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Structural and Functional Aspects of the Ecology of Submerged Aquatic Macrophyte Communities in the Lower Chesapeake Bay Volume I I: Submarine Light Quantity and Quality in the Lower Chesapeake Bay and Its Potential Role in the Ecology of Submerged Seagrass Communities

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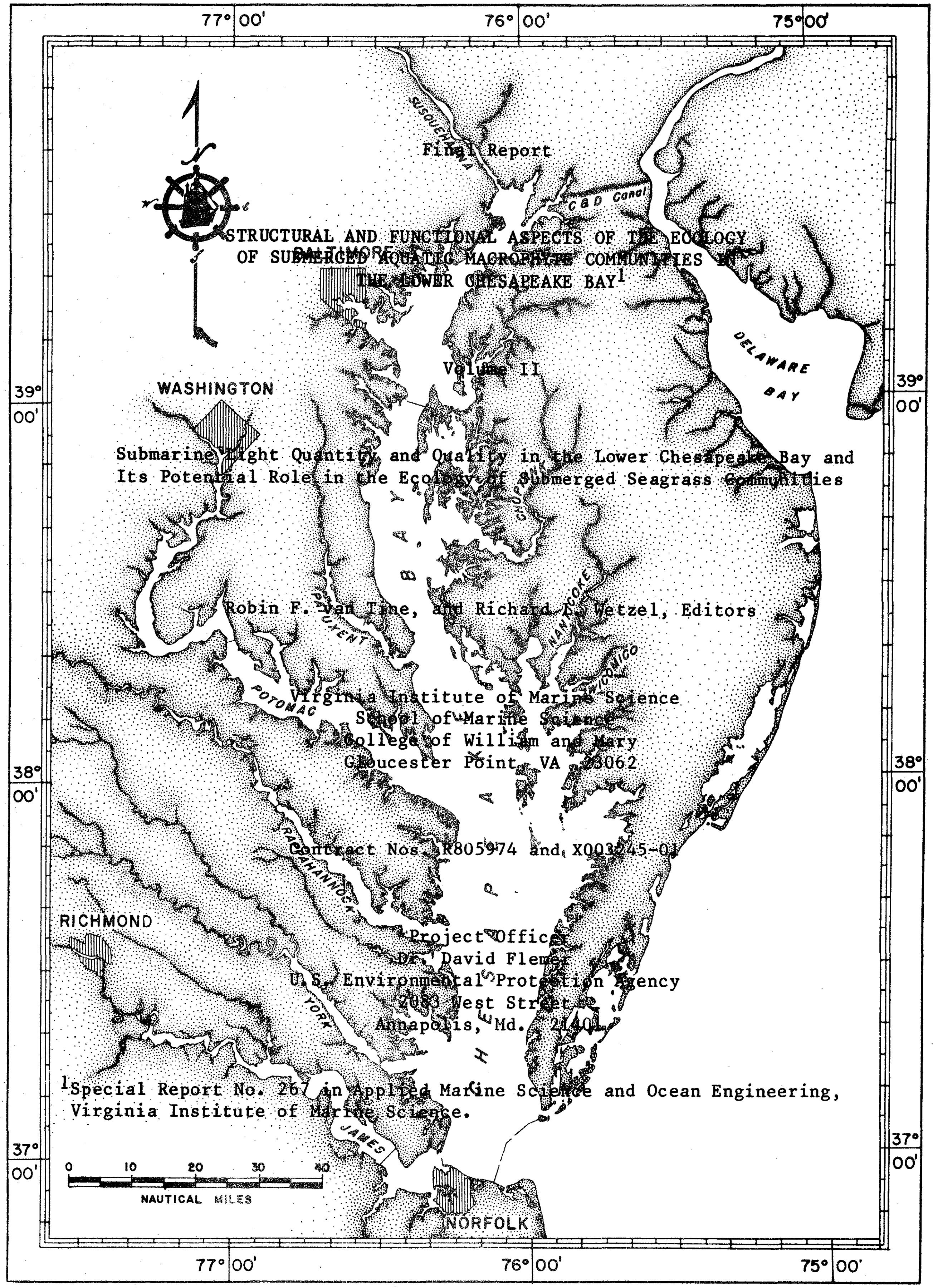
Recommended Citation

Van Tine, R. F., & Wetzel, R. L. (1982) Structural and Functional Aspects of the Ecology of Submerged Aquatic Macrophyte Communities in the Lower Chesapeake Bay Volume I I: Submarine Light Quantity and Quality in the Lower Chesapeake Bay and Its Potential Role in the Ecology of Submerged Seagrass Communities. Special Reports in Applied Marine Science and Ocean Engineering (SRAMSOE) No. 267 V2. Virginia Institute of Marine Science, College of William and Mary. https://doi.org/10.21220/V5BT95

Mike Bender



Final Report

STRUCTURAL AND FUNCTIONAL ASPECTS OF THE ECOLOGY OF SUBMERGED AQUATIC MACROPHYTE COMMUNITIES IN THE LOWER CHESAPEAKE BAY[1]

Volume II

Submarine Light Quantity and Quality in the Lower Chesapeake Bay and Its Potential Role in the Ecology of Submerged Seagrass Communities

Robin F. Van Tine, and Richard L. Wetzel, Editors

Virginia Institute of Marine Science
School of Marine Science
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Gloucester Point, VA 23062

Contract Nos. R805974 and X003245-01

Project Officer
Dr. David Flemer
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PREFACE

The research reported on in this volume is concerned with the underwater light environment and its relationship to submerged aquatic vegetation. Since light energy is the force by which all ecosystems are driven and since it has been suggested by some researchers that the light environment of the Chesapeake Bay has deteriorated coincident with declining SAV distribution, a research program was devised to analyze the underwater light environment of the lower Chesapeake Bay with respect to seagrasses. As estuarine waters are frequently heavily laden with both autochthonous and allochthonous loads of both organic and inorganic suspended and dissolved materials--all of which affect the spectral distribution of light underwater--we determined it was important to measure not only white light, but also specific light energies across the entire photosynthetically significant portion of the spectrum.

The results of these studies along with an analysis of past and present research on this topic reported for the Chesapeake Bay, a primer on aquatic optics and a comparative report on underwater irradiance in a tropical seagrass bed are presented in this report.

It is hoped that the results presented in this document will be an aid to those charged with managing the Chesapeake Bay and a stimulus for further research.

Robin van Tine
Gloucester Point, VA
August 1982

ACKNOWLEDGEMENTS

The authors would like to take this opportunity to thank some of the many people who helped in various phases of the research reported herein: Bill Cook and Walt Valentine, formerly of the Chesapeake Bay Program for their unusually enthusiastic support and ideas; Rick Hoffman, Denise Mosca and Sandy Sotsky for their technnical help in the field and lab; Mike Castagna and the staff of the V.I.M.S. Wachapreague field station for physical support; Mike Bender for financial support for one of us (R.v.T.) allowing the completion of the analysis of data and writing of this report; Gene Silberhorn for Wetlands Department boat time; Dennis Clark of NOAA for his helpful suggestions and preliminary analysis of the underwater irradiance at Vaucluse Shores; Nancy White and Carole Knox and the V.I.M.S. Word Processing staff for their tireless retyping of endless revisions of this report.

