The bio-optical state of ocean waters and remote sensing[1]

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Abstract

The diffuse attenuation coefficient for irradiance, K_T, is a physical measure of the bio-optical state of ocean waters. From an analysis of irradiance, K_T, and pigment concentration, the specific attenuation due to chlorophyll-like pigments is found to be 0.016 ± 0.003 [m^{-1} (mg pigment m^{-3})$^{-1}$]. The bio-optical state of ocean waters can be remotely sensed by spacecraft sensors. K_T is readily measured at sea and is highly correlated with and dependent on the chlorophyll-like pigment concentration, C_K. This pigment concentration and K_T provide a measure of the fraction of radiant energy attenuated by phytoplankton. This fraction, in turn, is closely related to the production equations formulated by Bannister and can be directly incorporated into a general theory of phytoplankton dynamics. C_K may also be used as an index of primary productivity. The determination of the bio-optical state of ocean waters by surface vessel provides direct information concerning the productivity of these waters; to the extent that the bio-optical state can be determined by satellite, it may be possible to examine important parameters of the marine ecosystem rapidly and repeatedly.

The remote sensing from spacecraft of the upwelling spectral radiant energy from the ocean's surface makes it possible to determine marine pigment concentrations due to phytoplankton. This, in turn, suggests the potential for obtaining rapid worldwide assessments of primary productivity over time scales required to link this productivity to commercially important fisheries. Continuous worldwide data on ocean productivity would assist synoptic ecological studies of ocean regions of special interest, provide otherwise unattainable data for the dynamic modeling of phytoplankton, and allow for the continuous monitoring of variations in productivity.

If these expectations for remote sensing are to be fully realized, technical methods for detecting and analyzing the upwelling radiant energy must be perfected and relationships between ocean optical properties and the biological parameters affecting these optical properties must be quantitatively investigated. Possible techniques for detecting upwelling spectral radiant energy from the ocean and the relationship of this signal to ocean optical properties have been discussed (Clarke et al. 1970; White 1969; Arvesen et al. 1971; Mueller 1976). We here describe the relationships between the optical properties of ocean waters and the biological properties influencing them.

We introduce the concept of "bio-optical state" to represent a measure of the total effect of biological processes on the optical properties of natural waters. It is the bio-optical state of ocean waters that can be remotely sensed by means of spacecraft sensors. The studies reported below indicate that the bio-optical state can be usefully related to the concentration of chlorophyll *a* and primary productivity. A complete analysis of the bio-optical state of natural waters requires consideration of the optical properties as a function of wavelength. However, to present general concepts and to compare our results with those of previous workers, we will consider here only total quanta or total energy. The spectral characteristics of the bio-optical state are discussed by Smith and Baker (1978).

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Bio-optical state of ocean waters

Biological constituents, particularly phytoplankton pigments and associated degradation products, play a significant role in determining the optical properties of natural waters. The combined effect of the absorption and scattering due to suspended and dissolved biogenous material establishes the bio-optical state of these waters. The concept of a bio-optical state will prove useful to the extent that diverse constituents in natural waters can be described by a few optical parameters which represent a meaningful average status of the biological material in the ocean water at a particular time and place.

The total diffuse attenuation coefficient for irradiance can be used to describe physically the bio-optical state of ocean waters as determined from Eq. 1:

$$K_T = K_W + k_c \times C + K_x, \qquad (1)$$

where K_T (m^{-1}) is the total diffuse attenuation coefficient for irradiance, K_W (m^{-1}) = 0.027 m^{-1} is the diffuse attenuation coefficient for clear ocean waters (e.g. Sargasso Sea), k_c [m^{-1} (mg pigment m^{-3})$^{-1}$] is the specific attenuation coefficient for irradiance due to plankton (chlorophyll-like) pigments, C (mg pigments m^{-3}) is the concentration of chlorophyll a and pheopigments in the water column, and K_x (m^{-1}) is the contribution to attenuation not directly attributable to chlorophyll-like pigments.

We chose K_T to characterize the bio-optical state of ocean waters for several reasons. First, many workers (Riley 1956; Holmes 1965; Aruga and Ichimura 1968; C. Lorenzen 1972) have demonstrated a strong correlation between the total diffuse attenuation coefficient for irradiance, K_T, and Chl a concentration. Second, Gordon and McCluney (1975) have shown that about 90% of the diffusely reflected irradiance originates from <1 attenuation length, i.e. a depth such that

$z = K_T^{-1}$. Third, K_T is the optical parameter relating irradiance just beneath the ocean surface, $E(0)$, to irradiance at depth, $E(z)$:

$$E(z) = E(0) e^{-(K_T z)}. \qquad (2)$$

Fourth, Preisendorfer (1976) has shown that K_T can be related, by means of the theory of radiative transfer, to the radiant energy reflected from the upper layer of the ocean. Thus K_T can be linked to the signal available to a remote sensor.

Techniques for determining K_T experimentally, by measuring energy or quanta as a function of depth, have been developed (Jerlov and Nygård 1969; Tyler and Smith 1966, 1970; Smith 1969; Smith and Wilson 1972; Booth 1976) and are widely used.

Because the concentration of chlorophyll in ocean waters adds a component to the total diffuse attenuation coefficient, the remotely sensed chlorophyll signal is derived from a depth in the ocean that depends on the chlorophyll concentration itself. In order to compare waters of various chlorophyll concentrations consistently we define

$$C_K = \frac{1}{K_T^{-1}} \int_0^{K_T^{-1}} C(z) \cdot dz, \qquad (3)$$

where C_K is the average chlorophyll concentration in the water column to a depth of 1 attenuation length K_T^{-1}, and $C(z)$ is the chlorophyll concentration (in mg m^{-3}) at depth z (in m). C_K will directly influence K_T and, hence, the upwelling remote signal and thus provides a link between the physical measurements and the biological status of ocean waters.

