f. 77-2

February 1977

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Sponsored by
U. S. Department of Commerce
National Oceanic and Atmospheric Administration
National Environmental Satellite Service
Contract No. USDC 5-35406
Grant No. 04-6-158-44033

SIO Ref. 77-2
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UNIVERSITY OF CALIFORNIA SAN DIEGO

SCRIPPS INSTITUTION OF OCEANOGRAPHY

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The work reported herein was performed by the Visibility Laboratory of the Scripps Institution of Oceanography under the sponsorship of the U. S. Department of Commerce, National Oceanic and Atmospheric Administration, National Environmental Satellite Service. Support was provided by Contract No. USDC 5-35406 and Grant No. 04-6-158-44033. Technical Monitor for both the contract and the current grant is John W. Sherman III of the NOAA/NESS SPOC Group.

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ABSTRACT

The diffuse attenuation coefficient for irradiance K_T has been shown to be a physical measure of the bio-optical state of ocean waters that is both physically and biologically meaningful. From an analysis of irradiance K_T and pigment concentration, the specific attenuation due to chlorophyll-like pigments has been found to be 0.016 ± 0.003 $[m^{-1} \cdot (\text{mg pigment} \cdot m^{-3})^{-1}]$. The bio-optical state of ocean waters can be remotely sensed by means of appropriate spacecraft sensors. In addition, K_T is readily measured at sea and has been shown to be highly correlated with and dependent upon 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 as formulated by Bannister and can be directly incorporated into a general theory of phytoplankton dynamics. Further, C_K may be used as an index of primary productivity. Thus, the determination of the bio-optical state of ocean waters by surface vessel provides direct information concerning the potential productivity of these waters. To the extent that the bio-optical state can be determined by satellite, it may be possible to rapidly and repeatedly examine important parameters of the marine ecosystem.

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INTRODUCTION

The remote sensing from spacecraft of the upwelling spectral radiant energy from within the upper layer of the ocean holds the potential for determining marine pigment concentrations due to phytoplankton. This, in turn, suggests the potential for obtaining rapid world-wide assessments of primary productivity over time scales required to link this productivity to commercially important fisheries. Continuous world-wide data on ocean productivity would assist synoptic ecological studies of ocean regions of special interest, would provide otherwise unattainable data for the dynamic modeling of phytoplankton, and would allow for the continuous monitoring of both short and long-term changes in this 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 the upwelling spectral radiant energy from the ocean and the relationship of this signal to ocean optical properties have been discussed by several investigators [Clarke, *et al.* (1970); White (1969); Arvensen, *et al.* (1971); Mueller (1976)], and will be the subject of a subsequent publication by the authors. We confine the present work to describing the relationships between the optical properties of ocean waters and the biological properties which influence them.

We have introduced 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 appropriate 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. We seek to understand these relationships in order to assess the potential accuracy of remotely sensing such marine biological data and to determine possible applications and practical limitations of such an effort.

A complete analysis of the bio-optical state of natural waters requires consideration of the optical properties as a function of wavelength. However, in order to present general concepts and to compare

our results with those of previous workers, the following discussion will consider only total quanta or total energy. In a subsequent publication the spectral characteristics of the bio-optical state will be considered in detail.

We wish to thank R. W. Eppley for allowing us the use of unpublished data from the Southern California Bight Studies obtained by the Food Chain Research Group (Institute of Marine Resources, Scripps Institution of Oceanography) and for helpful advice and discussions. We also wish to thank R. W. Austin, D. Clark, D. A. Kiefer, J. E. Tyler, and W. Wilson for constructive discussions concerning this work.

BIO-OPTICAL STATE OF OCEAN WATERS

It has long been recognized that biological constituents, particularly phytoplankton pigments and associated degradation products, play a significant role in determining the optical properties of natural waters. We use the term ''bio-optical state'' to represent a measurement of the total effect of biological material on the optical properties of natural waters. It is the combined effect of the absorption and scattering due to suspended and dissolved biogenous material that established the bio-optical state of these waters. The concept of a bio-optical state will prove useful to the extent that diverse biological constituents in natural waters can be described by a few optical parameters which, in turn, can be shown to practically represent a meaningful average status of the biological material in the ocean water at a particular time and place.

For reasons discussed below, we have chosen to work with the total diffuse attenuation coefficient for irradiance, K_T, to physically describe the bio-optical state of ocean waters. The value of K_T may be determined as indicated in Eq. 1,

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

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

In a subsequent report we will show that the bio-optical state can be characterized in detail by determining these optical parameters as a function of wavelength. Indeed, a complete description of the coefficients in Eq. 1 can only be made by considering their characteristics as a function of wavelength.

K_T has been chosen to characterize the bio-optical state of ocean waters for several reasons. Many authors [Riley (1956), Holmes (1965), Aruga and Ichimura (1968), Lorenzen (1972)] have shown that a strong correlation exists between the total diffuse attenuation coefficient for irradiance, K_T, and the chlorophyll *a* concentration. In a following report we have shown that this relationship, as a function of

wavelength, can be quantitatively utilized for the classification of water types based upon the fraction of available radiant energy attenuated by phytoplankton. In addition, we have derived values for K_w and k_c from our results. The relation between K_T and the concentration of chlorophyll *a*, C[mg Chl *a* · m^{-3}], takes an added significance since the fraction of available radiant energy absorbed by viable phytoplankton can now be calculated from measurements of C and K_T. In short, K_T and C are highly correlated and have been shown to be related in a manner that is both physically and biologically meaningful.

A second reason for choosing K_T as a measure of the bio-optical state is that K_T may be used to describe the depth above which 90 percent of the diffusely reflected irradiance (excluding specular reflectance) originates. Gordon and McCluney (1975) have shown that approximately 90 percent of the diffusely reflected irradiance, that upwelling signal to be remotely sensed, originates from less than 1 attenuation length, i.e., a depth such that $z = K_T^{-1}$. Further, K_T is the optical parameter that relates the irradiance just beneath the ocean surface, E(o), to the irradiance at depth, E(z), viz:

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

In addition, Preisendorfer (1976) has shown 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.

Finally, techniques for experimentally determining K_T, by measuring energy or quanta as a function of depth, have been developed [Jerlov and Nygard (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, and because the upwelling optical signal from these waters mostly originates from less than one attenuation length, the actual physical depth from which the remote signal originates is, in part, determined by the chlorophyll concentration. In other words, the remotely sensed chlorophyll signal is derived from a depth in the ocean which depends upon the chlorophyll concentration itself. In order to consistently compare waters of various chlorophyll concentrations we define

$$C_K[\text{mg Chl} \cdot m^{-3}] = \frac{1}{K_T^{-1}\,[m]} \int_0^{K_T^{-1}} C(z)\,[\text{mg Chl} \cdot m^{-3}]\, dz\,[m] \qquad (3)$$

where C_K is the average chlorophyll concentration in the water column to a depth of one attenuation length K_T^{-1} and C(z) is the chlorophyll concentration at depth z. It is C_K that will directly influence K_T and, hence, the upwelling remote signal. C_K thus provides a link between the physical measurements and the biological status of ocean waters. If this link can be shown to be widely applicable and accurate, then potential uses for remote sensing are achievable.

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, have been obtained by the Visibility Laboratory on several cruises (Fresnel I and II and the Discoverer Expedition). These data are referred to as "Vis Lab" data in the discussion below and are distinguished by the inclusion of complete spectral irradiance data obtained using the Scripps Spectroradiometer (Tyler and Smith 1966, 1970). This spectral irradiance data will be used in a subsequent report to show how the upwelling spectral signal from ocean water may be used to establish the bio-optical state of these waters. For present purposes, only the total irradiance (watts or quanta; see Morel and Smith 1974) data are used. The 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. These data are characteristic of very low to moderately productive waters.

The "Climax" data are from the Central Pacific Ocean. (Climax I, 1974; Climax II, 1975). Data from Climax I were taken from the gyre-like circulation of the North Central Pacific water mass. This water mass, representing an area approximately 1200 by 4500 nautical miles, is relatively homogeneous with respect to physical, chemical, and biological properties. These data are representative of the large gyre-like areas of the world's oceans (McGowan 1974; McGowan and Williams 1973). Although there are seasonal variations in these properties within the upper layer, the range is comparatively small, and there is little spatial heterogeneity above the thermocline during large parts of the year. Oceanographic data obtained on this expedition were taken while the research ship followed a pair of parachute drogues. To the extent that the ship managed to take data between the drifting drogues, the data were obtained in a reasonably coherent body of water. On the Climax II Expedition, data were obtained in both the North and South Pacific Central water masses.

Data from the Southern California Bight Studies were obtained by the Food Chain Research Group (Institute of Marine Resources, Scripps Institution of Oceanography, R. W. Eppley, private communication). Data from these studies include upwelling areas and are characteristic of productive coastal waters.

For these data chlorophyll *a* and phaeopigments were determined by the fluorescent technique described by Yentsch and Menzel (1963) as modified by Holm-Hansen *et al.* (1965) and outlined by Strickland and Parsons (1968, Section IV.3). The rate of assimilation of carbon by phytoplankton were estimated from the ^{14}C method of Steemann Nielsen (1952) as outlined by Strickland and Parsons (1968, Section V.3), generally with an incubation period of one-half day. Detailed descriptions of methods are given in the cruise data reports (Climax I, 1974; Climax II, 1975; Tyler, 1973).

The diffuse attenuation coefficient for total irradiance, K_T, was calculated by fitting a straight line to data of the total quanta (measured directly or calculated from spectral irradiance) versus depth (from the surface to roughly the 1 percent 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; it ignores the fact that K_T is an apparent, rather than inherent, optical property of the water (Preisendorfer, 1976); and, for total quanta, it ignores effects caused by changes in spectral irradiance with depth. In spite of these limitations the above procedure for determining K_T is consistent, widely used, and provides a good first order estimate for the parameters that

Table 1. Cruises, general locations, and number of optical, chlorophyll *a* plus phaeopigments and primary productivity measurements used.