Finally and especially we would like to thank our wives, Melissa van Tine and Beverly Wetzel and our children, Tristan van Tine, Paige and Chris Wetzel for thier support and understanding during many long absences in the field, and many long nights and weekends in the lab, at the computer center and during much time spent scribbling on yellow pads.

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LIGHT IN AQUATIC ENVIRONMENTS:
A REVIEW OF BASIC CONCEPTS

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LIGHT IN AQUATIC ENVIRONMENTS

INTRODUCTION

The study of the interaction of solar energy with the watery milieu necessitates not only an understanding of the properties of light and H_2O but must also take into account the myriad living and non-living entities, both dissolved and suspended, which impinge upon the propagation of light in aquatic environments. During the hundred years since the first crude underwater measurements of light were made with photographic plates, technological evolution has provided a vast array of increasingly sophisticated measuring devices. Complex and competitive sets of terminologies coevolved with the instrumentation resulting in a rather confusing body of knowledge for the non-specialist.

In this section the author intends to unravel and clarify enough of the assumptions and jargon of marine optics to provide a basic conceptual framework to allow the reader to understand light research in the Chesapeake Bay and elsewhere and relate it to submerged aquatic vegetation.

Some Basic Physics and Terminology

The sun emits electromagnetic radiation in discrete packets or quanta (Q) of energy termed photons. The energy content (ε) of each quantum is directly proportional to the frequency (ν),

$$\varepsilon = h\nu$$

and indirectly proportional to the wavelength (λ),

$$\varepsilon = \frac{hc}{\lambda}$$

where h is Planck's universal constant and c is the speed of light in a vacuum. This means that quanta of shorter wavelengths contain more energy than quanta of longer wavelengths.

The spectral energy distribution of incoming solar radiation at both the top of the earth's atmosphere and the surface of the planet, for a clear sky, is shown in Fig. 1a (Gates, 1971). Most of the energy reaching the earth's surface is contained within the shorter wavelengths [.4-10 μ or 400-1000 nanometers[1] (nm)]. Not surprisingly, this also includes the region of greatest biological import--visible light, approximately 350-750 nm (Table I

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[1] 1 nm = 10^{-3} μm = 10^{-9}m

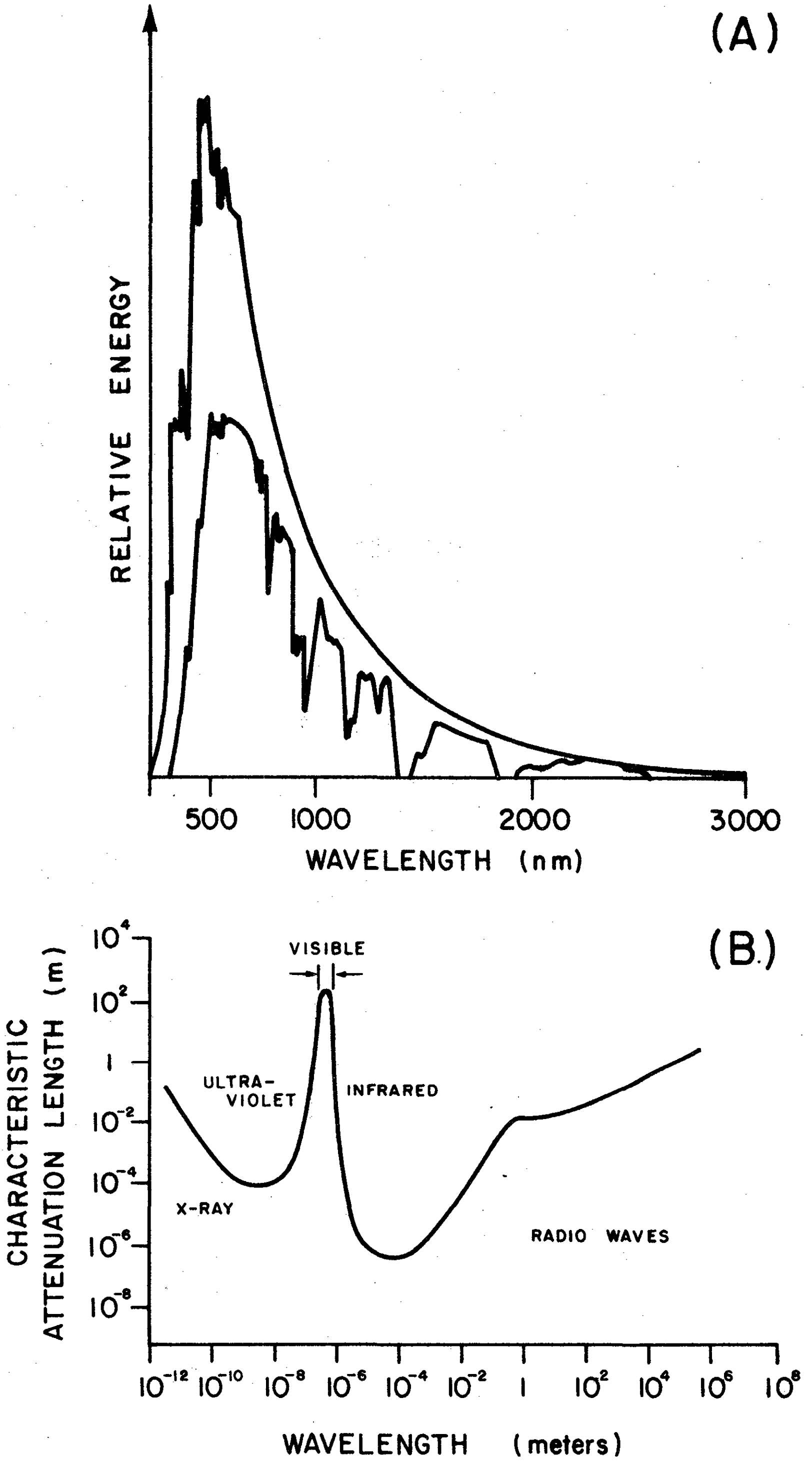

Figure 1. (a) Spectral distribution of solar radiation reaching the earth at the top of the atmosphere (upper curve) and the ground (lower curve) (After Gates, 1971). (b) The attenuation of electromagnetic energy in seawater (After Williams, 1970).

Table I

Approximate Wavelength Ranges of Colors

Color	(nm)
Ultraviolet	<380
Violet	380-450
Blue	450-490
Green	490-560
Yellow	560-590
Orange	590-630
Red	630-760
Infrared	>760

lists the approximate wavelength ranges for perceived color). In fact, visible light is the only portion of the electromagnetic spectrum which appreciably penetrates seawater - with the exception of very high frequency x-rays and very low frequency radio waves (Fig. 1b) (Williams, 1970). If the quanta distribution and the energy distribution are compared (Fig. 2) for the Photosynthetically Available Radiation (usually defined as 400-700 nm and termed (PAR or PhAR) it can be seen that the relative quanta and energy distributions differ in accordance with the physical nature of light. By integrating quanta and energy over the PAR

$$Q_{PAR} = \int_{400}^{700} \frac{dQ_\lambda}{d\lambda} \cdot d\lambda \qquad \varepsilon_{PAR} = \int_{400}^{700} \frac{d\varepsilon_\lambda}{d\lambda} \cdot d\lambda$$

and expressing the results as a ratio, comparisons can be made between differing water bodies (Fig. 3), sky conditions, depth, etc. (Morel and Smith, 1974; Jerlov, 1976; Dubinsky and Berman, 1979). Notice that the energy content per quantum decreases from clear oceanic to more turbid coastal waters (Fig. 3).

