyendranath et al. 1989).

Now consider a *collimated beam with zenith angle* θ_d after refraction at the surface. Equation 8 is then further elaborated as

$$P^B(z) = \int f[I(z, \lambda, \theta_d); \alpha^B(z, \lambda, \theta_d), P_m^B(z)] d\lambda. \quad (9)$$

Equation 9 need not be integrated over θ as we have assumed that I contains only one discrete angular component, θ_d . The angular dependence of α^B is to be determined next.

Recall that the quantum yield ϕ_m is defined by an expression similar to Eq. 2a, but in terms of light *absorbed*:

$$\phi_m = \left. \frac{\partial P}{\partial I_a} \right|_{I \rightarrow 0} \quad (10)$$

where I_a is the light absorbed by photosynthetically active pigment (Platt and Jassby 1976). Note that ϕ_m refers to the maximum *realized* quantum yield (obtained when I tends to zero) and not to the theoretical maximum *realizable* quantum yield. Note also that I refers to a flux per unit of area whereas I_a refers to energy absorbed per unit of volume. Comparison of Eq. 2a and 10 leads to the well-known result (Platt and Jassby 1976, p. 428; Kirk 1983, p. 243) that α is directly proportional to ϕ_m , the constant of proportionality being the optical absorption coefficient for phytoplankton. For normal incidence, therefore,

$$\alpha(z, \lambda) = \phi_m(z, \lambda) a_c^*(\lambda) B(z) \quad (11)$$

where the normalization of α has been written explicitly on the right-hand side. Use of B in Eq. 11 rather than C as in Eq. 7 ensures that we restrict the computation to absorption by photosynthetic pigments, to the exclusion of their degradation products.

Now for light of any zenith angle θ_d , absorption by phytoplankton in a thin layer of vertical extent dz is dI_a , where

$$dI_a = I(z, \lambda, \theta_d) a_c^*(\lambda) B(z) \sec \theta_d dz. \quad (12)$$

Hence, for light incident at angle θ_d to the zenith, the effective value of absorption is increased by a factor $\sec \theta_d$ over that for normally incident light. The value of α is increased by the same factor. In other words,

$$\alpha(z, \lambda, \theta_d) = \alpha(z, \lambda) \sec \theta_d. \quad (13)$$

The final result for a collimated beam of arbitrary zenith angle is then found by putting Eq. 13 into Eq. 9:

$$P^B(z) = \sec \theta_d \int f[I(z, \lambda, \theta_d); \alpha^B(z, \lambda), P_m^B(z)] d\lambda. \quad (14)$$

The next level of complexity concerns the *diffuse source*. Equation 9 becomes

$$P^B(z) = \int \int f[I(z, \lambda, \theta_s); \alpha^B(z, \lambda, \theta_s), P_m^B(z)] d\lambda d\theta_s. \quad (15)$$

Each and every angular component of Eq. 15 obeys Eq. 13. It will be convenient to have an alternative statement of Eq. 15 that is already integrated over θ . To do so, we follow the same sequence of arguments as in Eq. 10 through 14 except that in this case we base the absorption (Eq. 12) on Eq. 6b rather than 6a. Then, the analog of Eq. 13 is

$$\alpha(z, \lambda, s) = \alpha(z, \lambda) / \langle \cos \theta_s \rangle \quad (16)$$

where the symbol s denotes a diffuse source. It is clear that Eq. 13 is just a special case of Eq. 16.

It remains to determine $\langle \cos \theta_s \rangle$. The physical principle behind Eq. 6a and b is that the effective volume absorption coefficient increases as θ increases because of the increased path length of the photons for a given vertical excursion. For collimated light, the relevant factor is $\cos \theta_d$. For diffuse light, the relevant factor is $\langle \cos \theta_s \rangle$, the average of $\cos \theta$, weighted according to the angular distribution of the source, $L(\theta_s, \phi_s)$, where ϕ_s is the azimuthal angle (e.g. Kirk 1983). Hence

$$\langle \cos \theta_s \rangle = \frac{\int L(\theta_s, \phi_s) \cos \theta_s d\Omega}{\int L(\theta_s, \phi_s) d\Omega} \quad (17)$$

where $d\Omega = \sin \theta d\theta d\phi$ is an element of solid angle, and the integrations are taken over the upper hemisphere. The general expression for $P^B(z)$ in a diffuse light field is then

$$P^B(z) = \int f[I(z, \lambda); \alpha^B(z, \lambda), P_m^B(z), \langle \cos \theta_s \rangle^{-1}] d\lambda \quad (18)$$

where $I(z, \lambda)$ is the total downwelling irradiance due to the diffuse source.