Cruise	Location	K_T	Pigments	Primary Productivity
Fresnel I (11/28 – 12/13, 1968)	Gulf of Calif.	12	12	11
Discoverer (5/3 – 6/3, 1970)	Sargasso Sea	3	3	1
	Gulf of Mexico	7	7	5
	Cent. E. Pacific	11	11	11
Fresnel II (3/16 – 3/31, 1971)	Gulf of Calif.	11	8	5
Climax I (9/19 – 9/25, 1969)	Cent. N. Pacific	–	7	7
Climax II (8/27 – 10/8, 1969)	Cent. N & S. Pacific	–	16	16
SCBS1 (9/14 – 9/18, 1974)	Calif. Coastal Waters	12	15	15
SCBS2 (2/26 – 3/5, 1975)	Calif. Coastal Waters	15	14	15
SCBS3 (6/16 – 6/24, 1975)	Calif. Coastal Waters	13	13	15
SCBS4 (9/6 – 9/14, 1975)	Calif. Coastal Waters	15	15	15
SCBS 5 (12/2 – 12/10, 1975)	Calif. Coastal Waters	17	17	17

characterize 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 duphotic depth, is consistent with the accuracy of other data and methods which are used below.

k_T AND PIGMENT CONCENTRATION

Several authors (Riley, 1965; Aruga and Ichimura, 1968; Lorenzen, 1972) have shown that a strong correlation exists between K_T and the average chlorophyll concentration in the water column and have derived analytical formulae to relate these two variables. Figure 1 gives the results of these workers, plotted in terms of attenuation length versus log chlorophyll concentration, compared to our own data

and best fit to these data. (A discussion of statistical procedures used in this report is given in Appendix 1). The best fit to our data as plotted is represented by the analytical equation,

$$K_T^{-1}[m] = 8.78 - 7.51 \log C_K [\text{mg Chl} \cdot m^{-3}] \quad (4)$$

and shows the same strong correlation between K_T^{-1} and chlorophyll concentration as observed by previous workers. The curves and data shown in Fig. 1 represent data from several hundred oceanographic stations covering the full range of ocean chlorophyll concentrations. The relationship between K_T^{-1} and log C_K would appear to be widely applicable, and the correlations obtained indicate that roughly two-thirds of the variation in either variable is explained by the correlation with the other. It should be noted, however, that the combined data represented in Fig. 1 were obtained from waters whose dissolved and suspended material was largely of biogenous origin. Areas noticeably affected by terrigenous material were avoided or excluded.

The curves for the previous workers, shown in Fig. 1, refer to the average chlorophyll concentration within the euphotic zone, i.e., 4.61 attenuation lengths. Because the upwelling signal available to a remote sensor originates primarily from above one attenuation length, we have presented our data in terms of C_K^*, as defined in Eq. 3. That is, we have presented in Fig. 1 our physical measurement of the bio-optical state K_T^{-1} versus the average chlorophyll concentration to the depth to which a remote sensor "measures" the bio-optical state.

The correlation shown in Fig. 1 is highly significant and is strong evidence that the remotely sensed bio-optical state of ocean waters may be used to estimate, with useful accuracy, the value of C_K in ocean waters. Several points should be emphasized.

First, a plot of K_T^{-1} versus log C has been presented rather than a plot of K_T versus C as suggested theoretically by Eq. 1. This has been done by previous workers and we have added our own data and fit for comparison to this previous data. Historically, these data have been interpreted as being more or less linearly related when plotted as K_T^{-1} versus log C but nonlinear when plotted as K_T versus C. It will be shown below that, as physically expected, a linear fit can be found between K_T and C_K when nonlinear biological effects are accounted for. Until these effects are taken into account, the data shown in Fig. 1 should not be used to calculate the parameters of Eq. 1.

Second, a signal derived from within the upper optical depth of the ocean is somewhat more than just a "surface" signal. A depth of one attenuation length represents the upper 22 percent of the euphotic zone and is the layer in which 63 percent of the incident irradiance, having passed through the surface, is attenuated.

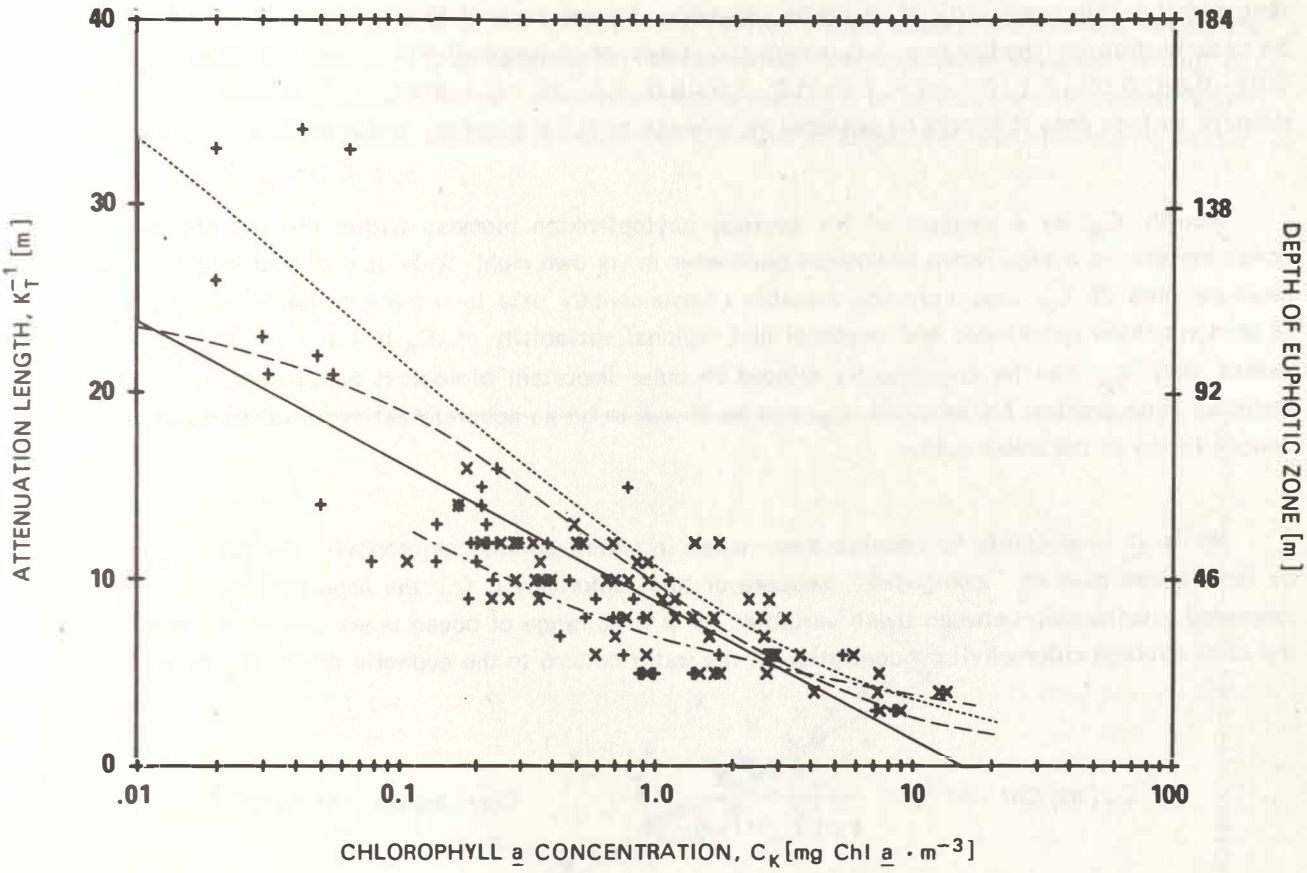

Fig. 1. Attenuation length, K_T^{-1}[m], versus log average chlorophyll a concentration [mg Chl a · m^{-1}]. The data points are from the cruises listed in Table 1 (+'s Vis Lab data, x's SCBS data) and the solid line is a least squares fit to these data (number of data points, N = 108; linear correlation coefficient, r = 0.806; probability that the observed data could have come from an uncorrelated parent population, $P_c < 0.01$; (see e.g., Bevington, 1969). The dashed lines show previous results of other workers: ——— Riley (1956), ····· Aruga and Ichimura (1972) as presented by Takahashi and Parsons (1972), —·—· Lorenzen (1972).

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

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

Third, even if K_T could be precisely determined from satellite data, the value of C_K can only be determined within some error of estimate. However, the accuracy of this estimate is such that C_K can be clearly distinguished among, say about six, zones of chlorophyll-like pigment concentrations, e.g., 0.01–0.05, 0.05–0.1, 0.1–0.5, 0.5–1.0, 1.0–5.0, 5.0–10 mg pigment m^{-3}. Further, given complementary surface data it should be possible to enhance both the accuracy and precision in estimating C_K.

Fourth, C_K, as a measure of the average phytoplankton biomass within the top optical depth of ocean waters, is a significant biological parameter in its own right. Wide spatial and long-term temporal measurements of C_K would provide valuable complementary data to surface measurements for the study of phytoplankton patchiness and seasonal and regional variability of C_K in the world's oceans. To the extent that C_K can be consistently related to other important biological parameters, its significance becomes even greater. For example, C_K can be shown to be an accurate estimator of the total chlorophyll concentration in the water column.

While it is possible to imagine many ways in which surface chlorophyll, C_0 (or C_z as defined by Eq. 3), can give an "ambiguous" measure of total chlorophyll, C_T, the important issue is the actual measured relationship between these variables for a wide range of ocean areas and water types. We take the total average chlorophyll concentration in the water column to the euphotic depth, C_T, to be

$$C_T[\text{mg Chl} \cdot m^{-3}] = \frac{1}{4.61\, K_T^{-1}[\text{m}]} \int_0^{4.61\, K_T^{-1}} C(z)[\text{mg Chl} \cdot m^{-3}]\, dz[\text{m}] \quad , \qquad (5)$$

where, as above, C(z) is the chlorophyll concentration at depth z. Holmes (1965) summarized physical, chemical and biological data from 16 oceanographic cruises (between 1925 and 1962) in the northeastern tropical Pacific. He observed a correlation (significant at the 1 percent level, $r = 0.818$) between the concentration of chlorophyll *a* within the first two meters of the surface and the total chlorophyll *a* in the water column within the euphotic zone, and suggested "that the chlorophyll *a* concentration in the upper few meters may be used to give a rough estimate of the chlorophyll *a* concentration in the water column." In 1970 Lorenzen presented the analysis of 91 samples collected during four cruises in the Atlantic and Pacific, covering a range of surface chlorophyll concentrations from 0.04 to 28.3 mg m^{-3}. His analysis showed a highly significant correlation between surface chlorophyll and measurements of total chlorophyll in the euphotic zone and also with primary productivity of the phytoplankton in the waters studied.