The most useful units and conversions for working with marine optics are listed in Table II. Only radiometric units are shown and not those for photometry (illumination, lumens, candles, lux, etc.) since the latter are biased for the "average human eye" and are not truly convertible to absolute energetic or quantum values. Recent measurements of light for ecological and biological purposes are almost always made as *irradiance*, i.e. the flux of energy or quanta per unit area. It is especially appropriate to use quanta measurements in biological or ecological studies since that is what organisms respond to.

Some Properties and Concepts of Optical Oceanography

The properties and concepts of optical oceanography are usually divided into two mutually exclusive classes: (1) *inherent* and (2) *apparent*. Inherent properties, such as *absorption* and *scattering*, are independent of changes in *insolation* (incoming light), whereas apparent properties, such as underwater *irradiance*, vary with changing solar and atmospheric conditions. Figure 4 illustrates some of the interrelationships between these properties and other parameters (Zaneveld, 1974).

Inherent Optical Properties

As light passes through the water column its energy content and spectral quality are changed by absorption and scattering due to the water molecules themselves, dissolved substances and suspended particles. The combined effect of these processes is termed *attenuation* and can be measured by a *beam transmissometer* (see Fig. 5). The ideal transmissometer emits a *collimated* (parallel) beam of light which is allowed to pass through the environment for a known distance and is then measured by a photocell after the scattered (non-parallel) rays are eliminated by a system of lenses and apertures. The circuitry of modern instruments, after compensating for ambient light,

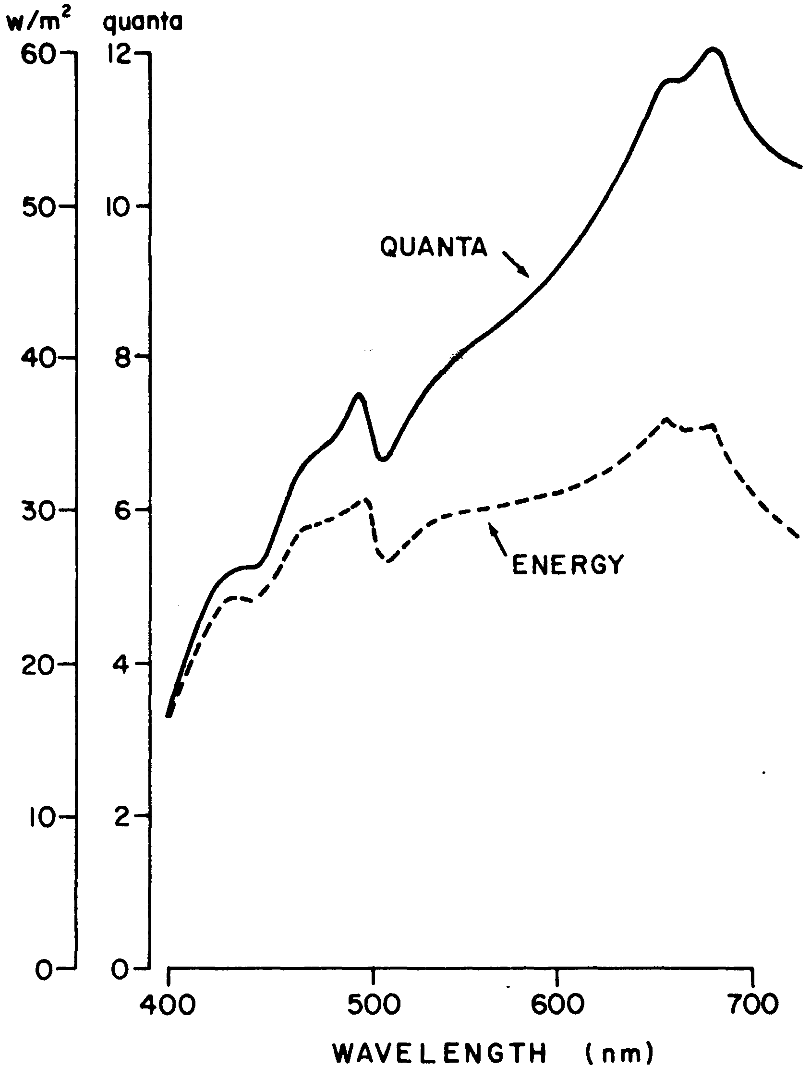

Figure 2. The relative spectral distribution of light quanta and energy in air off Sweden. (After Halldal, 1974).

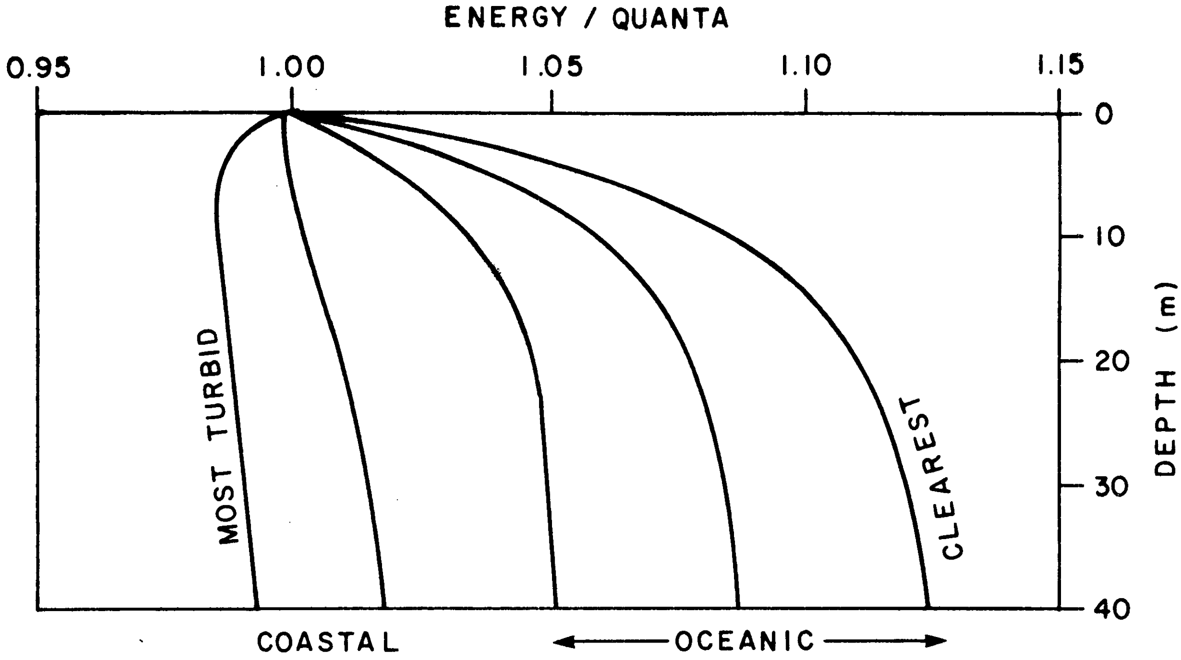

Figure 3. The ratio of energy irradiance to quanta irradiance as a function of depth for different characteristic water masses (After Jerlov, 1976).