In computing $\langle \cos \theta_s \rangle$, the problem is to evaluate Eq. 17, which is written in terms of the angular distribution of radiance in water given only the angular distribution of radiance in air. Let $L(\theta'_s, \phi'_s)$ be the distribution of diffuse radiance above water. Then, following Gershun (1939),

$$L(\theta_s, \phi_s) = n^2 L(\theta'_s, \phi'_s) \quad (19)$$

where n is the refractive index of water relative to air. Equation 19 disregards reflec-

tion losses at the interface. Noting that $d\Omega = \sin \theta \, d\theta \, d\phi$ and dropping the subscripts s we have

$$\langle \cos \theta \rangle = \frac{n^2 \int_0^{2\pi} d\phi' \int_0^{\pi/2} L(\theta') \cos \theta \sin \theta \, d\theta}{n^2 \int_0^{2\pi} d\phi' \int_0^{\pi/2} L(\theta') \sin \theta \, d\theta} \quad (20)$$

where axial symmetry is assumed. Now $\sin \theta = n^{-1} \sin \theta'$ and $\cos \theta = n^{-1} \cos \theta' \, d\theta'$ for refraction at a flat sea surface. Thus

$$\langle \cos \theta \rangle = \frac{\int_0^{\pi/2} L(\theta') \cos \theta' \sin \theta' \, d\theta'}{\left[n \int_0^{\pi/2} L(\theta') \sin \theta' \cos \theta' \times (n^2 - \sin^2 \theta')^{-1/2} \, d\theta' \right]} \quad (21)$$

Evaluation of Eq. 21 requires that we specify $L(\theta')$. A special case of Eq. 21 arises when the radiance distribution of the source is such that all angular contributions in $L(\theta'_s, \phi'_s)$ are equally represented. For this case $L(\theta')$ is constant and may be taken outside the integrals, such that

$$\langle \cos \theta \rangle = \frac{\int_0^{\pi/2} \cos \theta' \sin \theta' \, d\theta'}{n \int_0^{\pi/2} \cos \theta' \sin \theta' (n^2 - \sin^2 \theta')^{-1/2} \, d\theta'} \quad (22)$$

The substitution $x = \sin \theta'$ reduces the denominator to standard form and we find $\langle \cos \theta_s \rangle = 0.83$, or $\langle \cos \theta_s \rangle^{-1} = 1.20$.

We can now proceed to write down the production equation for *natural illumination* with its two components: direct sunlight I_d , and diffuse sky light I_s (Eq. 5). Let us first make explicit the functional form $f(I)$. We choose the equation of Smith (1936), which in nonspectral form is

$$P^B(z) = \frac{P_m^B [I(z)/I_k(z)]}{\sqrt{1 + [I(z)/I_k(z)]^2}} \quad (23)$$

Substituting from Eq. 3 and noting that $P(z) = B(z)P^B(z)$, we find

$$P(z) = \alpha(z)I(z) \cdot \left\{ 1 + \left[\frac{\alpha(z)}{P_m(z)} I(z) \right]^2 \right\}^{-1/2} \quad (24)$$

Applying this equation in the extended formalism with $I(z, \lambda)$ given by Eq. 5, we have

$$P(z) = \Pi(z) \{ 1 + [\Pi(z)/P_m(z)]^2 \}^{-1/2}, \quad (25)$$

with

$$\begin{aligned} \Pi(z) = & \sec \theta_d \int \alpha(\lambda, z) \times I_d(z, \lambda, \theta_d) \, d\lambda \\ & + \langle \cos \theta_s \rangle^{-1} \times \int \alpha(\lambda, z) I_s(z, \lambda) \, d\lambda \end{aligned} \quad (26)$$

where the first integral derives from Eq. 14 and the second from Eq. 18.