Data and methods

The data used for these studies are summarized in Table 1. Optical and related biological and oceanographic data appropriate for remote sensing studies, obtained by the Visibility Laboratory on several cruises (Fresnel I and II, Discoverer Expedition), are referred to as "Vis Lab" data in the discussion below and are distinguished by the inclusion of complete spectral irradiance measure-

ments made with the Scripps spectrora-diometer (Tyler and Smith 1966, 1970). Fresnel I and II data are from the Gulf of California, a subtropical area with exceptionally high rates of primary productivity (Zeitzschel 1969). Data from the Discoverer Expedition are from the Sargasso Sea, Gulf of Mexico, and central eastern Pacific and are characteristic of very low to moderately productive waters. The Climax data are from the central Pacific Ocean. Climax I data were taken from the gyrelike circulation of the North Central Pacific Water mass. On Climax II, data were obtained in both the North and South Pacific Central Water masses. These data are representative of the large gyrelike areas of the world's oceans (McGowan 1974; McGowan and Williams 1973). Data from the Southern California Bight Studies obtained by the Food Chain Research Group (R. W. Eppley pers. comm.) include upwelling areas and are characteristic of productive coastal waters.

For these data chlorophyll *a* and pheopigments were determined by the fluorescence technique outlined by Strickland and Parsons (1968). The rate of assimilation of carbon by phytoplankton was estimated from the ^{14}C method as outlined by Strickland and Parsons (1968), generally with a half-day incubation period. Detailed descriptions of methods are given in the cruise data reports (Climax I 1974: Scripps Inst. Oceanogr. Ref. 74-20; Climax II 1975: Scripps Inst. Oceanogr. Ref. 75-6; Discoverer Exped. 1973: Scripps Inst. Oceanogr. Ref. 73-16).

K_T (as well as K_W for clear ocean waters) was calculated by fitting a straight line to data of the total quanta (measured directly or calculated from spectral irradiance) vs. depth (from the surface to roughly the 1% irradiance level). This procedure, while providing a single parameter with which to characterize ocean waters, is an oversimplification since it assumes the water column is homogeneous with depth, ignores the fact that K_T is an apparent, rather than inherent, optical property of the water (Preisendorfer 1976),

Table 1. Cruises, general locations, and number of measurements used.

Cruise	Location	K_T	Pigments	Primary Productivity
Fresnel I 28 Nov – 13 Dec 68	Gulf of Calif.	12	12	11
Discoverer 3 May – 3 Jun 70	Sargasso Sea	3	3	1
	Gulf of Mexico	7	7	5
	Cent. E Pacific	11	11	11
Fresnel II 16 – 31 Mar 71	Gulf of Calif.	11	8	5
Climax I 19 – 25 Sep 69	Cent. N Pacific	–	7	7
Climax II 27 Aug – 8 Oct 69	Cent. N & S Pacific	–	16	16
SCBS1 14 – 18 Sep 74	California coastal waters	12	15	15
SCBS2 26 Feb – 5 Mar 75	California coastal waters	15	14	15
SCBS3 16 – 24 Jun 75	California coastal waters	13	13	14
SCBS4 6 – 14 Sep 75	California coastal waters	15	15	15
SCBS5 2 – 10 Dec 75	California coastal waters	17	17	17

and ignores effects caused by changes in spectral irradiance with depth. In spite of these limitations, the procedure is consistent, widely used, and provides a good first-order estimate for the parameter that characterizes the depth dependence of total quanta. Further, the use of a single K_T to characterize the optical property of the water column to the euphotic depth is consistent with the accuracy of the biological data used.

K_T *and pigment concentration*

Riley (1956), Aruga and Ichimura (1968), and C. Lorenzen (1972) have developed analytical formulae to relate K_T and the average chlorophyll concentration in the water column. Figure 1 gives their results, plotted in terms of attenuation length vs. log chlorophyll concentration. We show below that a linear fit can be found between K_T and C_K only when nonlinear biological effects are taken into account. Until this is done, the data
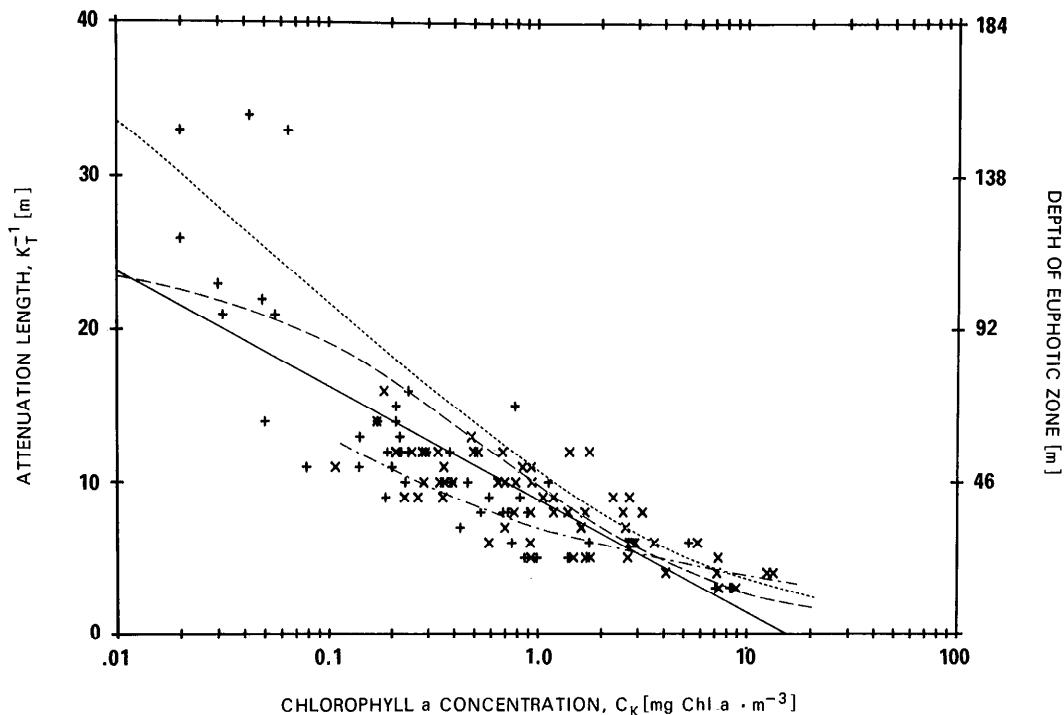
Fig. 1. Attenuation length vs. log average Chl a concentration. Data points are from cruises listed in Table 1 (+—Vis Lab data, ×—SCBS data); solid line is least-squares fit to these data (number of data points, $N = 108$; linear correlation coefficient, $r = 0.806$; probability that observed data could have come from uncorrelated parent population, $P_c < 0.01$: *see* Bevington 1969); dashed lines show previous results (— — — Riley 1956; - - - - Aruga and Ichimura *cited in* Takahashi and Parsons 1972; - — - — - C. Lorenzen 1972).