In agreement with Holmes and Lorenzen, 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 percent level; $\log C_T = 0.073 + 0.678 \log C_0$). Of more importance, from the point-of-view of remote sensing, is the correlation between C_T and C_K, shown in Fig. 2. This correlation is higher than that between C_T and C_0, as is to be expected since an integral to a depth of K_T^{-1} meters includes more of the chlorophyll *a* depth profile than the surface value.

We conclude that, on the average, C_K may be used as an accurate estimator of C_T. While detail may be lost (in particular the shape of the chlorophyll *a* profile versus depth), the average values are important complementary data to those obtained by surface ship. The regression equation in Fig. 2 indicates that, for low chlorophyll waters, relatively more chlorophyll is below one attenuation length $C_{1T}/C_{1K} > 1$, i.e., the chlorophyll maximum is below one attenuation length. For high chlorophyll waters the converse ($C_{1T}/C_{1K} < 1$) is true.

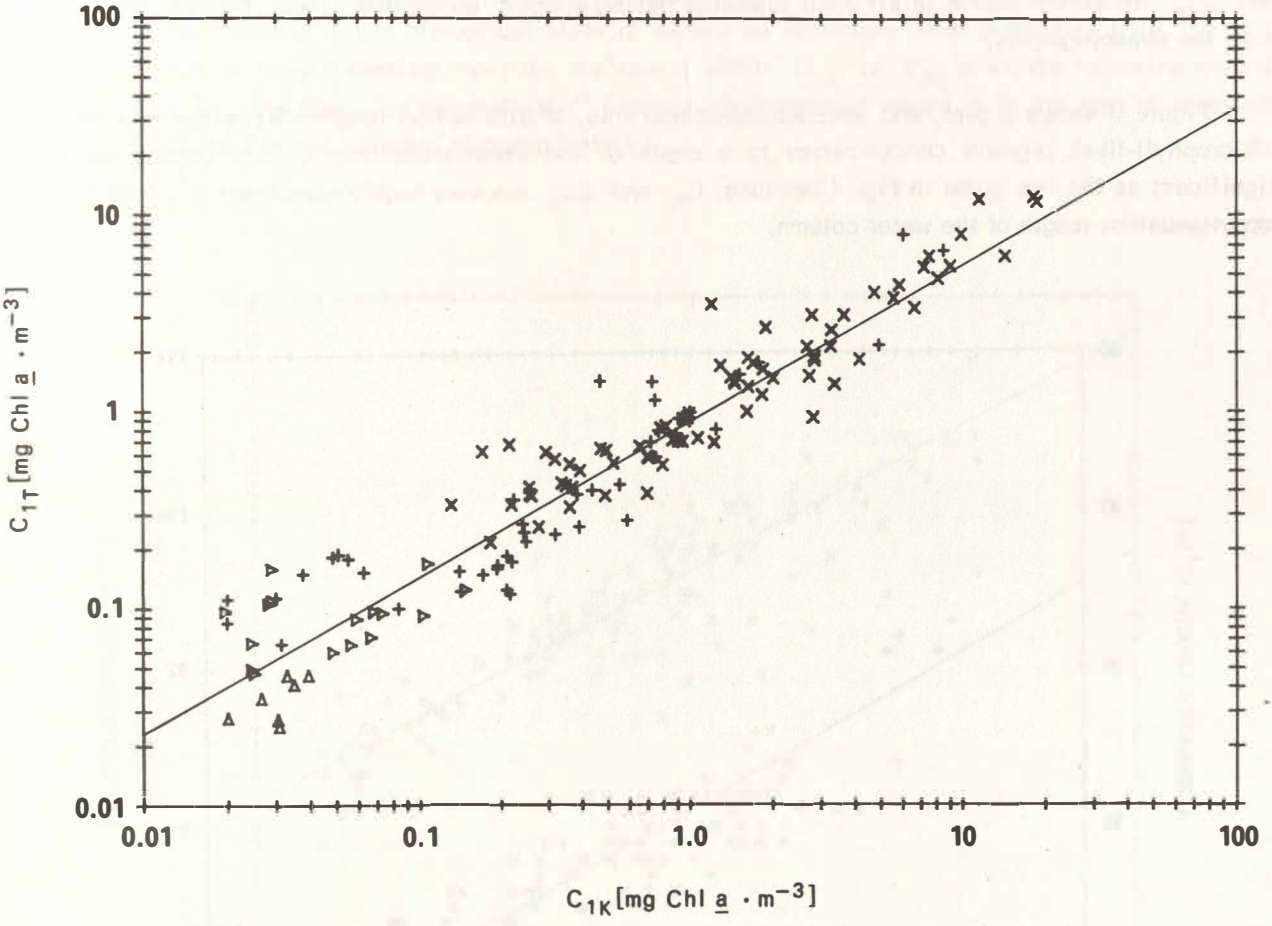

Fig. 2. Logarithm of the average total chlorophyll a concentration C_{1T}[mg Chl a · m^{-3}] in the euphotic zone versus log average chlorophyll concentration C_{1K}[mg Chl a · m^{-3}] in the depth zone of one attenuation length (N = 140, r = 0.955, $P_c < 0.01$). The solid line is a least squares fit to the data given by log $C_{1T} = -.020 + 0.788$ log C_{1K}. Vis Lab data indicated by +'s, SCBS data by x's, Climax I data by Δ's and Climax II data by ▷'s. These symbols are used consistently in the remaining figures.

Thus far we have considered only the relationship of K_T^{-1} to chlorophyll *a*. This was to facilitate comparison with the results of previous workers. The bio-optical state of ocean waters is dependent upon the total pigment, not just the chlorophyll *a* concentration. In particular, the phaeopigments are not separable from chlorophyll *a* using current *in situ* or remote sensing techniques. Consequently, we re-define C_K to be

$$C_K = C_{1K} + C_{2K} , \tag{6}$$

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

Figure 3 shows a plot, and best fit regression line, of attenuation length versus the average total (chlorophyll-like) pigment concentration to a depth of one attenuation length. This correlation is as significant as the one given in Fig. 1 because C_K and C_{1K} are very highly correlated ($r = 0.997$) in the top attenuation length of the water column.

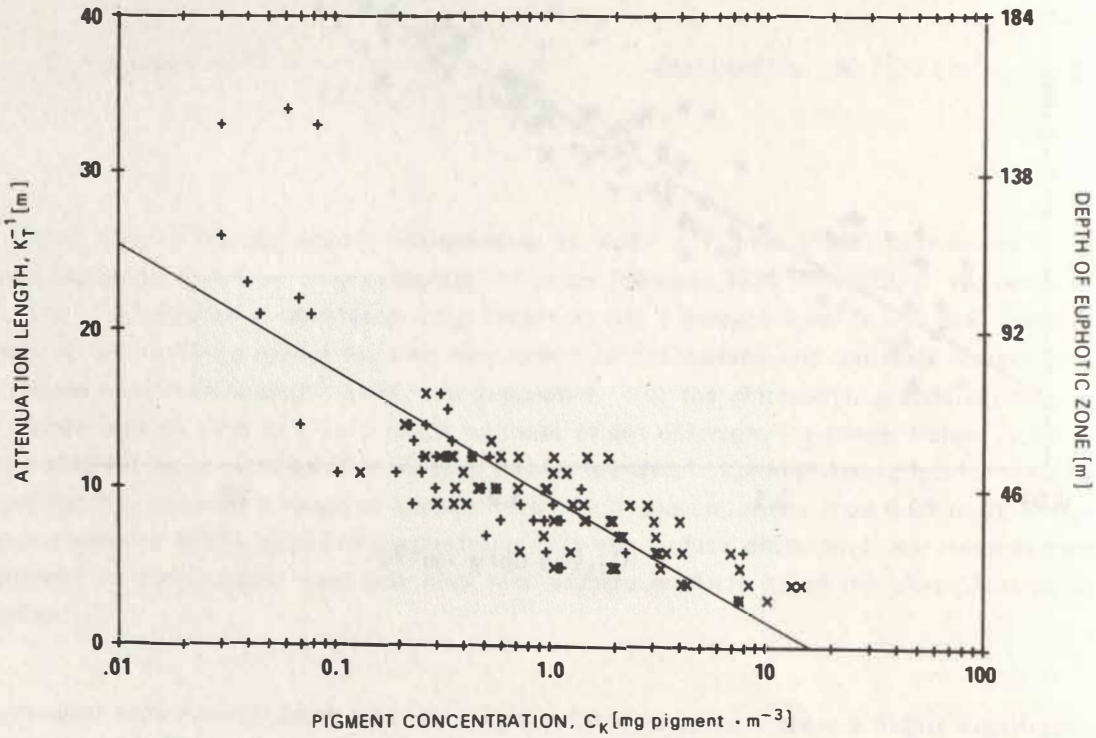

Fig. 3. Attenuation length, K_T^{-1} [m], versus log average "chlorophyll-like" (see text) pigment concentration C_K [mg pigments m^{-3}] in the depth zone to one attenuation length. Solid line is a least squares fit to the data given by $K_T^{-1} = 9.46 - 7.90 \log C_K$ ($N = 104$, $r = 0.806$, $P_c < 0.01$).

This very high correlation follows because in the top K_T^{-1} meters of the ocean, C_{1K} and C_{2K} are highly correlated (Fig. 4) and, on the average, C_{2K} is roughly one-fourth the concentration of C_{1K}. Indeed, this correlation between C_{1K} and C_{2K} may be used to estimate the relative contribution of C_{1K} and C_{2K} to the total pigment concentration C_K.

From the regression equation given with Fig. 4, the ratio of chlorophyll *a* to the total pigment concentration versus chlorophyll *a* may be calculated. It is found that C_{1K}/C_K varies from about 60 percent for $C_K = 0.01$ mg $\cdot$ m^{-3} to greater than 90 percent for $C_K = 10$ mg $\cdot$ m^{-3}. Thus, as the productivity of the waters increases the ratio C_{1K}/C_K increases, indicating a higher proportion of viable phytoplankton in highly productive, as compared to low productivity, waters.

As a consequence of this correlation, C_K remains a good measure of phytoplankton biomass in spite of the contribution to the bio-optical state of waters by nonviable plant pigments. Thus, we may, for the purposes of remote sensing, consider the use of either C_{1K} or C_K. In all the following we will consider only C_K, the total "chlorophyll-like" pigment concentration, since it is the sum of pigments that influences the bio-optical state of ocean waters.