Table II

Useful Physical Terms, Units and Conversions

Symbol	Term	Energy	Photons	Conversions
Q	Quantity	Joule (J) erg g-cal	Quanta Einstein	1 Einstein = 6.02×10^{23} Quanta 1 g-cal = 4.185 J 1 erg = 10^{-7} J
F	Radiant Flux (time rate of flow or power)	Watt (W)	Quanta$\cdot^{-1}$	1 g-cal = 4.185 WATTS^{-1} 1 $J\cdot m^{-2}\cdot s^{-1}$ = $1 W\cdot m^{-2}$
E	Irradiance (flux per area)	Watt$\cdot m^{-2}$ g-cal$\cdot cm^{-2}$ Langley (Ly)	Quanta$\cdot m^{-2}\cdot s^{-1}$ μEinstein$\cdot m^{-2}\cdot s^{-1}$ (photon flux density)	1 μEinstein$\cdot m^{-2}\cdot s^{-1}$ $= \frac{119.7}{\lambda\ (nm)}\ W\cdot m^{-2}$ 1 g-cal$\cdot cm^{-2}$ = 1 Ly

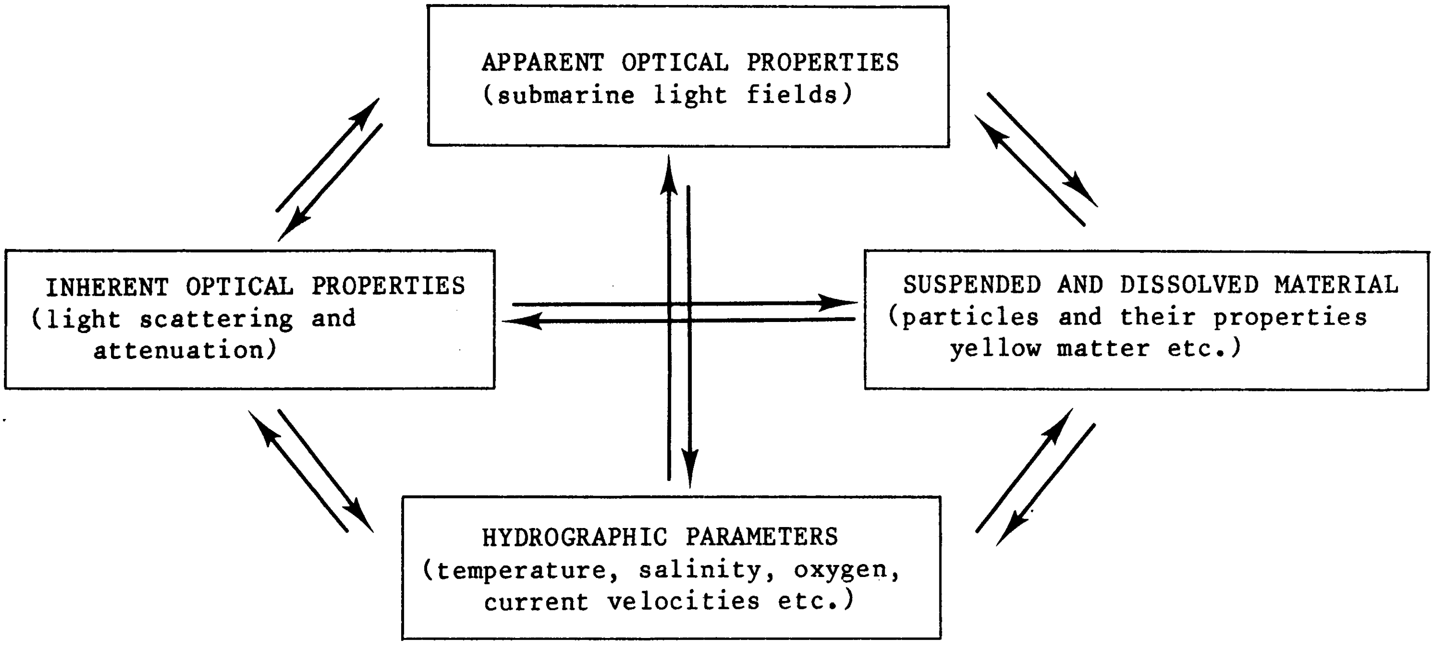

Figure 4. The interrelationships of the various groups of concepts in optical oceanography (After Zaneveld, 1974).

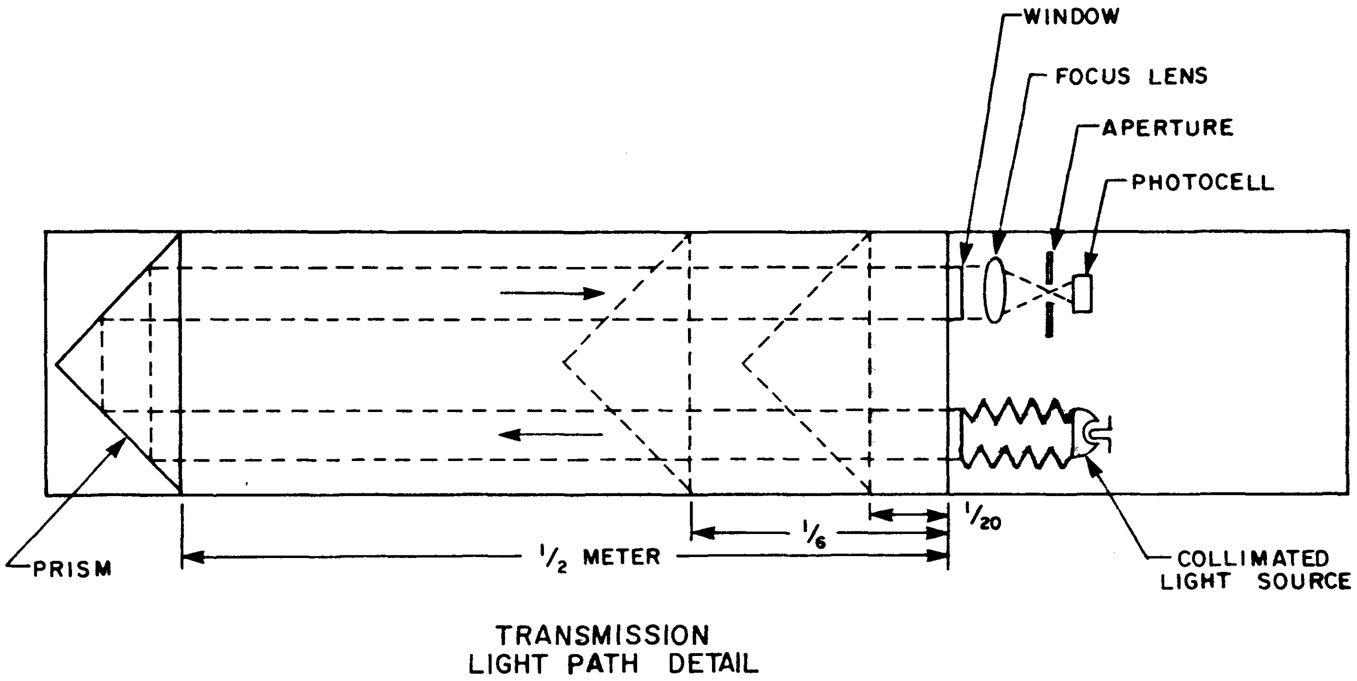

Figure 5. Light path detail of a beam transmissometer. (After Montedoro-Whitney Corp., 1980).