Riley's analysis based on open ocean observations in western North Atlantic (Sargasso Sea, New England coast, Georges Banks) with range of Chl a concentrations of about 0.02–20 mg m^{-3}; Aruga and Ichimura's data obtained in western North Pacific (Kuroshio and Oyashio Current areas) with chlorophyll ranges from 0.01–50 mg m^{-3}; Lorenzen's data obtained on cruises in both Pacific and Atlantic oceans (including upwelling regions off Peru and Southwest Africa) with chlorophyll ranges of about 0.04–28 mg m^{-3}.

If compensation depth taken to be depth at which there is 1% of surface radiation, then euphotic depth, z_e is equal to 4.61 K_T^{-1} (since $e^{-4.61} = 0.01$). Thus vertical axis may be plotted as attenuation length (K_T^{-1}, left-hand scale) or as depth of euphotic zone (z_e, right-hand scale).

shown in Fig. 1 should not be used to calculate the parameters of Eq. 1. Our own data, added to Fig. 1, are represented by the analytical equation

$$K_T^{-1} = 8.78 - 7.51 \log C_K, \qquad (4)$$

which shows the same strong correlation between K_T^{-1} and chlorophyll concentration observed by previous workers. Figure 1 presents data from a variety of oceanographic areas covering the full range of ocean chlorophyll concentrations and indicates that the relationship between K_T^{-1} and log C_K is widely appli-

cable. It should be noted, however, that the data came from waters whose dissolved and suspended material was largely of biogenous origin. Areas primarily affected by terrigenous material were not included.

While we can imagine many ways in which surface chlorophyll, C_o (or C_K as defined by Eq. 3), can give an ambiguous measure of total chlorophyll, C_T, the important issue is the actual relationship measured between these variables. We take the total average chlorophyll concentration in the water column to the eu-
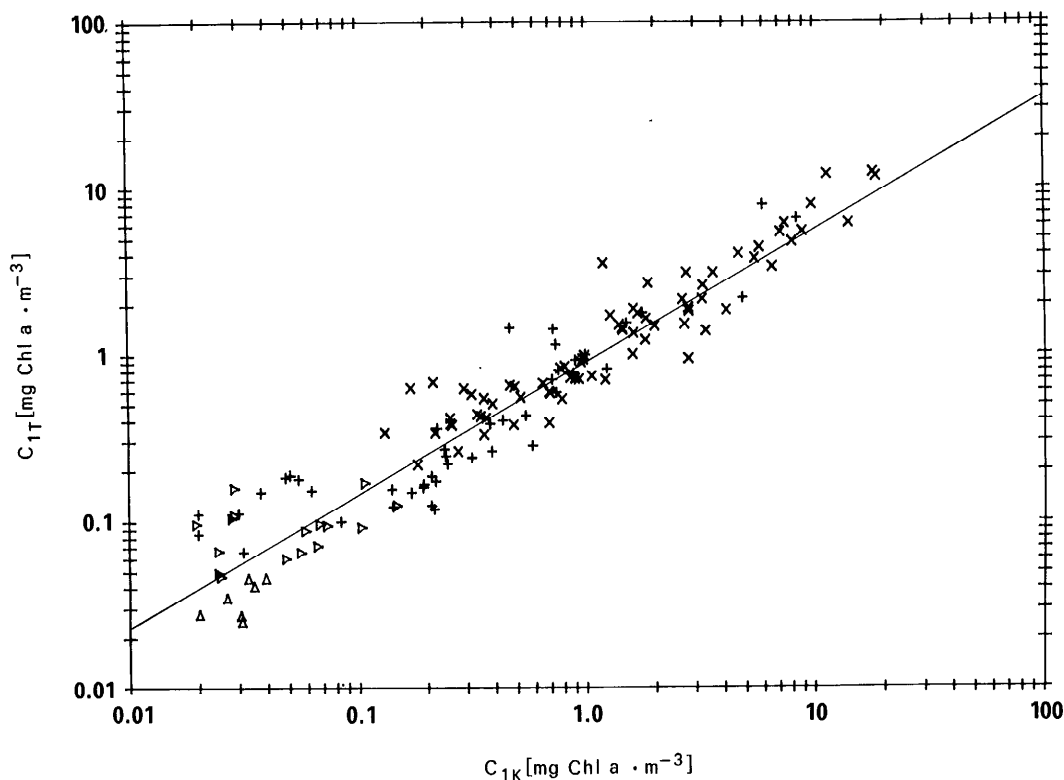
Fig. 2. Logarithm of average total Chl a concentration C_{1T} in euphotic zone vs. log average chlorophyll concentration C_{1K} in depth zone of 1 attenuation length ($N = 140$, $r = 0.955$, $P_c < 0.01$). Solid line is least-squares fit to data given by $\log C_{1T} = -0.020 + 0.788 \log C_{1K}$. +—Vis Lab data; ×—SCBS data; △—Climax I data; ▷—Climax II data.