We will assume for simplicity of exposition (although the assumption is easily relaxed) that α and P_m do not vary with depth. With the further assumptions of equal angular weighting in air for the sky-light component and refraction at a flat sea surface, the final form of Eq. 26 is

$$\Pi(z) = \int \alpha(\lambda) [I_d(z, \lambda, \theta_d) \sec \theta_d + 1.20 I_s(z, \lambda)] \, d\lambda \quad (27)$$

We now proceed to estimate the *magnitude of the errors* that can be expected if the angular effect on α is neglected. To this end we computed primary production at 33 stations using archived data from various of our cruises in the North Atlantic, covering a range of conditions from oligotrophic to very productive waters (Table 1). For these stations, both in situ measurements of primary production and incubator-based measurements of photosynthetic parameters were available. Incubations were carried out in collimated light. Chlorophyll and phaeophytin profiles measured at each station were also used in the computations.

A single set of standard (nonspectral) photosynthetic parameters (P_m^B and α^B) was assigned to data from each locality, based on the observations in that area. To construct the $\alpha^B(\lambda)$ values required for the computations, we took the *shape* of $\alpha^B(\lambda)$ to be

Table 1. Stations for which daily primary production ($\text{mg C m}^{-2} \text{ d}^{-1}$) was calculated. Results of calculation shown for both the extended formalism, Eq. 27, and restricted formalism (θ dependence suppressed). The last column gives the percent correction that must be applied to the result of restricted calculation to bring it up to value computed by extended formalism.

Position		Daily production		Correction (%)
		Restricted	Extended	
14°39.3'N, 64°54.0'W	3 Dec 84	184	202	9.5
14°38.6'N, 64°55.2'W	5 Dec 84	282	306	8.3
14°38.5'N, 65°00.0'W	6 Dec 84	334	363	8.9
75°45.9'N, 80°30.0'W	16 Aug 83	978	1,080	10.3
76°03.5'N, 82°20.0'W	18 Aug 83	2,320	2,550	9.8
76°07.0'N, 82°22.0'W	20 Aug 83	868	979	12.8
74°21.0'N, 81°49.0'W	24 Aug 83	428	477	11.5
73°52.9'N, 81°46.5'W	25 Aug 83	319	340	6.4
74°22.0'N, 82°30.0'W	26 Aug 83	276	305	10.3
76°14.7'N, 82°45.0'W	28 Aug 83	442	493	11.6
76°15.8'N, 82°36.5'W	29 Aug 83	249	275	10.6
72°12.0'N, 65°40.0'W	6 Sep 83	233	260	11.7
76°04.5'N, 82°12.0'W	13 Sep 83	264	288	8.9
76°03.0'N, 82°24.0'W	14 Sep 83	485	522	7.6
43°54.3'N, 49°08.0'W	13 Oct 84	1,720	1,840	7.0
43°57.8'N, 49°05.5'W	14 Oct 84	1,690	1,810	6.8
43°54.5'N, 49°10.4'W	15 Oct 84	733	783	6.8
43°48.5'N, 49°01.6'W	16 Oct 84	579	617	6.6
35°20.0'N, 62°32.0'W	13 Oct 83	144	152	5.3
35°20.0'N, 62°32.3'W	16 Oct 83	174	183	5.2
35°18.9'N, 62°32.6'W	17 Oct 83	187	197	4.9
35°19.7'N, 62°30.6'W	18 Oct 83	200	210	4.9
35°19.9'N, 62°31.9'W	19 Oct 83	174	183	5.1
36°55.7'N, 58°53.9'W	15 Jun 87	95.9	106	10.5
34°35.1'N, 56°52.8'W	18 Jun 87	144	159	10.2
34°33.0'N, 56°51.1'W	19 Jun 87	194	214	10.1
34°49.4'N, 56°36.6'W	21 Jun 87	179	197	10.0
34°39.8'N, 54°15.6'W	23 Jun 87	176	194	10.3
34°39.5'N, 54°13.7'W	24 Jun 87	163	180	10.1
34°34.7'N, 50°56.0'W	28 Jun 87	166	183	10.3
34°35.9'N, 50°59.1'W	29 Jun 87	150	164	10.0
31°58.2'N, 55°38.2'W	2 Jul 87	102	112	10.0
31°57.6'N, 55°37.8'W	3 Jul 87	103	113	10.1

invariant (Lewis et al. 1986, figure 7; Sathyendranath et al. 1989) but scaled the *magnitudes* for each locality such that the mean value was equal to the nonspectral value of α^B assigned to that locality.