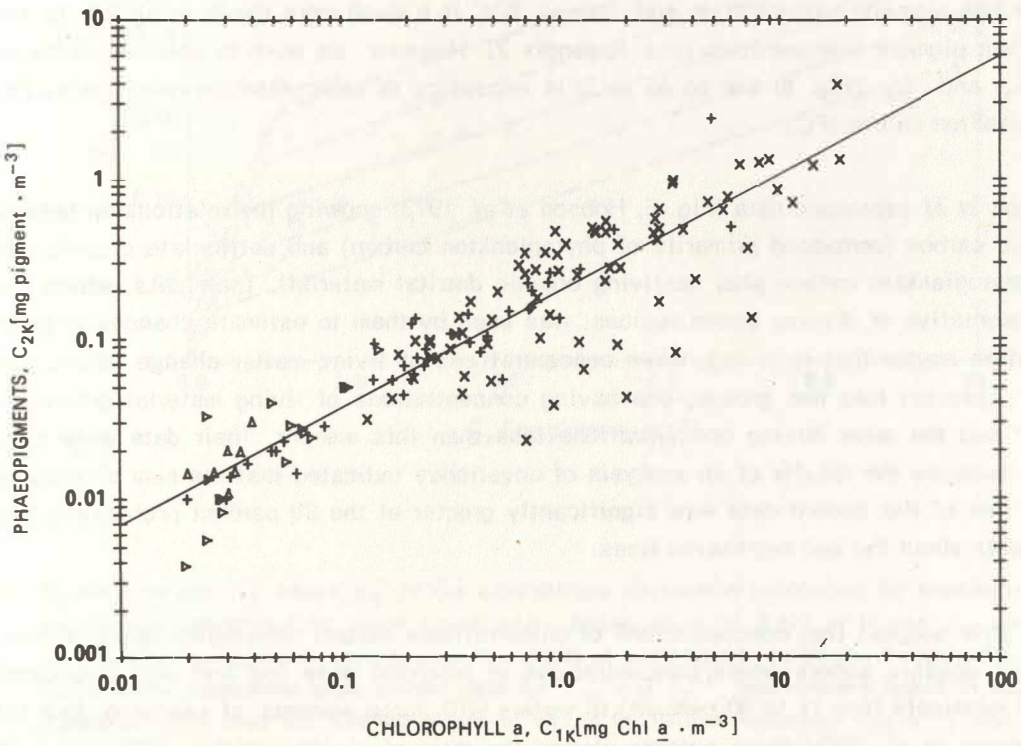

Fig. 4. Logarithm of the concentration of phaeopigments, C_{2K} [mg pigment $\cdot$ m^{-3}], versus log concentration of chlorophyll *a*, C_{1K} [mg Chl *a* $\cdot$ m^{-3}], in the depth zone of one attenuation length ($N = 136$, $r = 0.910$, $P_c < 0.01$). The least squares regression formula for these data is given by $\log C_{2K} = -0.708 + 0.729 \log C_{1K}$, as shown by the solid line.

NONLINEAR BIOLOGICAL EFFECTS

On the basis of Beer's Law (Eq. 1), we would expect a linear relationship between the total diffuse attenuation coefficient K_T and the total chlorophyll-like pigment concentration C_K. As noted above (Fig. 3), a nonlinear fit has historically been chosen to indicate the relationship between these parameters. A plot of $K_T - K_W$ versus C_K is shown in Fig. 5. It can be seen, and will be shown quantitatively, that an optimum fit requires more than a single straight line in order to match the data over the full range of C_K.

The slope k_c is due not only to chlorophyll-like pigment concentration C_K but also is due to all biological factors influencing the total attenuation coefficient that partially co-vary with pigment concentration, e.g.: cell size and cell composition including the pigment/cell ratio, t. pigment/carbon ratio and the ratio of chlorophyll *a*/accessory pigments, variations in species composition, and, especially, variations in the ratio of living to dead plant material. Thus the slope k_c will be influenced by all the biological material, including detritus, that is associated with viable plant material and co-varies with it.

Particulate organic carbon (POC) is a measure of these biological constituents which co-vary with chlorophyll-like pigment concentration and, indeed, POC is a much more likely candidate to vary linearily with K_T than pigment concentration (see Appendix 2). However, we wish to understand the relationship between K_T and C_K (Fig. 5) and to do so it is necessary to understand the relationship between POC and phytoplankton carbon (PC).

Hobson *et al.* presented data (Fig. 6, Hobson *et al.* 1973) showing the relationship between identifiable organic carbon (composed primarily of phytoplankton carbon) and particulate organic carbon (composed of phytoplankton carbon plus nonliving organic detrital material). Their data, which they claimed to be representative of diverse ocean regions, was used by them to estimate changes in percentages of the particulate matter that is living, when concentrations of living matter change. When this was done their data separated into two groups, one having concentrations of living material greater than 150 to 200 mg/m^3 and the other having concentrations less than this amount. Their data were separated into two groups because 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 percent probability level than the sum of squares about the two regression lines.

Their data suggest that concentrations of unidentifiable carbon contributed about 50 percent to the POC in most oceanic waters where concentrations of plankton were low and that this detrital carbon contributed relatively less (1 to 30 percent) in waters with large amounts of plankton. In a related curve (Fig. 2, Hobson *et al.* 1973) these authors plotted the ratio of plankton carbon (PC) versus POC carbon and showed that this 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 from the data of Hobson *et al.* that in ocean waters with low to medium chlorophyll-like pigment concentrations the ratio of viable to detrital carbon is relatively lower than for waters where the pigment concentrations are high. It should also be noted that, while C_K is plotted linearly in Fig. 5, the C_K data covers three orders of magnitude. Thus two orders of magnitude of data are poorly illustrated by this linear figure.

Based upon this assumption the data of Fig. 5 were fit with two straight lines such that the following equations were satisfied:

$$K_T - K_W = K_{x1} + k_1 \cdot C_K \qquad C_K < C_B \tag{7a}$$

$$K_T - K_W = K_{x2} + k_2 \cdot C_K + K_B \qquad C_K > C_B \tag{7b}$$

$$K_{x1} + k_1 \cdot C_B = K_{x2} + k_2 \cdot C_B + K_B \qquad C_K = C_B \ . \tag{7c}$$

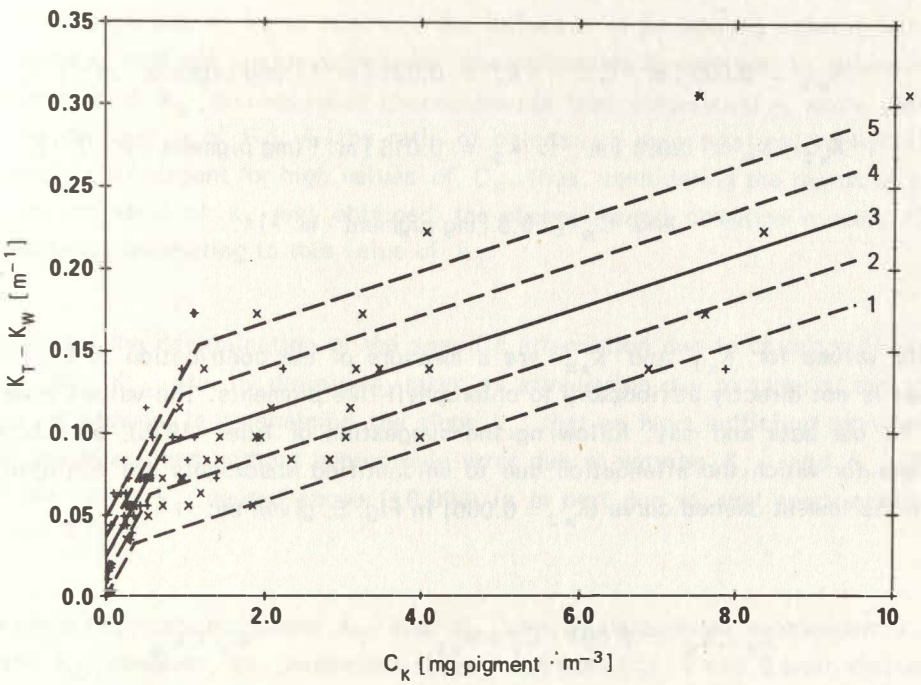

Fig. 5. $K_T - K_W$ versus C_K where K_T is the total diffuse attenuation coefficient for irradiance, K_W the attenuation coefficient for clear ocean water (taken equal to 0.027 m^{-1}) and C_K the average chlorophyll-like pigment concentration to a depth of one attenuation length. Points calculated from individually determined experimental data for C_K and K_T^{-1} from cruises listed in Table 1. The numbered solid lines are graphed values of Eqs. 8 for various values of $K_{x1}[m^{-1}]$ and $K_{x2}[m^{-1}]$:

(1) $K_{x1} = 0.00$, $K_{x2} = 0.00$ (3) $K_{x1} = 0.024$, $K_{x2} = 0.054$

(2) $K_{x1} = 0.012$, $K_{x2} = 0.027$ (4) $K_{x1} = 0.036$, $K_{x2} = 0.081$

(5) $K_{x1} = 0.048$, $K_{x2} = 0.108$

Line 3 is the least squares fit to the data where the parameters for the regression are given by Eqs. 7 where $K_{x1} = 0.023\,[m^{-1}]$, $K_{x2} + K_B = 0.081\,[m^{-1}]$, $k_1 = 0.091\,[m^{-1} \cdot (\text{mg pigment} \cdot m^{-3})^{-1}]$, $k_2 = 0.016\,[m^{-1} \cdot (\text{mg pigment} \cdot m^{-3})^{-1}]$, and $C_B = 0.8\,[\text{mg pigment} \cdot m^{-3}]$.

When our data are fit with two lines, rather than a single line, the results of an analysis of covariance indicates that the sum of squares about the regression line for the pooled data (single line) was significantly (at the 99 percent level) greater than the combined sum of squares about the two regression lines. A more complex fit to these data is the subject of continued investigation.