photic depth, C_T (in mg Chl m^{-3}), to be

$$C_T = \frac{1}{4.61\,K_T^{-1}} \int_0^{4.61 K_T^{-1}} C(z) \cdot dz. \quad (5)$$

In agreement with Holmes (1965) and Lorenzen (1970), the data listed in Table 1 show a highly significant correlation between C_T and C_0 (linear correlation coefficient, $r = 0.89$; significant at the 0.1% level; $\log C_T = 0.073 + 0.678 \log C_0$). Of more importance for remote sensing is the even higher correlation between C_T and C_K shown in Fig. 2. The regression line in Fig. 2 indicates that, for low chlorophyll waters, there is relatively more chlorophyll below 1 attenuation length ($C_{1T}/C_{1K} > 1$). This implies the chlorophyll maximum is below 1 attenuation length. For high chlorophyll waters the converse ($C_{1T}/C_{1K} < 1$) is true.

Thus far we have considered only the relationship of K_T^{-1} to Chl a to facilitate comparison with the results of previous workers. However the bio-optical state of ocean waters is dependent on total pigment, not just Chl a concentration. Since the pheopigments are not separable from Chl a by presently available in situ or remote sensing techniques, we redefine C_K to be

$$C_K = C_{1K} + C_{2K}, \quad (6)$$

where C_K is the total chlorophyll-like pigment concentration, C_{1K} the concentration of Chl a, and C_{2K} the concentration of all other pigments having spectral absorption similar to that of Chl a, e.g. the pheopigments.

Figure 3 shows a plot, and best fit regression line, of attenuation length vs.
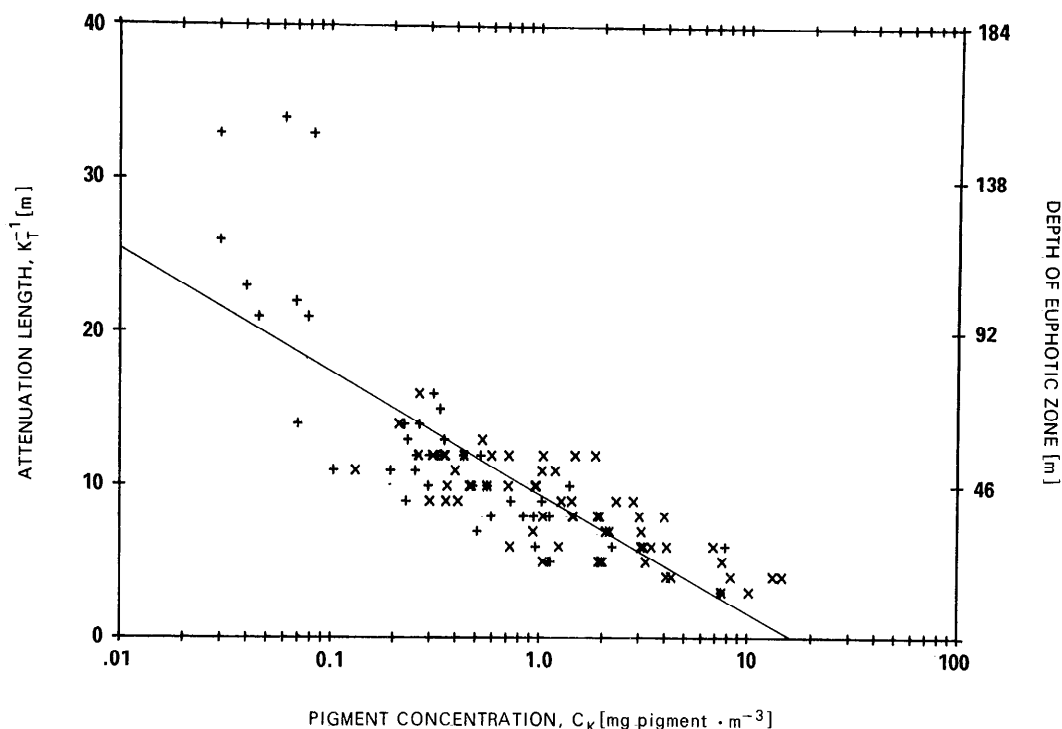
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Fig. 3. Attenuation length vs. log average chlorophyll-like *(see text)* pigment concentration in depth zone to 1 attenuation length. Solid line is least-squares fit to data given by $K_T^{-1} = 9.46 - 7.90 \log C_K$ ($N = 104$, $r = 0.806$, $P_c < 0.01$). Symbols as in Fig. 2.

average total (chlorophyll-like) pigment concentration to a depth of 1 attenuation length. This correlation is as significant as that of Fig. 1, so we consider C_K to be a good measure of phytoplankton biomass in spite of the contribution by degraded plant pigments to the bio-optical state of waters. In all the following we will consider C_K rather than C_{1K}.

Figure 4 shows that C_{1K} and C_{2K} are highly correlated and that C_{2K} is roughly a fourth the concentration of C_{1K}. From the regression equation given with Fig. 4, we find that C_{1K}/C_K varies from about 60% for $C_K = 0.01$ mg m^{-3} to >90% for $C_K = 10$ mg m^{-3}. Thus as the productivity of the waters increases, there is a higher proportion of viable phytoplankton.

Nonlinear biological effects

On the basis of Beer's Law (Eq. 1), we would expect a linear relationship be-

tween K_T and C_K. As noted above (Fig. 3), a nonlinear fit has historically been chosen to indicate the relationship between these parameters. A plot of $K_T - K_W$ vs. C_K is shown in Fig. 5. We see, and will show quantitatively, that an optimum fit requires more than a single straight line to match the data over the full range of C_K.