For the location and date appropriate to each station, surface irradiance was calculated according to Bird (1984) and the underwater irradiance field constructed using Eq. 6a and b and the observed chlorophyll profiles as described in Sathyendranath and Platt (1988). Primary production was computed for each station using the spectral model as in Eq. 27. We also computed primary production with Eq. 27 but with the effect of angular distribution on α suppressed. The measurements in the arctic

were made on days of heavy cloud cover such that the clear-sky model grossly overestimated light at the sea surface. This was also true of one of the stations on the Grand Banks. Therefore, the estimated production for these stations was multiplied by the ratio of the measured irradiance to the estimated clear-sky irradiance at the surface as a rough correction for cloud effect.

In evaluating the *time dependence* of errors, we found in a sample calculation that the error is maximum (around 16%) in early morning when solar elevation is low and minimum at local noon (about 5%) when solar elevation is maximum (Fig. 1). The error in daily integrated production in this example is 8.7%. The correction that should

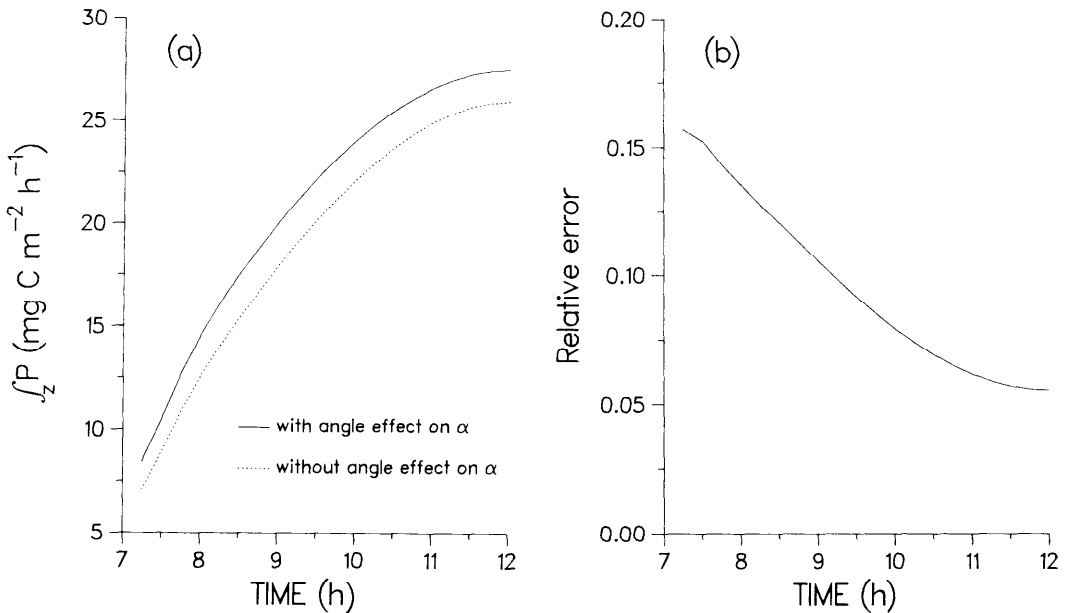


Fig. 1. a. Computed values of column-integrated primary production (hourly), for a station in the tropical Atlantic ($14^{\circ}39.3'\text{N}$, $64^{\circ}54.0'\text{W}$) occupied on 3 December 1984. Continuous line—the computed production (P_1) takes into account the dependence of α on the angular distribution of underwater light field. Dotted line—the computed production (P_2) does not account for angular dependence of α . b. Relative error in estimated production arising from neglecting the angular dependence of α , computed as $(P_1 - P_2)/P_1$.

be applied to *daily integrated* production to allow for the effect of the angular structure of the irradiance field on light absorbed by phytoplankton (see Table 1) varied from 5 to 13% among the 33 stations.