compares the emitted flux (F_o) to the transmitted flux (F_t) and reads out the beam transmittance (T) as a ratio:

$$T = \frac{F_t}{F_o}$$

The <u>attenuance</u> (C) is the ratio of the flux lost (F_c) to the flux emitted (F_o):

$$C = \frac{F_c}{F_o}$$

Since the flux transmitted added to the flux lost equals the original flux

$$F_t + F_c = F_o$$

then

$$\frac{F_t}{F_o} + \frac{F_c}{F_o} = 1$$

and it follows by substitution that

$$T + C = 1$$

<u>Transmissivity</u> is defined as the beam transmittance (T) divided by the path length (r) in meters. The rate of change in attenuance per meter of beam is termed the <u>total attenuation coefficient</u> (α or c) and is defined as a log function of the beam transmittance (T)

$$c = \frac{-\ell n\ T}{r}$$

where r is the path length of the beam. "c" is a convenient and often used descriptor of the combined inherent properties of absorption and scattering (the units of c are m^{-1}).

The spectral distribution of the total attenuation coefficient (c) generally shows high attenuance at both ends of the PAR (see Fig. 6a). Since it is an aggregated coefficient it is informative to consider the component parameters which cause the observed attenuance. Much of the attenuance in the long wavelengths is due to the water itself as shown by James and Birge (1937) for pure water, and Clarke and James (1939) for filtered seawater (see Fig. 6b). Note that there is little appreciable difference in the two curves, indicating that the effect of sea salts on attenuance is small (Yentsch, 1960). Light attenuation in pure water or pure seawater is a constant. Of course, natural water bodies (particularly estuaries) are not pure, but contain constantly varying particulate and dissolved substances. Burt (1958), using uncontaminated filtered seawater samples, was able to determine the attenuance due to dissolved substances. By subtracting this from the total attenuation coefficient of non-filtered seawater he was able to calculate the light attenuance due to particulate matter. These results (for the eastern tropical Pacific) are shown in Fig. 6c. Notice that the shorter wavelengths

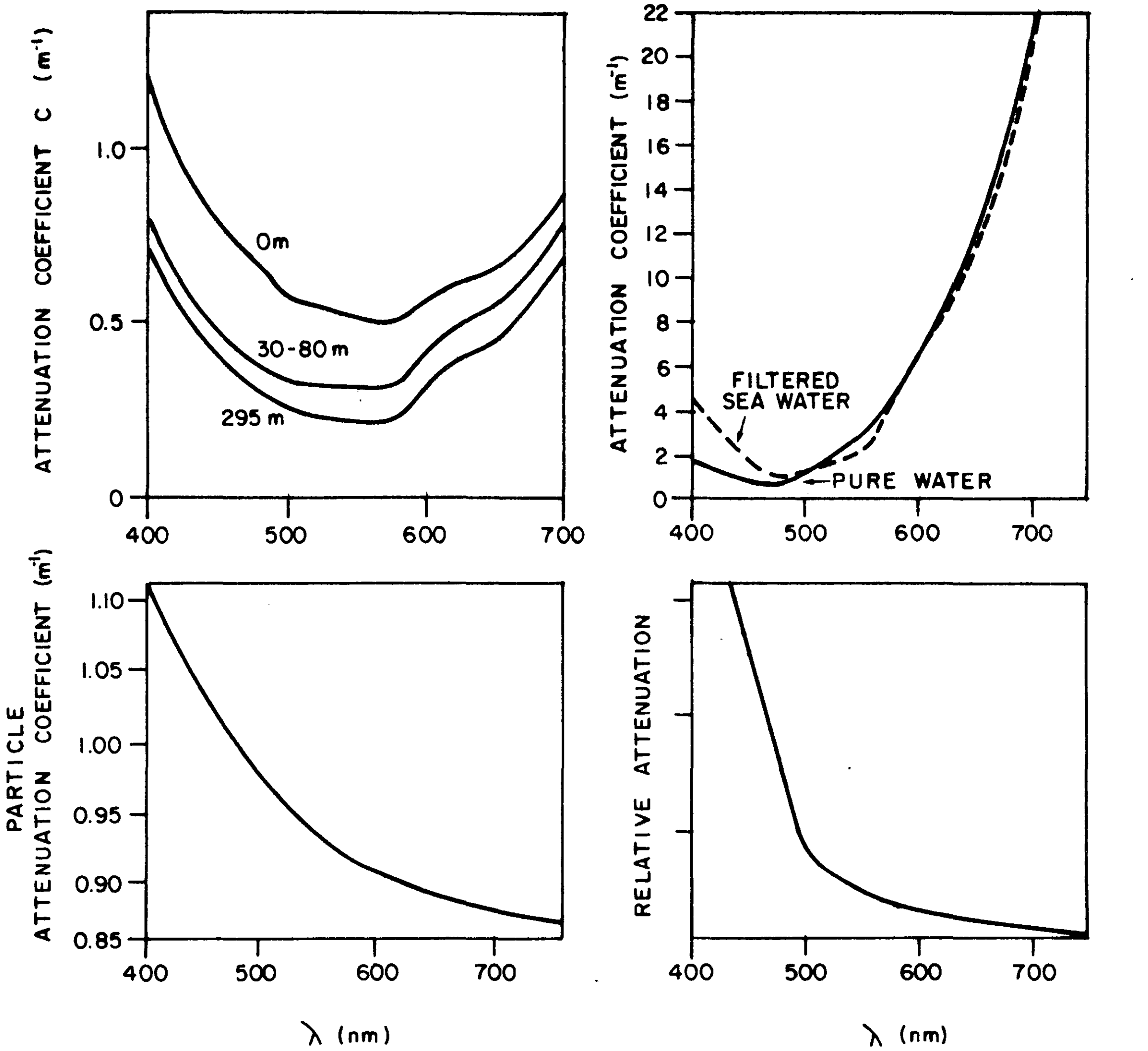

Figure 6. Spectral distribution of the total attenuation coefficient and its component parameters. (a) Spectral distribution of the total attenuation coefficient at different depths in the Baltic Sea (After Lundgren, 1975). (b) Comparative attenuation of pure water (After James and Birge, 1937) and filtered sea water--(After Clark and James, 1939). (c) Light attenuance caused by particulate matter (After Burt, 1959). (d) Absorption curve for Gelbstoff (After Kalle, 1966).

are selectively attenuated by particles. The shorter wavelengths are also attenuated by yellow substance or Gelbstoff (see Fig. 6d), the collective name given to a complex mixture of organic compounds by Kalle (1966). Gelbstoff is formed from carbohydrates resulting from organic matter decomposition in a "Maillard" reaction. Sources are both allochthonus (swamps, marshes, land runoff) and autochtonus (planktonic, and benthic organisms). Flocculation of fine suspended and colloidal materials in estuaries probably encourages the reaction, as does the presence of amino acids (Kalle, 1966).