To account for nonlinear effects we rewrite Eq. 1:

$$K_T - K_W = K_x + k_c \times C_K + K_y, \quad (7)$$

where the additional term, K_y(m^{-1}), represents biological material that influences the total attenuation coefficient and that covaries with C_K. This covariance can be expressed as

$$K_y = k_y \times \alpha C_K, \quad (8)$$

where k_y[m^{-1}(mg pigment m^{-3})$^{-1}$] is the specific attenuation coefficient for this
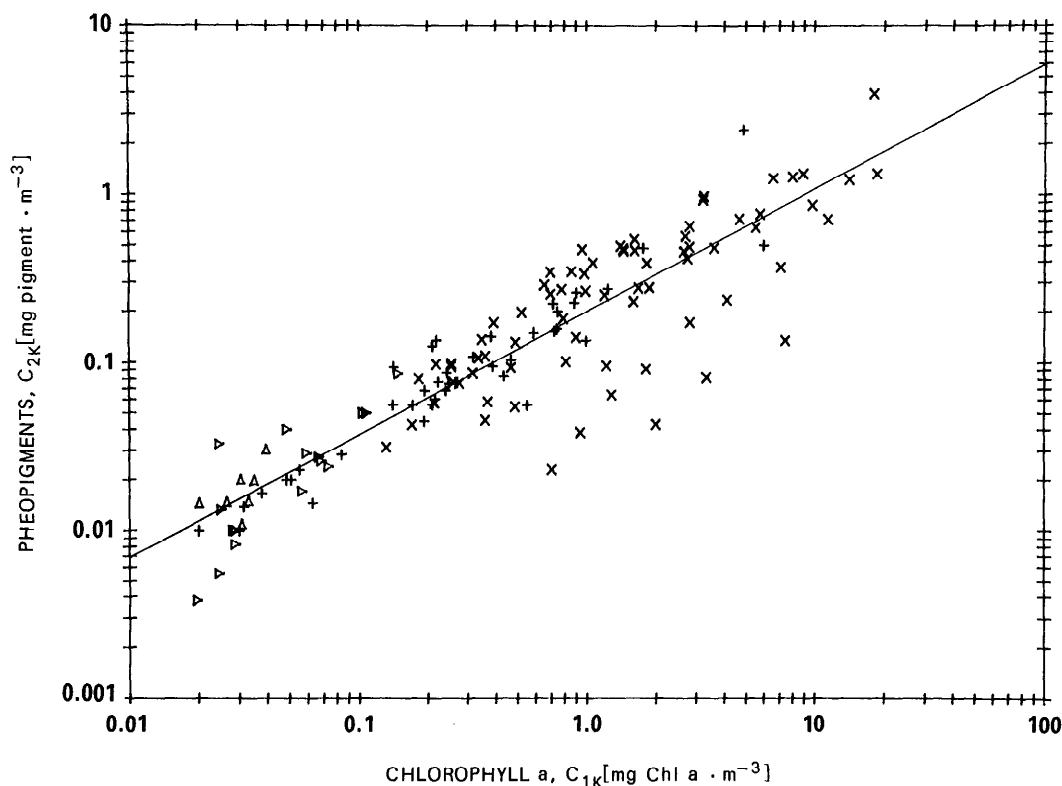
Fig. 4. Logarithm of concentration of pheopigments vs. log concentration of Chl *a* in depth zone of 1 attenuation length ($N = 136$, $r = 0.910$, $P_c < 0.01$). Least-squares regression formula for these data given by $\log C_{2K} = -0.708 + 0.729 \log C_{1K}$, as shown by solid line. Symbols as in Fig. 2.

biogenous material and α is a proportionality constant linking the concentration of this material to C_K. Thus, Eq. 7 can be written

$$K_T - K_W = K_x + (k_c + \alpha k_y) \times C_K, \quad (9)$$

which explicitly recognizes that the slope of a plot of $K_T - K_W$ vs. C_K is due not only to pigment concentration but also to covarying material. Particulate organic carbon (POC) is a measure of this biological material which covaries with chlorophyll-like pigment concentration. It is necessary to understand the relationship between POC and phytoplankton carbon (PC) in order to understand the relationship between K_T and C_K.

Hobson et al. (1973: fig. 6) presented data showing the relationship between identifiable organic carbon (composed primarily of phytoplankton carbon) and POC (composed of phytoplankton carbon plus nonliving organic detrital material). Their data are representative of diverse ocean regions and were used to estimate the change in the percentage of the particulate matter that is living as the concentration of living matter changes. Their data thereupon separated into two groups, one having concentrations of living material >150 to 200 mg m^{-3} and the other having concentrations below this: the results of an analysis of covariance indicated that the sum of squares about the regression line of the pooled data was significantly greater at the 99% probability level than the sum of squares about the two regression lines. The data of Hobson et al. suggest that unidentifiable carbon contributed about 50% to the
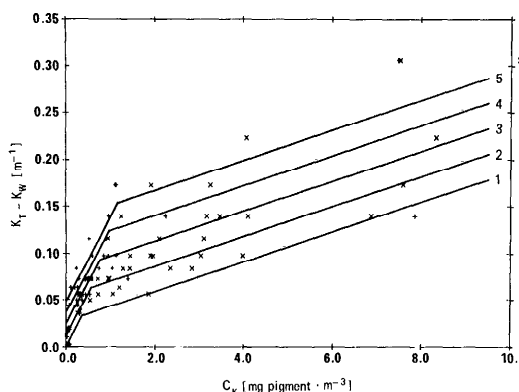
Fig. 5. $K_T - K_W$ vs. C_K where K_T is total diffuse attenuation coefficient for irradiance, K_W is attenuation coefficient for clear ocean water (taken equal to 0.027 m^{-1}: determined experimentally from Sargasso Sea spectral irradiance data), and C_K is average chlorophyll-like pigment concentration to depth of 1 attenuation length. Points calculated from individually determined experimental data for C_K and K_T^{-1} from cruises listed in Table 1. Numbered lines are graphed values of Eq. 12 for various values of K_{x1} and K'_{x2} (m^{-1}): 1—$K_{x1} = 0.00$, $K'_{x2} = 0.00$; 2—$K_{x1} = 0.012$, $K'_{x2} = 0.027$; 3—$K_{x1} = 0.023$, $K'_{x2} = 0.054$; 4—$K_{x1} = 0.036$, $K'_{x2} = 0.081$; 5—$K_{x1} = 0.048$, $K'_{x2} = 0.108$. Line 3 is least-squares fit to data where parameters for regression are given by Eq. 14 where $K_{x1} = 0.023$, $K_{x2} = 0.081$, $k_1 = 0.091$, $k_2 = 0.016$, and $C_B = 0.8$. Symbols as in Fig. 2.