When the daily primary production, estimated with the angular spectral model, was regressed against measured production at these stations (Platt and Sathyendranath 1988, Fig. 1) a near one-to-one relation between the quantities was found. This result is promising, considering that the measured and computed values are strictly independent estimates of primary production. It should also be stressed that the specific absorption and scattering coefficients in the optical model were not tuned to suit local conditions, although they could be if additional information were available (Sathyendranath and Platt 1988).

The effect of angular distribution on α is not the only way that the angular structure of the underwater light field influences the magnitude of primary production. As discussed elsewhere (Sathyendranath and Platt 1988), the vertical attenuation coefficient K and the effective absorption coefficient of

phytoplankton a_E^* are both dependent on the angular distribution of the light field. However, these two effects have been taken into account here in the computation of available light at depth for estimating primary production with and without the angular dependence of α . In other words, the 5–13% correction to daily production stated in this section is due to the effect of angular distribution on α alone, *over and above any effects of angular distribution on the structure of the underwater irradiance field*.

Note also that the 5–13% error that we have been discussing is a *systematic error*. Neglecting to make the correction will always lead to an *underestimate* of primary production. In this respect its effect is to be distinguished from those of *random errors* in the estimation of α^B , P_m^B , and B . Note further that our estimate of this systematic error is *conservative*. We have calculated the *minimum possible* spread in the submarine light field (clear sky, flat ocean, and minimum turbidity). A rough sea surface, a cloudy sky, or multiple scattering in the water column (i.e. more turbid water) could render the submarine light field more diffuse

than we have assumed. The effect of the angular term would then be greater than we have estimated.

We now turn to an *interpretation* of the results presented above. We consider first the *distinction between light available and light absorbed*. Our analysis reveals a fundamental difference between formulations of the light-saturation curve in terms of light available and those in terms of light absorbed: the former are insensitive to the angular distribution of the light field and can lead to errors in estimating in situ production, except in the case where the light is incident normally to the free surface of the medium (approximated most closely at local noon with a cloud-free sky). The problem arises from using photosynthesis parameters measured in the laboratory for estimating production in nature. In the incubator, if the light is not incident at right angles to the sample, α will be overestimated unless the angle of incidence is taken into account in the computations. Then, even if α is known exactly, in situ production will be estimated incorrectly if the angular distribution of the light field is not taken into account. A scalar quantity, "available" light, is a sufficient descriptor of the light field for estimating in situ production from α if and only if the geometry of the in situ light field is identical in all respects to that in the incubator in which α is measured. Otherwise a correction must be applied.

On this analysis, formulation of the light-saturation curve in terms of light absorbed must be considered a more fundamental and a more rigorous approach than formulation in terms of light available (but nevertheless does not remove the obligation to take the angular distribution of the light field into account). Absorbed-light models separate what is a single property in available-light models into two properties: the biological property (quantum yield) is separated from the physical process (light absorption). The parameter α is a property of a sample. The product $\phi_m a_c^* B \sec \theta$ (Eq. 11) depends on the properties of the organisms (ϕ_m , a_c^* , B) and on the structure of the light field ($\sec \theta$). The apparatus for calculating production from an available-light model cannot assimilate information on the angular distri-

bution of the light field: it is indifferent to the direction from which the photons arrive.

On the other hand, absorbed-light models do have the ability to respond to the angular structure of the light field and if carefully applied can give unbiased estimates of in situ production. The results of such calculations show the correction factors that should be applied to the available-light models.

Although we conclude that ϕ_m models are more fundamental than α models, the fact remains that ϕ_m is not a directly observable property of a phytoplankton sample. The only avenue available at present to estimate ϕ_m is via measurements of α and a_c^* for the same sample. The importance of invoking Eq. 10 is that it leads to a procedure for correcting α according to the angular structure of the irradiance field. As a directly measurable property of a sample, α retains an importance at present denied to ϕ_m . The possibility exists, however, that in the future ϕ_m may be more directly measurable, for example by photoacoustic methods (Ortner and Rosencwaig 1977; Trees and Voss 1987) or by observations of solar-stimulated chlorophyll fluorescence (Topliss and Platt 1986).