In the above equations C_B is a somewhat arbitrary pigment concentration representing the division between low and high pigment concentration waters. The value of K_B is defined by Eq. 7c and is a parameter necessary to ensure a continuous curve at the "boundary" ($C_K = C_B$) between the two regions. C_B was determined by making use of the analogous division found by Hobson *et al.* (1973) for POC and by assuming a reasonable POC to pigment ratio. The data were then fit by Eqs. 7 and this fit was iterated until condition 7c was satisfied. This fit is shown by the solid line in Fig. 5 and the values for the constants from this fit are:

$$K_{x1} = 0.023\,[m^{-1}], \qquad k_1 = 0.091\,[m^{-1} \cdot (\text{mg pigment} \cdot m^{-3})^{-1}],$$

$$K_{x2} + K_B = 0.081\,[m^{-1}], \quad k_2 = 0.016\,[m^{-1}\,(\text{mg pigment} \cdot m^{-3})^{-1}],$$

$$\text{and} \quad C_B = 0.8\,[\text{mg pigment} \cdot m^{-3}] \ .$$

The finite values for K_{x1} and K_{x2} are a measure of the contribution of biogenous material to attenuation that is not directly attributable to chlorophyll-like pigments. The values given above are the mean values for our data and may, following the suggestion of Tyler (1975), be subtracted in order to obtain equations for which the attenuation due to unidentified absorbents are negligible. When this is done we obtain the lowest dashed curve ($K_{x2} = 0.000$) in Fig. 5, given by:

$$K_T - K_W = 0.091 \cdot C_K + K_{x1} \qquad C_K < C_B \tag{8a}$$

$$= 0.027 + 0.016 \cdot C_K + K_{x2} \qquad C_K > C_B \tag{8b}$$

where K_B was found to be $0.027\,[m^{-1}]$ (not to be confused with K_W) and C_B is determined, for various values of K_{x1} and K_{x2}, from Eq. 7c. Equations 8 have been graphed on Fig. 5 for several values of K_{x1} and K_{x2}.

It should be noted that, because we have analyzed the data in two independent groups, the mean values for K_{x1} and K_{x2} are different. This is because, for each group of data, the mean amount of attenuation due to material that does not co-vary with C_K is different. As a consequence, there is an artificial discontinuity in K_x between the two regions of high and low pigment concentrations. In principle, with a more complex fit to the data, this artificial discontinuity at $C_K = C_B$ could be eliminated. For the present analysis this added complexity is not necessary.

Thus the total diffuse attenuation coefficient has been defined for two groups of data. One for low C_K, where the relative contribution of detrital material to the slope of k_1 is appreciable. Another for high C_K, where the relative contribution of detrital material to the slope k_2 is significantly less. Because the relative contribution of unidentified organic carbon becomes small for high values of C_K we can, as a first approximation, consider k_2 to be the specific attenuation coefficient due to chlorophyll-like pigments.

Based upon the analysis shown in Fig. 5 the specific attenuation due to chlorophyll-like pigments k_2 is found to be 0.016 ± 0.003 [m^{-1}(mg pigment m^{-3})$^{-1}$]. This agrees with Bannister's (1974a) accepted value of k_2 which was obtained by averaging estimates, ranging from 0.013 to 0.020, of Megard (1972), Talling (1970), M. Lorenzen (1972), and C. J. Lorenzen (1972). We do not agree with the value obtained by 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 co-varying detrital material on our result. It should be noted that our analysis includes phaeopigments in addition to chlorophyll *a*. Some of the previous estimates of k_2 distinguished phaeopigments from chlorophyll *a*, while others did not. As explained in the discussion of Fig. 4, the ratio of chlorophyll *a* to total chlorophyll-like pigment concentration approaches 90 percent for high values of C_K. Thus, considering the region of pigment concentrations for which our value of k_2 was obtained, the phaeopigments comprise roughly 10 percent of the pigment concentration contributing to this value of k_2.

In this analysis for the determination of the specific attenuation due to chlorophyll-like pigments the parameters K_{x1} and K_{x2} are, by definition, taken as attenuation due to material that does not co-vary with C_K. Thus we assume, in determining the slope k_2, that we have sufficient representative data such that k_2 may be determined without appreciable error due to varying K_{x1} and K_{x2}. 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, Eqs. 8 can be used to calculate K_x. However, the parameters determined from Eqs. 7 and 8 were derived from data obtained from waters whose dissolved and suspended material were largely of biogenous origin and their direct application, for remote sensing, is limited to such waters. For waters noticeably affected by terrigenous material, an additional term would need to be added to the right-hand side of these equations in order 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.

There is a fine point, in the interpretation of the constants in Eqs. 7 and 8, that is due to the wavelength dependence of the parameters involved. Figure 5 presents data of the diffuse attenuation coefficient for total quanta, that is, it presents data for the attenuation of total quanta as a function of depth. However, the above arguments hold, and in a subsequent article Eqs. 7 will be fit to data with the attenuation coefficients expressed as a function of wavelength. Thus, the analysis shown in Fig. 5, and the magnitude of the constants obtained, are in part influenced by the spectral characteristic of the optical constants. In the present article we will continue to ignore the wavelength dependency of K_T.

Agreement between the slope k_2 and previous determinations of the specific attenuation coefficient due to chlorophyll lends support to our interpretation (suggested by the analysis of Hobson *et al.* 1973) of the nonlinear biological effects on Beer's Law. Thus we have achieved a useful result. For biogeneous natural waters the diffuse attenuation coefficient for irradiance has been cast into a form which is physically (satisfies Beer's Law) and biologically (k_2 represents the specific attenuation of an average ensemble of phytoplankton) meaningful.

C_K AND PRIMARY PRODUCTIVITY

Another example of the potential usefulness of C_K is its known relationship to primary productivity. Knowledge of primary productivity and its distribution in space and time is of sufficient importance to make averaged estimates of value. For circumstances where the remote sensing data is poorly complemented by surface data, it is still possible to estimate primary production. This may be done by taking C_K as an index of the standing stock of phytoplankton and by utilizing the general correlation between primary productivity and the concentration of phytoplankton (see, e.g., Koblentz-Mishke *et al.* 1970).

Figure 6 shows the correlation between the 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

$$P_T[\text{mg C} \cdot (12\text{h})^{-1} \cdot \text{m}^{-3}] = \frac{1}{4.61\ K_T^{-1}[\text{m}]} \int_0^{4.61\ K_T^{-1}} P(z)\,[\text{mg C} \cdot (12\text{ h})^{-1}\,\text{m}^{-3}] \cdot dz[\text{m}]\,, \qquad (9)$$

where $P(z)$ is the productivity per 12-hour day per m^3 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 may be used to estimate P_T from C_K provided uncertainties of several-fold are acceptable (see Appendix 3).

It has been pointed out by many authors (see, e.g., Patten 1961) that the consistently high correlation found between phytosynthesis and chlorophyll concentration is surprising when we consider: (1) the known loss of phytosynthetic efficiency at high concentrations brought about by high population densities, (2) the occurrence of inactive chlorophyll, (3) the association of large quantities of chlorophyll and its degradation products with nonliving detritus, and (4) the variations in the ratio of productivity per unit of chlorophyll *a* defined as the assimilation ratio, R_A [mg C · h^{-1} · (mg Chl *a*)$^{-1}$].

In spite of these reasons the correlation shown in Fig. 6 indicates that about three-fourths of the variance in P_T can be accounted for by corresponding differences in C_K. To the extent that the above listed causes can be shown to contribute to the variance between P_T and C_K it is possible, by utilizing both ancillary information which can be obtained by satellite and complementary surface data, to reduce the standard error in estimating P_T from C_K.

For example, total irradiance, time of year, and surface temperature are all ancillary data which can be obtained by means of remote sensing. Each of these variables (irradiance, season, temperature) have been suggested as a contributing cause for the variability of the assimilation ratio (Curl and Small 1965, Mandelli *et al.* 1970, Malone 1971). Thus to the extent that variations in the assimilation ratio can be accounted for by variability in irradiance, season or temperature, the standard error in estimating P_T from C_K can be reduced (Appendix 3).

As a further example of how surface data may usefully complement satellite data, consider the Climax I data (Δ's) shown in Fig. 6. For this set of data an effort was made, by using parachute drogues, to follow and sample a relatively coherent body of water. To the extent that this was successful, these data may be considered as "replicate" measurements, on successive days, of productivity and pigment

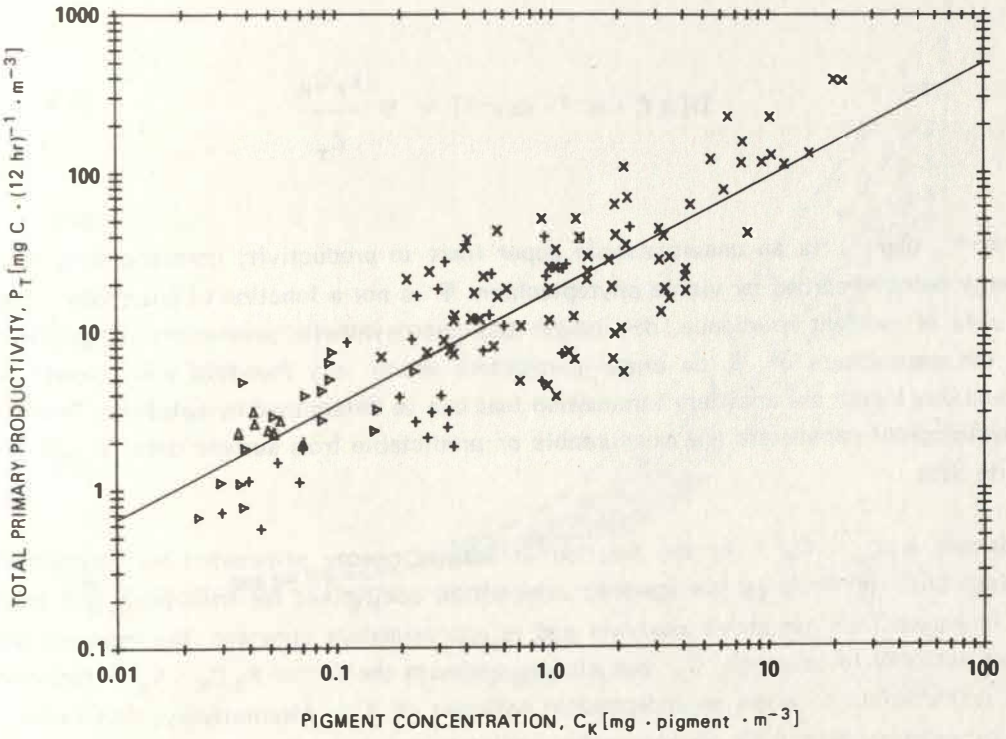

Fig. 6. Logarithm of the total average productivity, P_T[mg C · (12h)$^{-1}$ · m^{-3}], within the euphotic zone versus log chlorophyll-like pigment concentration to a depth of one attenuation length, C_K[mg pigment · m^{-3}] (N = 126, r = 0.855, $P_c < 0.01$). The least squares regression formula for these data is given by log P_T = 1.254 + 0.728 log C_K.

concentrations. The sample variance (the standard error of estimate squared) for the seven replicate Climax I data points shown in Fig. 6 is 0.0036. The sample variance for all the data is 0.1093. Thus, if replicate samples are taken as a measure of experimental error, about 3.3 percent of the observed variance between P_T and C_K can be ascribed to experimental error. While it may be anticipated this estimate of experimental error will be larger when combining data from diverse experimental investigations, these data do give an indication of the amount of variance due to the experimental error when estimating P_T from C_K.