POC in most oceanic waters, where concentrations of plankton were low, and that this detrital carbon contributed relatively less (1 to 30%) in waters with large amounts of plankton. Hobson et al. (1973: fig. 2) also showed that the ratio PC:POC approached 1.0 for high concentrations of PC. Since PC is a rough measure of Chl *a* and vice versa, we conclude that in ocean waters with low to medium chlorophyll-like pigment concentrations the ratio of viable to detrital carbon is relatively lower than in waters where pigment concentrations are high.

Based on these results we separated the data of Fig. 5 into two groups. One group is for low C_K, where the relative contribution of covarying detrital material to the slope is appreciable,

$$k_1 = k_c + \alpha\, k_y, \qquad C_K < C_B. \qquad (10)$$

The other is for high C_K, where the relative contribution of this material to the slope is significantly less,

$$k_2 \approx k_c, \qquad\qquad C_K > C_B, \qquad (11)$$

so that k_2, as a first approximation, is the specific attenuation coefficient due to chlorophyll-like pigments in this region. Equation 9 then becomes

$$K_T - K_W = K_{x1} + k_1 \times C_K, \\ C_K < C_B, \qquad (12a)$$

and

$$K_T - K_W = K_{x2} + k_2 \times C_K, \\ C_K > C_B. \qquad (12b)$$

Combining 12a and 12b:

$$K_{x1} + k_1 \times C_B = K_{x2} + k_2 \times C_B, \\ C_K = C_B. \qquad (12c)$$

An analysis of covariance indicates that the sum of squares about a single regression line through all the data was significantly (at the 99% level) greater than the combined sum of squares about the two regression lines. Since the C_K data cover three orders of magnitude, two orders of magnitude of data are poorly illustrated by the linear plot in Fig. 5.

We determined C_B for the above equations by making two least-squares linear fits to the data, Eq. 12a and b, while simultaneously satisfying 12c to ensure a continuous curve at the boundary ($C_K = C_B$) between the two regions. C_B is a somewhat arbitrary division between the low and high pigment concentration waters in that its value could be varied severalfold without significantly altering the statistical justification for a two-region fit (such a variation changed K_{x1} and K_{x2} but did not appreciably alter the slopes k_1 and k_2). This two-region division is analogous to that found by Hobson et al. (1973) and our boundary between regions is compatible with theirs. The fitted result is shown by the solid line in Fig. 5; the values for the constants are $K_{x1} = 0.023$(m^{-1}), $k_1 = 0.091$[m^{-1}(mg pigment m^{-3})$^{-1}$], $K_{x2} = 0.081$(m^{-1}), $k_2 =$
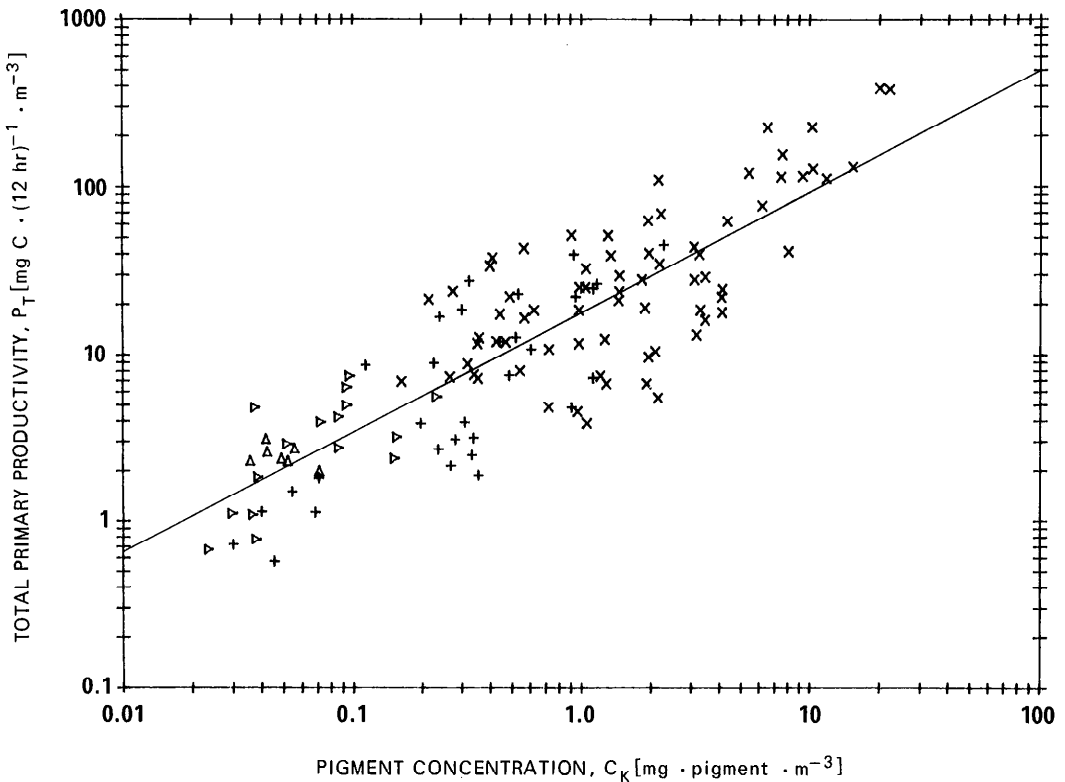
Fig. 6. Logarithm of total average productivity within euphotic zone vs. log chlorophyll-like pigment concentration to depth of 1 attenuation length ($N = 126$, $r = 0.855$, $P_c < 0.01$). Least-squares regression formula for data given by $\log P_T = 1.254 + 0.728 \log C_K$. Symbols as in Fig. 2.