We consider next the *choice of vector or scalar irradiance* as forcing variable. In the presentation of the theory, it has been assumed that the light available is given by the downwelling *vector* irradiance, i.e. the irradiance on a diffusing flat plate collector facing vertically upward. This quantity is related to the downwelling *scalar* irradiance \dot{I} through the equation

$$I(z, \lambda, \theta) = \dot{I}(z, \lambda, \theta) \cos \theta \quad (28)$$

in the case of a collimated beam incident at angle θ . For diffuse light, $\cos \theta$ will have to be replaced in Eq. 28 by $\langle \cos \theta \rangle$. Phytoplankton absorption per unit of vertical distance, given by Eq. 12, can be rewritten in terms of scalar irradiance as follows:

$$\begin{aligned} dI_a &= \dot{I}(z, \lambda, \theta) \cos \theta a_c^*(\lambda) B(z) \sec \theta dz \\ &= \dot{I}(z, \lambda, \theta) a_c^*(\lambda) B(z) dz. \end{aligned} \quad (29)$$

In other words, phytoplankton absorption of vector irradiance for a unit vertical distance is equivalent to their absorption of

scalar irradiance for the same distance but measured in the direction of the beam. Notice that in the equation for absorption as rewritten in terms of scalar irradiance the $\cos \theta$ terms cancel each other. The same is true in the production equation (Eq. 25). This fact might suggest that one way of avoiding the problems arising from angular distribution of the light field would be to measure or compute scalar irradiance instead of vector irradiance. The vertical attenuation coefficient for scalar irradiance (K) would still contain the $\cos \theta$ term, however, such that the angular distribution would nevertheless have to be taken into account.

Note that this issue is different from whether phytoplankton *collect* vector or scalar irradiance. Kirk (1983) has suggested that it is more appropriate to use scalar rather than vector irradiance to quantify light available, since phytoplankton are randomly oriented in water and therefore would not have a preferred angle for light absorption (vector irradiance for downwelling light favors the downward direction). If, therefore, available light were taken to be scalar irradiance, the $\cos \theta$ terms in the equations for absorption and photosynthesis would not be self-canceling.

Another point to note is that, if reflection losses are neglected, vector irradiance in air is conserved after refraction at the sea surface, whereas scalar irradiance is reduced. With

$$I = \int L(\theta, \phi) \cos \theta \, d\Omega,$$

comparison of the numerators in Eq. 17 and 21 in Table 1 shows that irradiance is invariant with refraction. Given that

$$\dot{I} = \int L(\theta, \phi) \, d\Omega,$$

comparison of the denominators of the same equations shows that refraction reduces the scalar irradiance by a factor $= n[(1 - \sin^2 \theta') / (n^2 - \sin^2 \theta')]^{1/2}$, where θ' is the zenith angle in air. If we assume the sky radiance to be uniformly diffused and the sea surface to be flat, the consequence is a reduction in scalar irradiance by a factor of 40% after refraction at the sea surface.

We next consider the *time dependence* of α . When the angular structure of the light field is taken into account, the effective α depends on the zenith angle of the sun (Eq. 13). Because the solar angle is a function of time, Eq. 13 implies that the effective value of α is also time-dependent. It will be a decreasing function of time from dawn to noon. Hence, estimates of daily photosynthesis where $P(z, t)$ is integrated over time will be biased if α is not corrected for angular effects. The appropriate equation for $P(z, t)$ is Eq. 26 with $\sec \theta = \sec \theta(t)$ to represent the direct sunlight component of total downwelling irradiance.

Note that the angular correction to α described above is not the same as the variation on a 24-h time scale of α measured in incubators (MacCaull and Platt 1977) where the geometry of the light source used to measure α is fixed and any time dependence observed in α is presumably a response of the cells themselves, either in ϕ_m or in a_c^* (change in numbers or structure of chloroplasts). Typically this variation (increasing α from dawn to noon) is in the opposite sense to that arising from angular effects.