PIGMENT CONCENTRATION AND PRODUCTION EQUATIONS

A method for the measurement of 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 authors (Talling 1957, Steel 1962, Steel and Menzel 1962, Vollenweider 1965, Fee 1969) have developed equations for gross-daily production in the water column based on environmental factors, including incident irradiance and chlorophyll concentrations and on factors dependent upon the physiology of the phytoplankton.

Recently, Bannister (1974a,b) has reviewed these earlier equations and has re-cast them into more fundamental and general forms. In particular, he has shown that equations for daily production can be written

$$\Pi[\text{g C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}] = \Psi \frac{k_2 C_K}{K_T} \tag{10}$$

Ψ [g C · m^{-2} · day^{-1}] is an unsurpassable upper limit to productivity corresponding to all available radiant energy being absorbed by viable phytoplankton. Ψ is not a function of chlorophyll concentration, but rather only of incident irradiance, day length and photosynthetic parameters. Bannister (1974b) has discussed the dependence of Ψ on algae parameters which vary four-fold with growth rate. Incident irradiance and day length are ancillary information that can be determined by satellite. Thus, to the extent that the physiological parameters are measureable or predictable from surface data, Ψ can be estimated from satellite data.

The factor $k_2 C_K \cdot K_T^{-1}$ is the fraction of radiant energy attenuated by phytoplankton, where k_2[m^{-1} · (mg Chl · m^{-3})$^{-1}$] is the specific attenuation coefficient for irradiance due to chlorophyll. Since k_2 is known from our above analysis and is approximately constant, the remotely sensed K_T^{-1} may be used not only to estimate C_K but also to estimate the factor $k_2 C_K \cdot K_T^{-1}$ (provided spectral information is sufficient to allow an independent estimate of K_x). Alternatively, this ratio may also be determined by means of Eqs. 8 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. Note that, unlike Bannister, we have combined chlorophyll and phaeopigments in our notation for C_K and must, therefore, utilize a relationship like that given in Fig. 4 in order 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 versus the chlorophyll concentration plotted logarithmically. This fraction can be represented either by the ratio $\Pi \cdot \Psi^{-1}$ from the production equations given by Bannister or by the experimentally measured ratio $k_2 C_K \cdot K_T^{-1}$. Thus this fraction links the production equations to the experimental data. By means of Eqs. 8a and b, we can calculate the ratio $k_2 C_K \cdot K_T$ and plot it versus log C_K as shown by the solid lines in Fig. 7 A particular data point plotted on this graph thus provides the following information.

First, the fraction of the incident irradiance that is actually attenuated by chlorophyll-like pigments, and thus (using Fig. 4) the fraction of radiant energy attenuated by viable phytoplankton, is obtained. This information allows one to calculate (Eq. 10) the potential productivity Π from the known radiant energy utilized by phytoplankton, provided Ψ (which depends on algae 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 non-chlorophyll-like material can be estimated by comparing a plotted data point with the family of K_x curves. Alternatively, K_x may be calculated using Eqs. 8 from experimentally determined values of K_T and C_K.

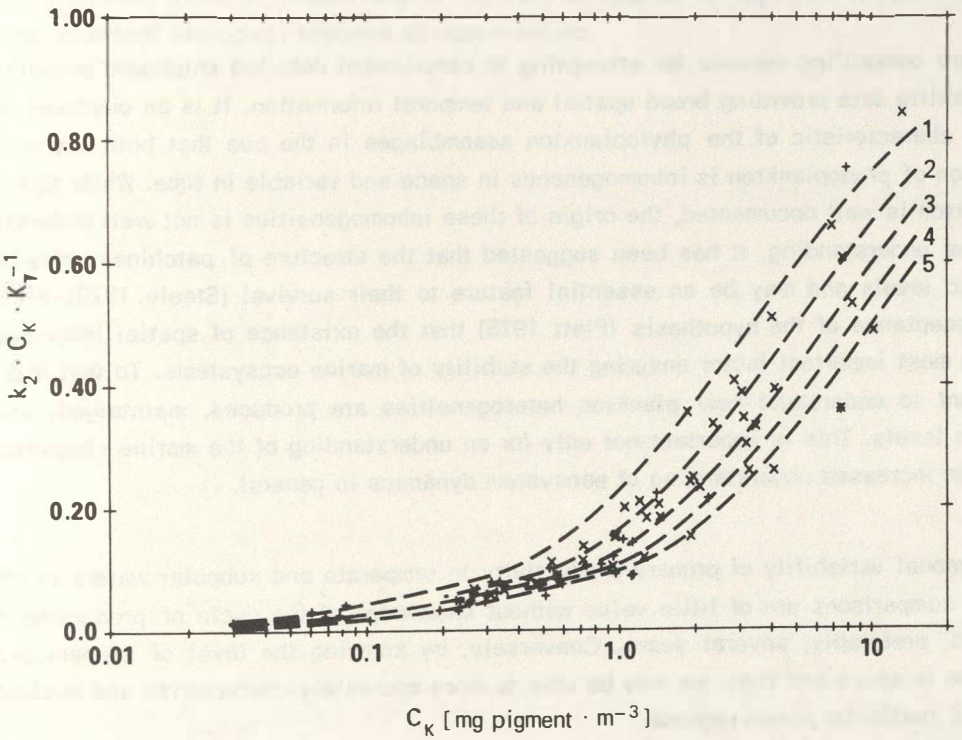

Fig. 7. Fraction of radiant energy attenuated by chlorophyll-like pigments, $k_2 \cdot C_K \cdot K_T^{-1}$, versus log chlorophyll-like pigment concentration to a depth of one attenuation length, C_K[mg pigment · m^{-3}]. Points calculated from individually determined experimental data for C_K and K_T^{-1} (Table 1) using $k_2 = 0.016$ [m^{-1} · (mg pigment · m^{-3})$^{-1}$]. The numbered solid lines are graphed values of $k_2 \cdot C_K \cdot K_T^{-1}$ using Eqs. 8 to determine K_T^{-1} for the same values of K_{x1} and K_{x2} listed for Fig. 5.

Third, by comparing Π with actual measured photosynthesis, the difference may be ascribed to non-radiant energy effects, e.g., grazing, nutrient limitation, mixing, etc. Thus limitations due to radiant energy have been separated and facilitate direct consideration of these other effects.

Bannister (1974a) has transformed the production equations of several workers into a form which is an explicit function of phytoplankton concentration and which does not contain parameters for coefficients dependent upon phytoplankton concentration. Further, in order to simplify theoretical analysis, the parameters of his transformed equations have been chosen so as to minimize the range of values needed to describe the variations of photosynthesis 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 also in a form which can be directly incorporated into a general theory of phytoplankton dynamics. By use of these production equations with satellite data (input irradiance, day length, 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.

DISCUSSION AND SUMMARY

There are compelling reasons for attempting to complement detailed shipboard primary productivity data with satellite data providing broad spatial and temporal information. It is an observed, and possibly fundamental, characteristic of the phytoplankton assemblages in the sea that both the environment and the distribution of phytoplankton is inhomogeneous in space and variable in time. While this "patchiness" of phytoplankton is well documented, the origin of these inhomogeneities is not well understood. In spite of this lack of understanding, it has been suggested that the structure of patchiness may be utilized by higher trophic levels and may be an essential feature to their survival (Steele 1973). Further, there is increasing acceptance of the hypothesis (Platt 1975) that the existence of spatial inhomogeneities may be the single most important factor ensuring the stability of marine ecosystems. To test this hypothesis, it is important to understand how plankton heterogeneities are produced, maintained, and related to higher trophic levels. This is important not only for an understanding of the marine ecosystem in particular, but for an increased understanding of ecosystem dynamics in general.

The seasonal variability of primary productivity in temperate and subpolar waters is often so great that regional comparisons are of little value without knowledge of the cycle of production throughout at least one and, preferably, several years. Conversely, by knowing the level of primary production and its distribution in space and time, we may be able to more accurately characterize and evaluate biological productivity of particular ocean regions.

The application of theoretical models of the photosynthetic productivity of planktonic algae to ecological situations would be more effective if estimates of integral photosynthesis could be made for prolonged periods and over wide spatial regions. In order for models of plankton dynamics to become less descriptive and more predictive, it is necessary for the input data to such models to be more comprehensive.

A basic objective of understanding primary productivity in the world's oceans is to increase our knowledge of the fundamental relationships between different trophic levels. To date, our knowledge of plankton production cannot be regarded as a satisfactory instrument with which to link the fisheries with their environment. This lack is in part due to the spatially and temporally limited data obtainable by surface vessels.

Satellite data will provide significant complementary, and otherwise practically unattainable, information to that gathered at the ocean surface. It will allow the detection and measurement of the growth and decay of plankton patchiness which, in turn, should lead to a more complete understanding of the stability of marine ecosystems. It will provide data to assess the seasonal variability of regions in the world's oceans. It will provide the required spatial and temporal information necessary for descriptive, and predictive, modeling of plankton dynamics. It will provide a real-time awareness of the ecosystem, thus allowing the system's oceanographer (Walsh 1972), while at sea, to adapt his experimental program to the spatial and temporal variations of the area under study. All of these factors converge toward providing a more complete experimental description and a better theoretical understanding with which to link fisheries' production to the environment through an understanding of primary productivity. Remote sensing will allow the spatial and temporal variability, inherent in this biological data, to be more completely assessed. For these reasons we have investigated how accurately our measure of the bio-optical state of ocean waters, K_T, can be related to C_K and, in turn, how C_K may be linked to other important biological features of ocean waters.