$0.016 [\text{m}^{-1}(\text{mg pigment m}^{-3})^{-1}]$, and $C_B = 0.8(\text{mg pigment m}^{-3})$.

The values for K_{x1} ($0.023\ \text{m}^{-1}$) and K'_{x2} (where $K_{x2} = K'_{x2} + 0.027 = 0.081\ \text{m}^{-1}$) are a measure of the mean contribution of biogenous material to attenuation that does not covary with chlorophyll. Following the suggestion of Tyler (1975), we take K_{x1} and K'_{x2} as zero when this material is not present. Thus, for waters where the contribution of noncovarying material is negligible, we have the equations

$$K_T - K_W = 0.091 \times C_K, \qquad C_K < C_B, \quad (13a)$$

and

$$K_T - K_W = 0.027 + 0.016 \times C_K, \qquad C_K > C_B. \quad (13b)$$

The quantity 0.027 in 13b is a necessary artifact of the two-line fit. Mathematically it indicates that when $K'_{x2} = 0$ and $C_K = 0$, the line 13b does not have an intercept through zero because $k_1 \neq k_2$. Physically this quantity need not be interpreted since 13b has meaning only in the $C_K > C_B$ region. These equations can also be generalized by adding varying amounts of detrital material, K_{x1} and K'_{x2}, which give

$$K_T - K_W = 0.091 \times C_K + K_{x1}, \quad (14a)$$

and

$$K_T - K_W = 0.027 + 0.016 \times C_K + K'_{x2}. \quad (14b)$$

Equations 14 have been plotted in Fig. 5 for several values of K_{x1} and K'_{x2}, including the lowest curve (where K_{x1}

$= 0.00$, $K'_{x2} = 0.00$) and curve three (where $K_{x1} = 0.023$, $K_{x2} = 0.081$, $K'_{x2} = 0.054$). It will be noted that, to ensure a continuous curve, C_B varies as K_{x1} and K'_{x2} are changed. In principle, with a more complex fit to the data, this artificial discontinuity at $C_K = C_B$ could be eliminated, but for the present analysis we have not added this complexity.

The specific attenuation due to chlorophyll-like pigments, $k_2 \approx k_c$, is found to be 0.016 ± 0.003 [m^{-1} (mg pigment m^{-3})$^{-1}$], which agrees with Bannister's (1974a) accepted value of k_2, obtained by averaging estimates, ranging from 0.013 to 0.020, of Megard (1972), Talling (1970), M. Lorenzen (1972), and C. Lorenzen (1972). This lends support to our interpretation of the nonlinear biological effects on Beer's Law. Our value does not agree with that of Tyler (1975), whose analysis suggested our own, because we have determined the specific attenuation due to chlorophyll-like pigments so as to minimize the influence of covarying detrital material on our result. We assume that we have sufficient representative data so that k_2 can be determined without appreciable error due to varying K_{x1} and K_{x2} since these parameters do not covary with C_K. The value of the uncertainty of the slope k_2 quoted above (± 0.003) is in part due to, and hence accounts for, any influence of K_{x1} and K_{x2}.

For oceanographic applications where K_T and C_K can be determined independently, Eq. 14 can be used to calculate K_x. For waters noticeably affected by terrigenous material, an additional term would have to be added to the right-hand side of these equations to account for the attenuation due to nonbiological material. This complicates the problem of remotely sensing the bio-optical state of natural waters and dictates the necessity for more complete (including spectral) information.

C_K *and primary productivity*

We take C_K as an index of the standing stock of phytoplankton by utilizing the general correlation between primary pro-

ductivity and the concentration of phytoplankton (e.g. *see* Koblentz-Mishke et al. 1970). Figure 6 shows the correlation between total productivity in the water column and C_K for the data listed in Table 1. P_T is the total average primary productivity in the water column above the euphotic depth, calculated as

$$P_T = \frac{1}{4.61 K_T^{-1}} \int_0^{4.61 K_T^{-1}} P(z) \cdot dz, \tag{15}$$

where $P(z)$ is the productivity (in mg C per 12-h day per cubic meter) at depth z. These data, plotted on a log-log scale, span more than three orders of magnitude in both productivity and pigment concentration. Hence, they come close to spanning the full range of these concentrations in ocean waters and are representative of the relationship between P_T and C_K. The correlation between the variables shown in Fig. 6 is significant and can be used to estimate P_T from C_K provided uncertainties of severalfold are acceptable. To the extent that variations in irradiance, season, or temperature (Curl and Small 1965; Mandelli et al. 1970; Malone 1971) can be taken into account, the standard error in estimating P_T from C_K can be reduced.

Pigment concentration and production equations

A method for measuring primary productivity was suggested by Ryther and Yentsch (1957) based on the use of the assimilation ratio, the intensity of photosynthesis (mg C m^{-3} h^{-1}) to chlorophyll concentration (mg Chl m^{-3}), and the irradiance penetrating to depths in the sea. Since this early work, several workers (Talling 1957; Steele 1962; Steele and Menzel 1962; Vollenweider 1965; Fee 1969) have developed equations for gross daily production in the water column based on such environmental factors as incident irradiance and chlorophyll concentrations and on factors dependent on the physiology of the phytoplankton. Bannister (1974a,b) reviewed these ear-

lier equations and recast them into more fundamental and general forms. In particular, he showed that equations for daily production can be written

$$\Pi \;(\text{g C m}^{-2}\,\text{d}^{-1}) = \Psi\,\frac{k_2 C_K}{K_T}. \qquad (16)$$

Ψ (in g C m^{-2} d^{-1}) is an unsurpassable upper limit to productivity corresponding to the absorption of all available radiant energy by viable phytoplankton. Ψ is not a function of chlorophyll concentration, but rather only of incident irradiance, day length, and photosynthetic parameters. Bannister (1974*b*) discussed the dependence of Ψ on algal parameters that vary fourfold with growth rate. Incident irradiance and daylength are ancillary information that can be determined by satellite. Thus, to the extent that the physiological parameters are measurable or predictable from surface data, Ψ can be estimated from satellite data.