We now consider *deviation* from the assumption that the radiance in air has *equiangular distribution*. If $L(\theta')$ is not uniform, it cannot be taken outside the integrations in Eq. 21. For example, it is often found that $L(\theta')$ is a cardioidal distribution with $L(\theta') \propto (1 + 2 \cos \theta')$. In this case,

$$\begin{aligned} \langle \cos \theta_s \rangle &= \frac{\int_0^{\pi/2} (1 + 2 \cos \theta') \cos \theta' \sin \theta' \, d\theta'}{\left[n \int_0^{\pi/2} (1 + 2 \cos \theta') \cos \theta' \right.} \\ &\quad \left. \times \sin \theta' (n^2 - \sin^2 \theta')^{-1/2} \, d\theta' \right]}. \end{aligned} \quad (30)$$

The numerator reduces immediately to two standard forms. The denominator is reduced to standard forms by the substitutions $x = \sin \theta'$ for the first integral and $x = \cos \theta'$ for the second. We then find $\langle \cos \theta_s \rangle = 0.85$ (cf. Morel and Prieur 1975), very little different from the result for the uniform distribution.

Another plausible case is that where the

angular distribution of radiance is *uniform in water*.

In this case, from Eq. 17,

$$\langle \cos \theta_s \rangle = \frac{\int_0^{\pi/2} \cos \theta \sin \theta \, d\theta}{\int_0^{\pi/2} \sin \theta \, d\theta} = 0.5. \quad (31)$$

It is to be noted that a rough sea surface would permit light to enter the sea at angles greater than the critical angle. Multiple scattering in the sea would also increase the spread of the light rays beneath the water. As a consequence of both these factors, the underwater radiance distribution would tend toward the uniform distribution discussed here. In very turbid waters, it may be more appropriate to use this approximation rather than either of the first two cases discussed here (see Kirk 1983). Note that in the case of multiple scattering within the vertical depth increment considered (Δz) it may be necessary to consider $\langle \cos \theta \rangle$ even lower than 0.5 to account for the increased path length.

We now turn to the *depth dependence* of $\langle \cos \theta_s \rangle$. In the presentation of our model, we have treated $\langle \cos \theta_s \rangle$ as a depth-independent parameter. Strictly speaking, $\langle \cos \theta_s \rangle$ is not independent of depth. As diffuse light penetrates water, rays with a near-vertical path will be attenuated less than those with paths closer to the horizontal. The radiance distribution will therefore change progressively until an "asymptotic radiance distribution" is reached in deep waters (e.g. Preisendorfer 1959; Tyler 1960), with a maximum toward the zenith and symmetry around the maximum. Beam spreading due to scattering also contributes to changing $\langle \cos \theta_s \rangle$ with depth and modifies the partition of incident light between direct and diffuse components. To describe such changes, we would have to do the book-keeping for light under water in terms of radiance at every angle rather than in terms of total downwelling irradiance. This requirement would add considerably to the complexities of the computations. But generally, depth dependence of $\langle \cos \theta_s \rangle$ for downwelling light has been found (both theoretically and experimentally) to be small for oceanic waters (Preisendorfer 1976; Prieur 1976), and depth-independent $\langle \cos$

$\theta_s \rangle$ is often a valid and useful approximation. It should, however, be used with caution in very turbid waters (Kirk 1983).

Finally we consider the special case of a *uniform biomass profile*. If the biomass profile and the photosynthetic parameters were uniform with depth, the computations could be simplified, if one were interested in only the column-integrated production rather than production at every depth. In this case, it can be shown that the fraction of incident light that is absorbed and stored by phytoplankton in the water column remains the same, irrespective of the angle of incidence. To demonstrate this equality, let us consider two cases: (1) light is incident at an angle θ just below the surface, and (2) light is incident normally. If z_{p1} is the euphotic depth in case 1, and z_{p2} that of case 2, then $z_{p2} = z_{p1} \sec \theta$. If K is the vertical attenuation coefficient for normal incidence, it is $K \sec \theta$ for the oblique incidence case. Let us divide the euphotic zone into an equal number of layers in both the cases. If the thickness of each layer is Δz in case 1, it is $\Delta z \sec \theta$ in case 2. The light incident at the top of the $n + 1$ th layer would be $I(z) = \exp(-Kn\Delta z \sec \theta)$ in both cases. Also, the light absorbed by the $n + 1$ th layer would be $dI_a = I(z)a_c^*C(z)\Delta z/\cos \theta$ in both cases. Thus, in the uniform distribution case, it would be possible to compute total water-column production without taking the angular distribution into account. Such simplifications would not be possible if the water column were not uniform in optical and photosynthetic parameters.