The total attenuance (C), as stated previously, is actually a combination of absorption (A) and scattering (B).

$$C = A + B$$

Likewise, the coefficient of attenuation (c or α) is a combination of the coefficients of absorptance (a) and scatterance (b).

$$c = a + b$$

Scattering is the change in direction of light propagation caused by diffraction, refraction and reflection due to particles, water molecules and dissolved substances. Scattering is wavelength dependent but in an irregular and complex manner. The particle size distribution and the index of refraction are important parameters related to scatterance. The major scatterers in estuaries are silts and clays (small particles about 1 μm in diameter) which, in general scatter the shorter wavelengths (blue end of visible spectrum) much more than the longer wavelengths (red end). Scatterance meters (nephelometers) designed to measure b at either fixed or variable angles have been devised. The most appropriate type is the integrating meter which measures scattering at all angles. Most scattering in natural water bodies is at small angles (50% at angles less than 3.5°), i.e. in the forward direction. Measurements of light in coastal regions have usually shown more foreward scattering than those in the open oceans (Jerlov and Fukuda, 1960; Pickard and Giovando, 1960; Morrison, 1970). Since the amount of energy scattered laterally out of a hypothetical water column should be balanced by an equal amount scattered into that water column from adjacent columns, the net effect of scattering is the increase of effective path length. This results in a greater opportunity for absorption. For estuaries one would expect blue light to be scattered more then red light and thus be subjected to more attenuation due to the added absorption by the additional particles and water molecules encountered in this longer path.

Absorption is a thermodynamically irreversible process wherein photons are converted to thermal, kinetic or chemical energy. Photosynthesis is an example. Table III (Jerlov, 1976) summarizes absorption and scattering characteristics in seawater.

Apparent Optical Properties

The apparent optical properties of a body of water are those resulting from the measurement of natural light fields underwater, i.e., the measurement of in situ radiant flux. There are two basic types of measurement made:

Table III. Summary of absorption and scattering characteristics (After Jerlov, 1976).

	Absorption character	Wavelength dependence	Scattering character	Wavelength dependence
Water	invariant at constant temp. and pressure	strong	invariant, small compared to absorption	λ^{-4}
Sea salts (inorganic)	negligible in the visible, weak in the ultraviolet	some increase towards short λ	appreciable	
Yellow substance	variable	increase towards short λ		
Particulate variable matter	variable	increase towards short λ	variable	variable

radiance and irradiance. Radiance (L) is defined in terms of flux per unit solid angle per projected area. Irradiance (E), the more common measurement, is simply the flux per unit area and is usually collected with a flat circular opal glass (or plastic) diffuser. The diffuser is designed so that light received from all angles is transmitted to the sensor according to Lambert's cosine law, i.e. the irradiance transmitted is proportional to the incident radiant intensity multiplied by the cosine of the angle of incidence. Spherical irradiance (E_s) is irradiance collected with a spherical diffuser and represents the total light coming from all directions. It is probably the best measure of light available for photosynthesis; however, very little data in this form presently exists in the literature. Jerlov (1976) reports that investigations of the ratio of cosine collection in the downward direction (E_d) to equal collection for the upward hemisphere (E_o) generally show a range of .75 to .85. So, cosine irradiance measures most of the irradiance collected by spherical sensors. Cosine irradiance is the most usual apparent property measured for biological purposes, and is used in the research reported herein. Irradiance and radiance can be expressed as either energy or quanta (see Table I) but quanta seem most apropriate for ecological studies. Instruments can be designed to measure board spectral regions, such as the PAR, or discrete wavelengths, i.e. spectral irradiance.

The complete spectrum of downward irradiance at sea level and at several depths of the open ocean is shown in Fig. 7. Notice that there is almost no energy outside of the PAR below 1 m. Most of the "missing" energy has been converted into heat via absorption. According to Clark and Ewing (1974), only 4-11% of incident irradiance between 300-700 nm is reflected from the surface or backscattered out of the water column (the combination is called albedo) (see Fig. 8). The spectral distribution of downward irradiance can be expressed graphically as a family of curves of energy (or quanta) versus wavelength at specific depths, as in Figs. 7 and 9 or as percentages of surface irradiance as in Fig. 10. Depth profile ranges of Jerlov's (1976) water types, from clearest oceanic to most turbid coastal are presented in Fig. 10 along with our Chesapeake Bay (Estuarine) profiles.

The diffuse downwelling (or vertical) attenuation coefficient[2] (K_d) expresses the decay of irradiance as a log function,

$$K_d = \frac{-\ell n \frac{E_2}{E_1}}{(Z_2 - Z_1)}$$

where ℓn is the natural log, E_2 is the irradiance at depth Z_2, E_1 is the irradiance at depth Z_1 and $(Z_2 - Z_1)$ is the distance between the two depths in meters. The units of K_d are m^{-1}. The spectral attenuation coefficient [K_d (λ)] is a particularly useful parameter for comparing underwater

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[2] Often termed extinction coefficient

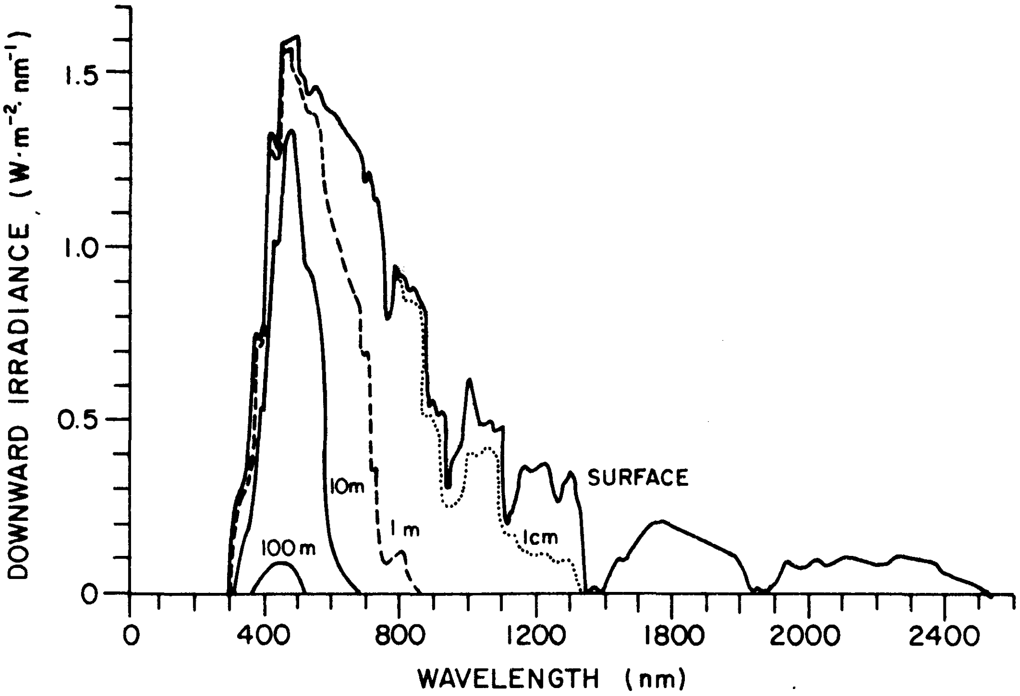

Figure 7. The complete spectrum of downward irradiance in the sea. (After Jerlov, 1976).