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APPENDIX 1

LINEAR REGRESSION AND CORRELATION ANALYSIS

Linear regression and correlation analysis used in this report follows the development of Bevington (1969). In particular, the program POLFIT, LINFIT, PCORRE, and REGRES were used. Briefly, the basic concepts used are as follows.

For data consisting of pairs of measurements (x_i, y_i) of an independent variable x and a dependent variable y the data were fit to

$$y = a + bx$$

by the method of least squares. We wish to determine whether or not the variations in the observed values of y are correlated with the variations in the measured values of x. Since we are considering the interrelation between the variables x and y, we can equally well consider x as a function of y and fit the equation

$$x = a' + b' y$$

The experimental linear-correlation coefficient is defined as

$$r \equiv \sqrt{b\, b'}$$

and is a measure of the degree of linear correlation between the variables x and y (calculated by LINFIT).

As pointed out by Bevington, "the correlation coefficient r cannot be used directly to indicate the degree of correlation." However, "a common test for r is to compare its value with the probability distribution for a parent population which is completely uncorrelated. Such a comparison will indicate whether or not it is probable that the data points could represent a sample derived from an uncorrelated

population.'' By means of the PCORRE program the probability $P_e(r,N)$ that a random sample of N uncorrelated experimental data points would yield an experimental linear-correlation coefficient as large as or larger than the observed value of $|r|$ can be calculated. Thus $P_e(r,N)$ indicates the probability that the observed data could have come from an uncorrelated parent population.

The square of the experimental linear-correlation coefficient, r^2, is called the coefficient of determination. It shows what proportion of the variance in the value of the dependent variable can be explained by, or estimated from, the concomitant variation in the value of the independent variable. Note that the fact that $100 \cdot r^2\%$ of the variance in y can be ''explained by'' corresponding differences in x does not in itself mean that the differences in x ''caused'' the differences in y. This statistical measure merely indicates how closely the variance in x was associated with the variance in y.

APPENDIX 2

NONLINEAR BIOLOGICAL EFFECTS

There is additional evidence supporting the hypothesis that low and high productivity waters are different with respect to the ratio of viable phytoplankton to total particulate organic carbon, PC/POC. Low productivity regions, where $C_K < C_B$, are heavily cropped by zooplankton which leads to a relatively large fraction of detrital material. In contrast, high productivity waters are subjected to less grazing pressure and detrital material contributes a smaller fraction of the POC.

As suggested in the text it is POC that, in biogenous waters, is expected to be linearly related to $K_T - K_W$. It is then the nonlinear relationship between PC and POC that introduces the nonlinearity between $K_T - K_W$ and C_K. Our analysis of $K_T - K_W$ versus POC indicates that a single linear fit to the data cannot be significantly improved by a two-region fit to the data.

Figure 4 shows that the relationship between phaeopigments, C_{2K}, and chlorophyll *a*, C_{1K}, is also nonlinear. This nonlinearity does not contribute significantly to the nonlinear $K_T - K_W$ versus C_K relationship. It does, however, indicate that the relative contribution of phaeopigments to the total pigment concentration decreases with increasing pigment concentration, at least to depths of one attenuation length.

Figure A2-a, a plot of C_{1K} versus C_K, shows that to a depth of one attenuation length the contribution of phaeopigments to the total pigment concentration is relatively small (i.e., the departure of the data points from the straight line, indicating $C_{1K} = C_K$ or $C_{2K} = 0$, is small). As is generally recognized, similar data from 3 to 4 attenuation lengths as shown in Fig. A2-b, shows a relatively greater contribution of phaeopigments to the total pigment concentration.

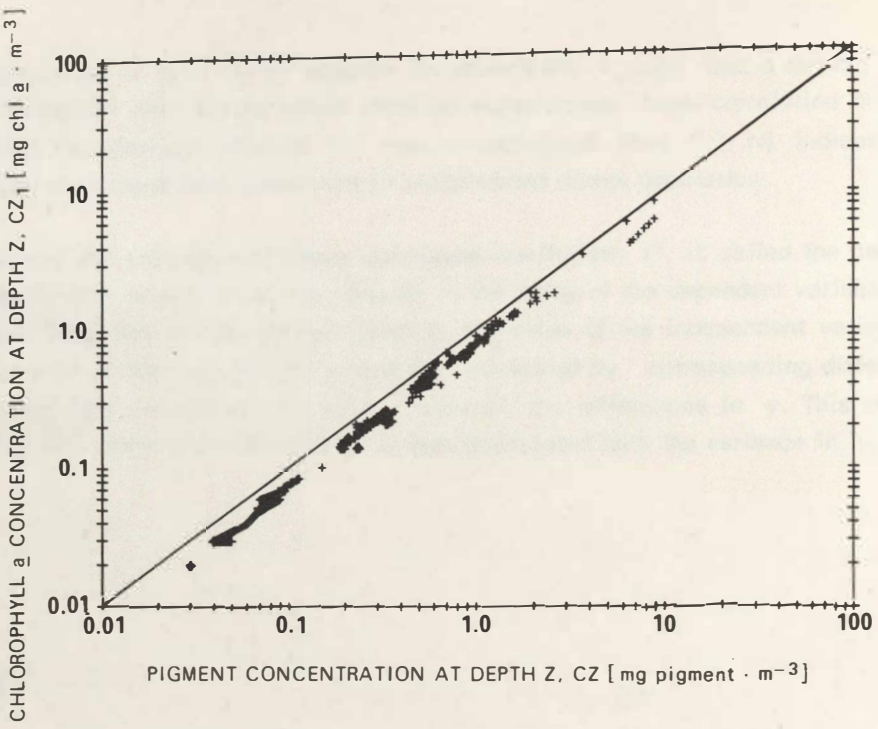

Fig. A2-a. Logarithm of the concentration of chlorophyll *a* [mg Chl *a* · m^{-3}] versus log total chlorophyll-like pigment concentration [mg pigment · m^{-3}], at a particular depth z within the range of depths from the surface to one attenuation length K_T^{-1}. Total pigment concentration is the sum of chlorophyll *a* plus phaeophyton.

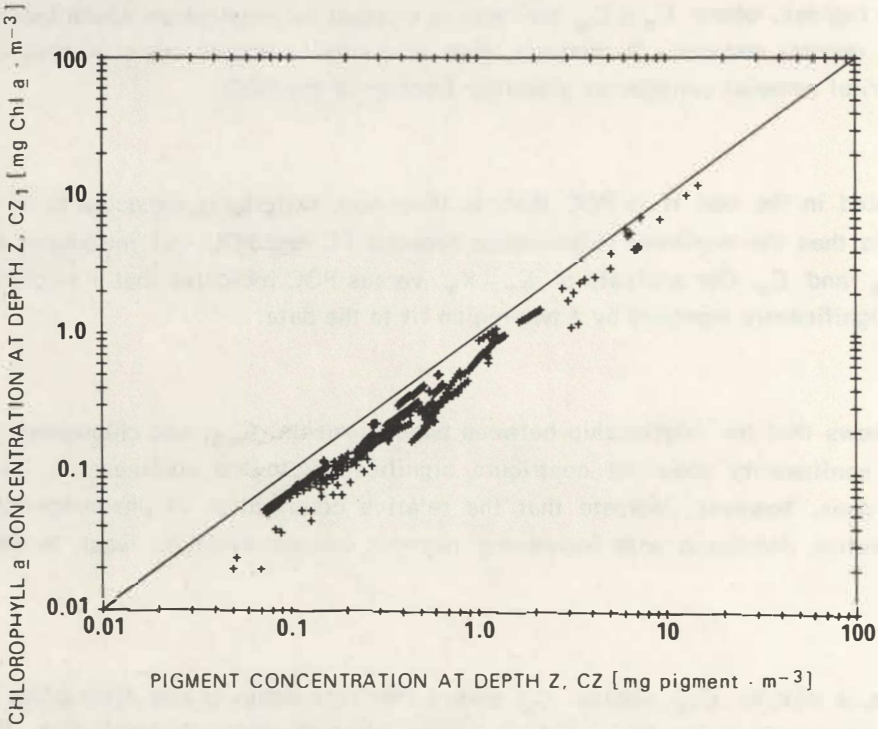

Fig. A2-b. Log of the concentration of chlorophyll *a* [mg Chl *a* · m^{-3}] versus log total chlorophyll-like pigment concentration [mg pigment · m^{-3}], at a particular depth z within the range of depths from $3 \cdot K_T^{-1}$ to $4 \cdot K_T^{-1}$.

APPENDIX 3

P_T VERSUS C_K

The logarithm of the total average productivity within the euphotic zone, P_T, versus log chlorophyll-like pigment concentration to a depth of one attenuation length, C_K, was presented in Fig. 6. The least squares regression formula for these data is given by

$$\log P_T = (1.254 \pm 0.030) + (0.7284 \pm 0.0398) \log C_K$$

and the standard error of estimate of log P_T from these data is 0.3209. Thus the standard error of estimate of P_T, for some arbitrary chosen C_K, is roughly plus or minus a factor of two ($10^{0.3209} \sim 2$).

As pointed out when discussing the Climax data only a fraction of this error of estimate can be attributed to uncertainties in experimental replication, the remainder is presumably due to environmental and physiological changes in the photosynthetic process. Our data were analyzed with the aim of seeing if any environmental factors, that could in principle be determined by appropriate satellite sensors, could be used to reduce the standard error of estimate of P_T from C_K. None of our analyses have succeeded in this aim. However, these "negative" results are of interest and are therefore reported here.

To investigate the possibility that variations in total daily irradiance contributed to the standard error of estimate for P_T from C_K these data were plotted indicating the total daily downwelling irradiance incident in the ocean surface (Fig. A3-a). The data were separated into several zones of differing total irradiance and no significant differences in P_T vs C_K, for the several irradiance zones, were

observed. This cursory analysis does not distinguish between a cloudy day in summer and a sunny day in winter, each having the same daily irradiance, and hence seasonal effects are not accounted for. It will require further investigation, with data analyzed with respect to both season and irradiance, in order to determine a possible influence of total daily irradiance on the standard error of estimate of P_T from C_K.