A requirement in present-day biological oceanography is the estimation of primary production in the ocean water column at large horizontal scale. It can be done most readily through applying an irradiance model to a remotely sensed biomass field (Platt and Sathyendranath 1988; Sathyendranath et al. 1989). We have shown that a systematic error will be incurred in the estimation if we ignore the dependence of the initial slope α on the angular distribution of the light field. In cases where it may be necessary to apply a rough and ready correction to estimated production, a rule of thumb might be to add 10% to conventional production estimates to account for angular effects on α . Such corrections would

apply to all computations of primary production from available light, including those where the light saturation function is a process model used as part of a general ecosystem model, those where primary production has to be estimated from oceanographic station data on pigments, as well as those in the remote-sensing context.

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Submitted: 22 February 1988

Accepted: 17 August 1988

Revised: 2 November 1988

Limnol. Oceanogr., 34(1), 1989, 198–205
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A steady state description of growth and light absorption in the marine planktonic diatom *Skeletonema costatum*

Abstract—Studies of the marine diatom *Skeletonema costatum* indicate that for a given irradiance and day length, increases in the rate of supply of a limiting nutrient cause linearly proportional increases in the growth rate and the Chl:C ratio. For a given irradiance, increases in day length cause decreases in the Chl:C ratio, and the growth rate is linearly proportional to the product of day length and the Chl:C ratio. For a given day length, increases in irradiance cause decreases in the Chl:C ratio and quantum yield, and the growth rate and irradiance are curvilinearly related.

These observations are incorporated into a formulation of steady state growth, which includes day length, irradiance, and the Chl:C ratio, and two coefficients, which are the product of the maximal quantum yield and the specific absorption coefficient and the product of the average absorption cross section of the photosynthetic unit and the minimal rate of turnover of the unit. The photosynthetic quantum yield is represented by a Poisson distribution and is a function of irradiance alone.

Present ability to predict rates of primary production of marine phytoplankton from

Acknowledgments

We thank D. Slagstad for the best-fit analysis of the data to the model and O. Holm-Hansen, J. Mork, B. G. Mitchell, and M. Vernet for discussions and criticisms of the manuscript.

Research was financed by Norwegian Research Council for Science and the Humanities grant D.5573.004 (E.S.), and by NASA grant NAGW-317 and Office of Naval Research grant 00014-87-K-0287 (D.A.K.).

Contribution 241, Trondhjem Biological Station.

measurements of parameters such as the concentration of chlorophyll, temperature, nutrient concentration, and incident light has been limited by a lack of knowledge about the interactive effects of these parameters on growth and photosynthesis. This limitation is particularly restrictive to all large-scale oceanographic studies in which the direct measurement of primary production is too time-consuming to provide good spatial or temporal coverage. In particular, the ability to estimate primary production from maps of temperature, chlorophyll concentration, and incident light available from satellite imagery will depend on an adequate description of the relationship between growth rate and light absorption.

To better understand the interactive regulation of phytoplankton growth, we have examined variations in the growth rate and chemical composition of the marine centric diatom *Skeletonema costatum* (Grev.) Cleve under a wide range of irradiances, day lengths, and rates of nutrient supply. *Skeletonema costatum* is a prominent species in most coastal waters and fjords (Steemann Nielsen and Jørgensen 1968) and is the most prominent phytoplankton species in the Trondheimsfjord (63°N), where it is exposed to extreme seasonal fluctuations in irradiance, day length, and nutrient supply (Sakshaug and Andresen 1986; Sakshaug and Olsen 1986). Variation in day length is particularly important at high latitudes; for