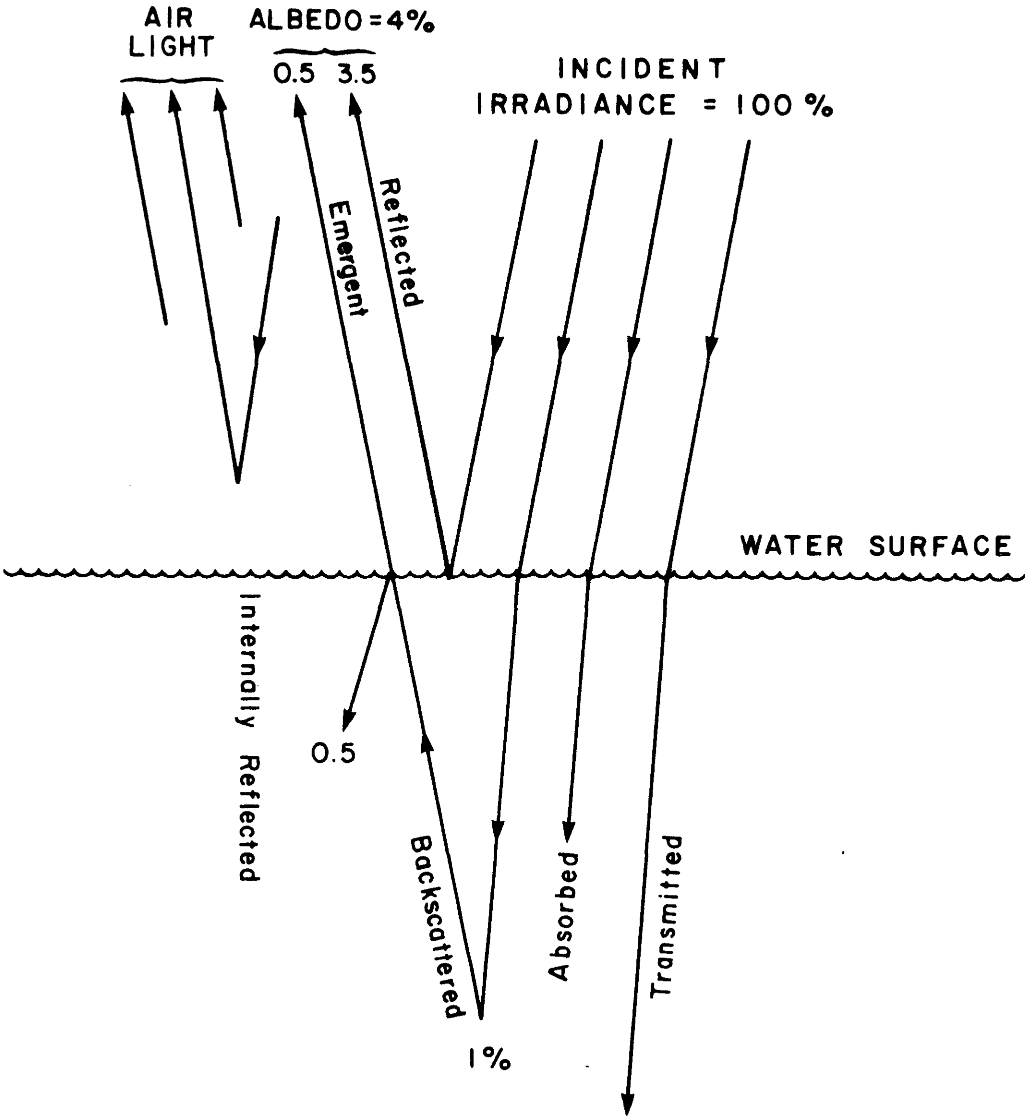

Figure 8. The fate of incident radiation in the PAR over the sea. (After Clark and Ewing, 1974).