Almost by definition part of the error in estimating P_T from C_K is due to variations in the assimilation ratio. Daily irradiance, season, and temperature have all been suggested (Curl and Small 1965, Mandelli *et al.* 1970, Malone 1971) as causes contributing to variations in R_A, where

$$R_A \equiv \frac{P_T\,[\text{mg carbon fixed} \cdot m^{-3} \cdot hr^{-1}]}{C_T\,[\text{mg chl } \underline{a} \cdot m^{-3}]} .$$

Our results, Figs. A3-b, c, do not show any usefully significant correlations of R_A with daily irradiance, season (separate Cruises), or surface temperature.

In spite of these negative results it is clear that the standard error of estimate of P_T from C_K could be reduced if R_A could be independently estimated. Since other workers have found useful correlations with R_A, further efforts to estimate R_A by satellite should be pursued.

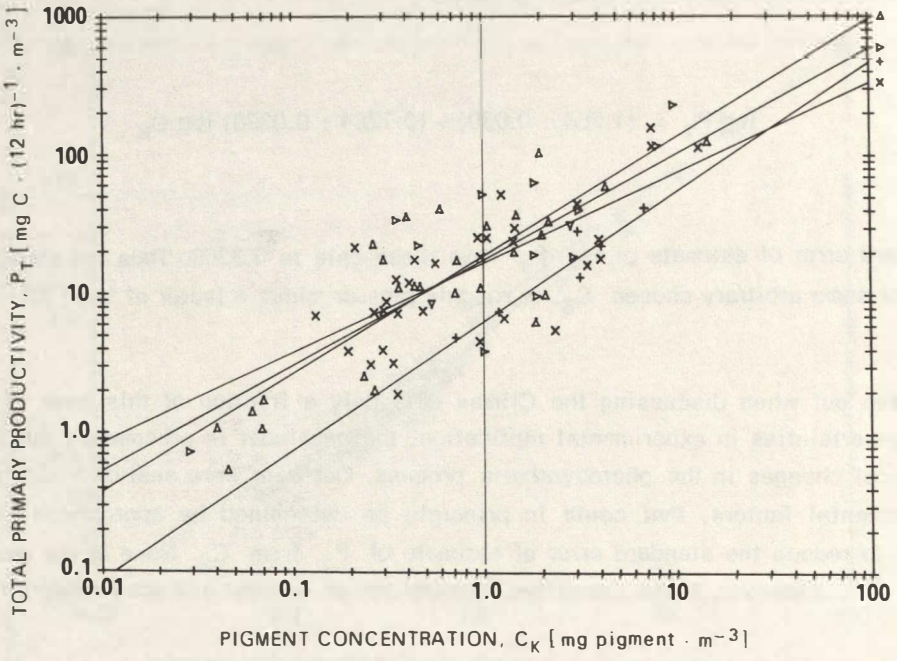

Fig. A3-a. Logarithm of the total average productivity within the euphotic zone, P_T, versus log chlorophyll-like pigment concentration to a depth of one attenuation length. The data are separated into several zones of total daily incident irradiance, in units of langleys per day, as follows: + 1-100, × 101-200, △ 201-300, ▷ 301-400, ▽ 401-500.

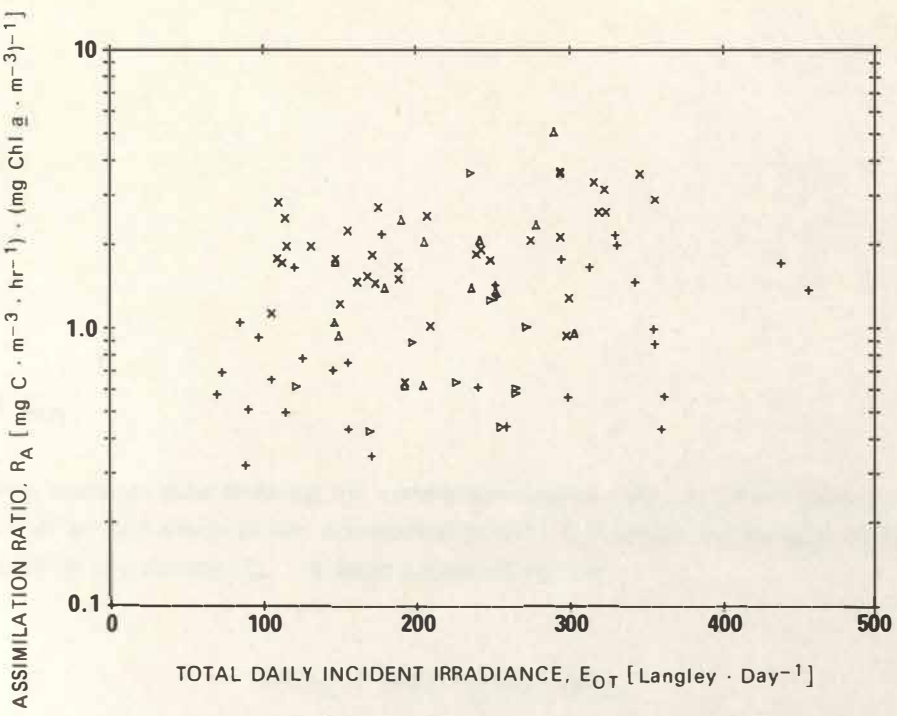

Fig. A3-b. Log of the assimilation ratio, R_A [(mg C · m^{-3} · hr^{-1}) · (mg chl *a* · m^{-3})$^{-1}$], versus total daily incident irradiance, E_{OT} [langley · day^{-1}]. The data are separated into four temperature zones, in degrees centigrade, as follows: + 10-15, × 16-20, ▲ 21-25, ▶ 26-30.

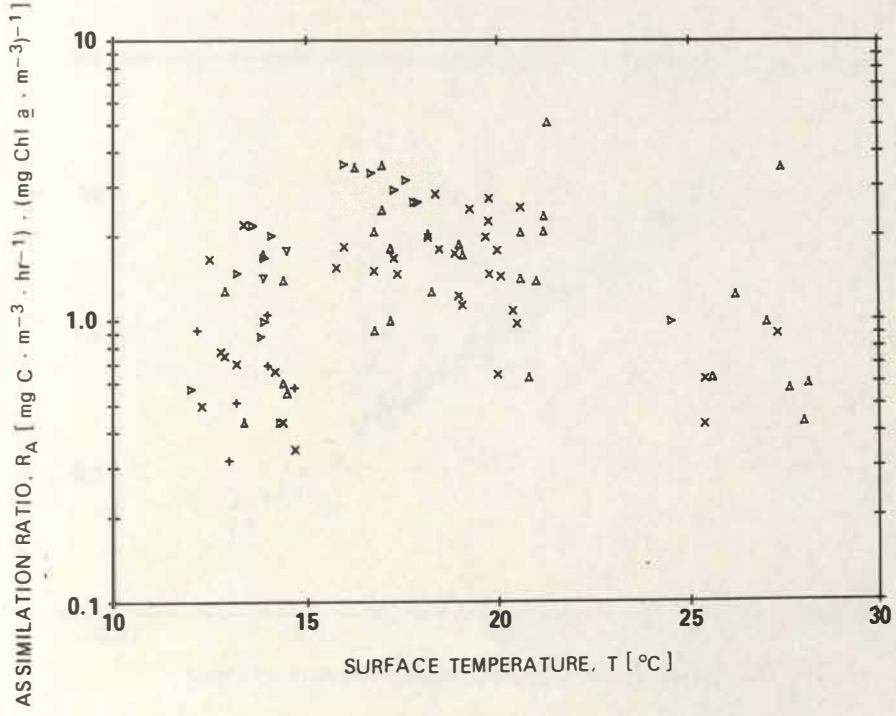

Fig. A3-c. Log of the assimilation ratio, R_A versus surface temperature, T [°C]. The data are separated into several zones of total daily irradiance, in units of langleys per day, as follows: + 1-100, × 101-200, ▲ 201-300, ▶ 301-400, ▼ 401-500.

APPENDIX 4

C_K VERSUS C_O

Figure A4-a presents data showing the correlation between the log of the average chlorophyll-like pigment concentration to a depth of one attenuation length, C_K, versus log average chlorophyll-like pigment concentration of the surface, C_O. A least squares fit gives

$$\log C_K = 0.031 + 0.961 \log C_O$$

where N = 104, r = 0.986, and $P_c < 0.01$. The high correlation coefficient implies that 97 percent of the variance in log C_K is associated with the variance in C_O. Thus the remotely sensed signal, C_K, is highly correlated with conventional surface measurement of the total chlorophyll-like pigment concentration.

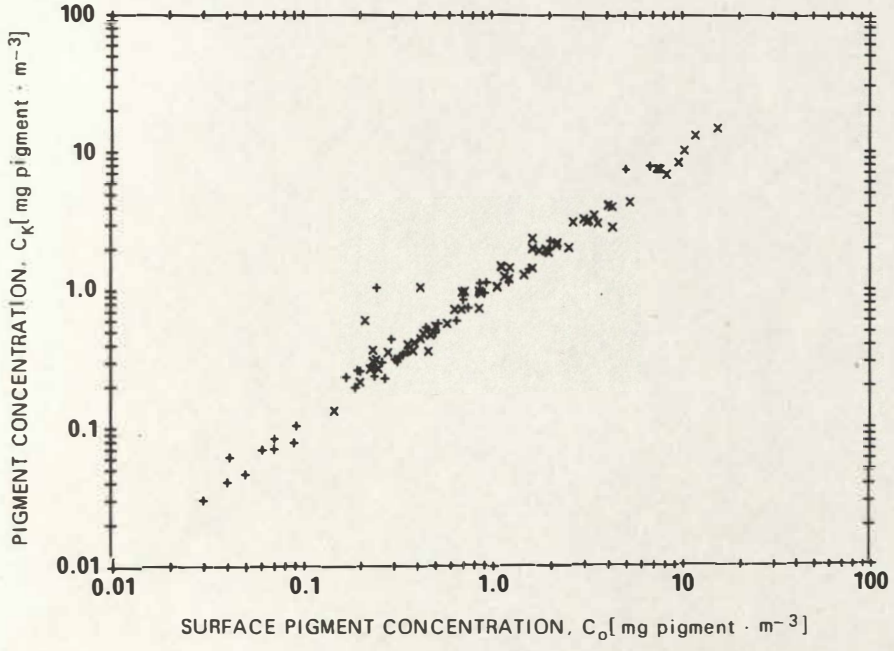

Fig. A4-a. Plot of log C_K versus log C_O where C_O is the average chlorophyll-like pigment concentration in the top meter of the water column.