The factor $k_2 C_K \times K_T^{-1}$ is the fraction of radiant energy attenuated by chlorophyll-like pigments, where k_2 is the specific attenuation coefficient for irradiance due to phytoplankton. Since k_2 is known from our above analysis and is approximately constant, the remotely sensed K_T^{-1} can be used not only to estimate C_K but also to estimate the factor $k_2 C_K \times K_T^{-1}$ (provided spectral information is sufficient to allow an independent estimate of K_x). Alternatively, this ratio can also be determined by means of Eq. 14 for oceanographic applications where K_T and C_K can both be measured. As Bannister has shown, the actual daily production, Π, in the layer depends on phytoplankton concentration solely through this factor. Unlike Bannister, we have combined chlorophyll and pheopigments in our notation for C_K and must, therefore, use a relationship like that given in Fig. 4 to find the fraction of energy attenuated by C_{1K} and C_{2K}.

Figure 7 shows a plot of the fraction of radiant energy attenuated by chlorophyll and pheopigments vs. the pigment concentration, C_K, plotted logarithmically. This fraction can be represented either
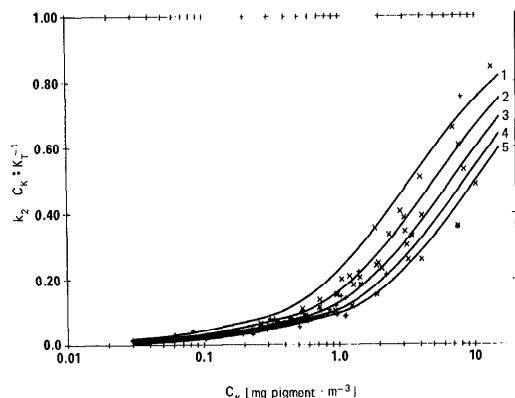

Fig. 7. Fraction of radiant energy attenuated by chlorophyll-like pigments, $k_2\,C_K{:}K_T$, vs. log chlorophyll-like pigment concentration to depth of 1 attenuation length, C_K. Points calculated from individually determined experimental data for C_K and K_T^{-1} (Table 1) using $k_2 = 0.016$. Numbered solid lines are graphed values of $k_2 C_K{:}K_T$ using Eq. 14 to determine K_T^{-1} for same values of K_{x1} and K_{x2} listed for Fig. 5. Symbols as in Fig. 2.

by the ratio $\Pi{:}\Psi$ from the production equations given by Bannister or by the experimentally measured ratio $k_2 C_K{:}K_T$. Thus this fraction links the production equations to the experimental data. By means of Eq. 14a and b we can calculate the ratio $k_2 C_K{:}K_T$ and plot it vs. log C_K as shown by the solid lines in Fig. 7. A particular data point plotted on this graph provides the following information. The fraction of radiant energy attenuated by viable phytoplankton can be obtained from Fig. 4. This information allows us to calculate by Eq. 16 the potential productivity Π from the radiant energy utilized by phytoplankton, provided that Ψ (which depends on algal properties) is known. Second, if K_T and C_K can be determined (both are routine measurements from a surface vessel) then the attenuation due to nonchlorophyll-like material can be estimated by comparing a plotted data point with the family of K_x curves. Alternatively, K_x can be calculated using Eq. 14 from experimentally determined values of K_T and C_K. Third, by comparing Π with actual measured photosynthesis, we can ascribe any differences found between the calculated and measured

productivity to the modeling parameters used in Ψ. In other words, the contribution of radiant energy to productivity has been separated from these other effects and facilitates their investigation.

Discussion and summary

Our understanding of the fundamental relationships between the environment and the higher trophic levels is limited by the data now obtainable. Satellite data will provide significant complementary information to that gathered at the ocean surface. It will allow the spatial and temporal variability inherent in the biological data to be more completely assessed. This is important to many questions, such as the structure of patchiness, that may significantly affect the higher trophic levels (Steele 1973) and that may influence the stability of the marine ecosystem (Platt 1975).

We have discussed how K_T can be linked to the signal available to a remote sensor and have investigated how accurately our measure of the bio-optical state of ocean waters, K_T, can be related to C_K. C_K may in turn be related to other important biological features of ocean waters. For biogenous natural waters the diffuse attenuation coefficient for irradiance has been cast into a form which is meaningful physically (satisfies Beer's Law) and biologically (k_2 represents the specific attenuation of an average ensemble of phytoplankton). Agreement between the slope k_2 and previous determinations of the specific attenuation coefficient due to chlorophyll supports our interpretation of the nonlinear biological effects on Beer's Law.

Bannister (1974a) transformed the production equations of several workers into a form which is an explicit function of phytoplankton concentration and which does not contain parameters or coefficients dependent on phytoplankton concentration. Further, in order to simplify theoretical analysis, the parameters of his transformed equations were chosen so as to minimize the range of values needed to describe the variations of photosyn-

thesis in ocean waters. As a consequence, these production equations provide a direct theoretical framework with which to connect remotely sensed data on the bio-optical state of ocean waters to the gross daily production in a water column. Bannister's production equations are in a form which can be incorporated directly into a general theory of phytoplankton dynamics. By use of these production equations with satellite data (input irradiance, daylength, K_T^{-1}, C_K) to complement surface measurements, plus a knowledge of important plankton physiological parameters, we have a theoretical framework and broad experimental evidence with which to study plankton production in the world's oceans.

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