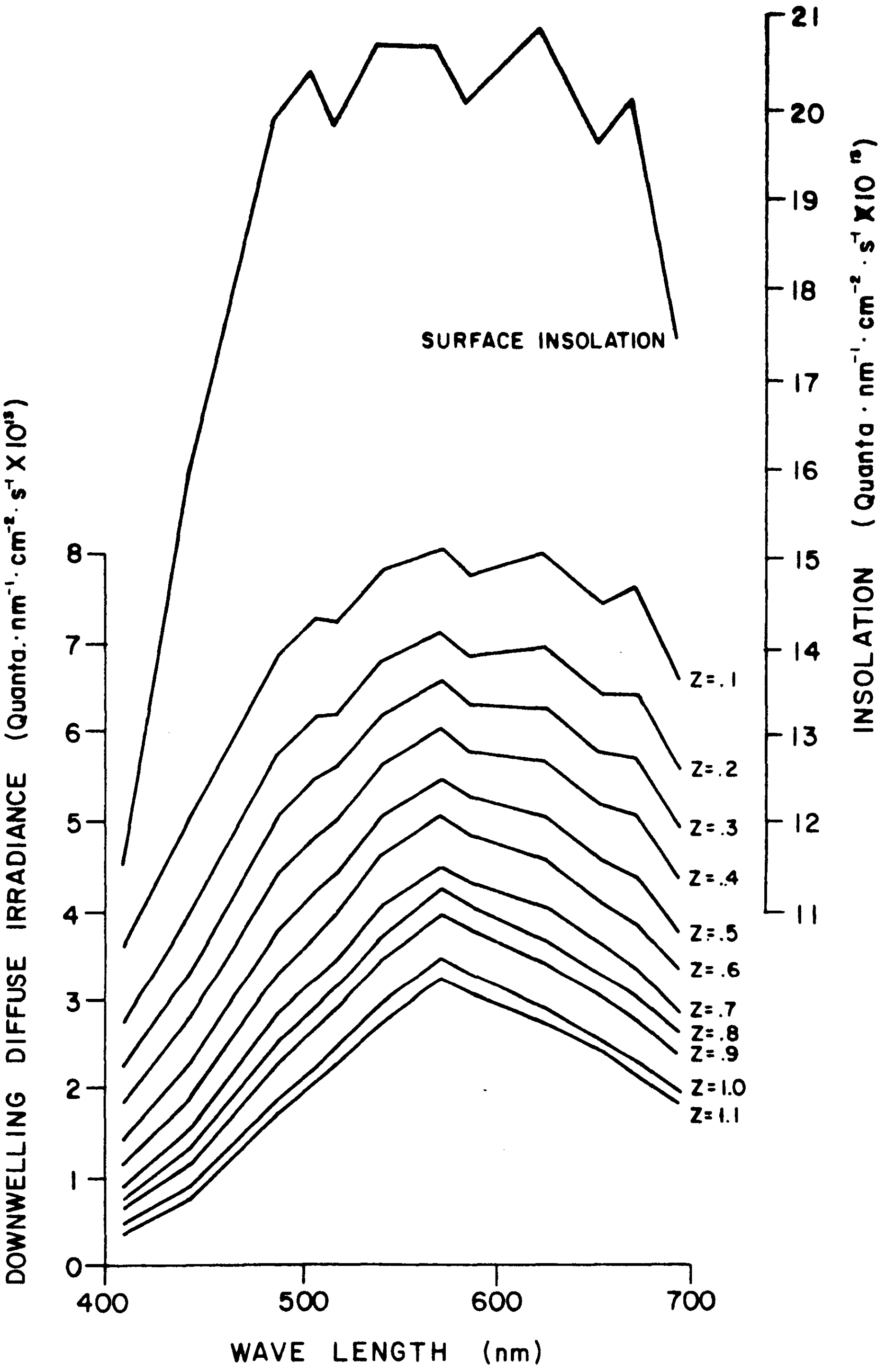

Figure 9. Spectral distribution of downward irradiance at different depths over a Zostera marina bed off the eastern shore of the Chesapeake Bay.

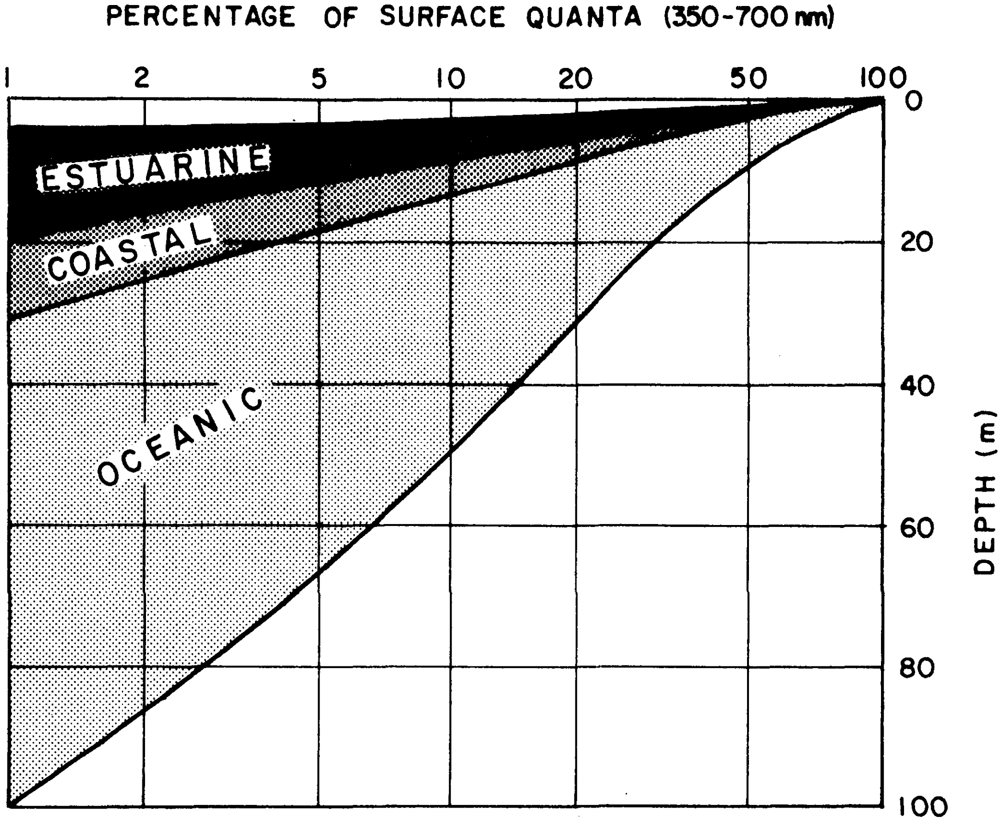

Figure 10. Depth profiles of percentage of surface quanta (350-700 nm) for different water types ranging from the clearest oceanic to coastal (After Jerlov, 1976) to estuarine (Lower Chesapeake Bay).

irradiance between water bodies, seasons and wavelengths. Since K_d differs at different depths in shallow water (<10 m) meaningful comparisons must be made at the same depths. This change in K_d can be seen in Fig. 11. Notice the inverse relationship between downwelling irradiance (E_d) and the attenuation coefficient (K_d). A progression of increasing K_d (λ) (spectral attenuation) from clear oceanic water (low attenuation) to turbid estuarine water (high attenuation) is shown in Fig. 12. Curve "a" is the Sargasso Sea, "b" for the Western Coast of Africa, and "c" for the clearest Chesapeake Bay measurements. Shallow lower Chesapeake Bay waters during summer exhibit a $k_d(\lambda)$ of from 1 to 12 m^{-1}!).

It must be kept in mind that the diffuse attenuation coefficient (K_d) derived from irradiance measurements and the total attenuation coefficient (c) derived from the beam transmissometer are two different properties with no simple relatedness. The total attenuation coefficient is calculated based on a spectrally defined and emission controlled collimated light source which is designed to eliminate diffuse (scattered) light not originating within the source and is thus an inherent property. K_d, however, is calculated based on the natural diffuse submarine light field and is therefore an apparent property. Secchi Disk readings (D_s) (an observer notes at what depth a standard white and black disk "disappears") are actually attempts to measure K_d. According to Idso and Gilbert (1974) the relationship

$$K = \frac{1.7}{D_s}$$

is valid for depths between 1.9 and 3.5 meters. However, others would argue that without the inclusion of c (α) in the relationship, unrealistic values would be obtained (Williams, 1970).

Temporal Variations in Light Energy Distribution

Temporal variations in light distribution, both in the atmosphere and underwater are due directly and indirectly to the relative motions of and distances between the earth, moon and sun. The seasonal variation in solar radiation outside the atmosphere (Fig. 13) is of course caused by the distance between the earth and the sun and the tilt of the earth on its axis. Notice that the variation increases with latitude, whereas the integrated annual energy decreases with latitude. Atmospheric patterns cause variations in this generalization.

Diurnal variations have two components: (1) solar elevation and (2) tidal amplitude and frequency. The interface between water and air is a boundary between media of different optical density thus an electromagnetic wave striking this interface splits into a reflected wave and a refracted wave. Reflection of combined sun and skylight from a horizontal, flat surface varies asymptotically with solar elevation, being between 3-6% at angles greater than 30°. Below 30° the reflectance increases dramatically up to 40% at 5°. Reflection below 30° is wavelength dependent (Fig. 14a) due to the changing amount of diffuse atmospheric light in the global light at low sun angles (Sauberer and Ruttner, 1941). As the solar elevation decreases, relatively

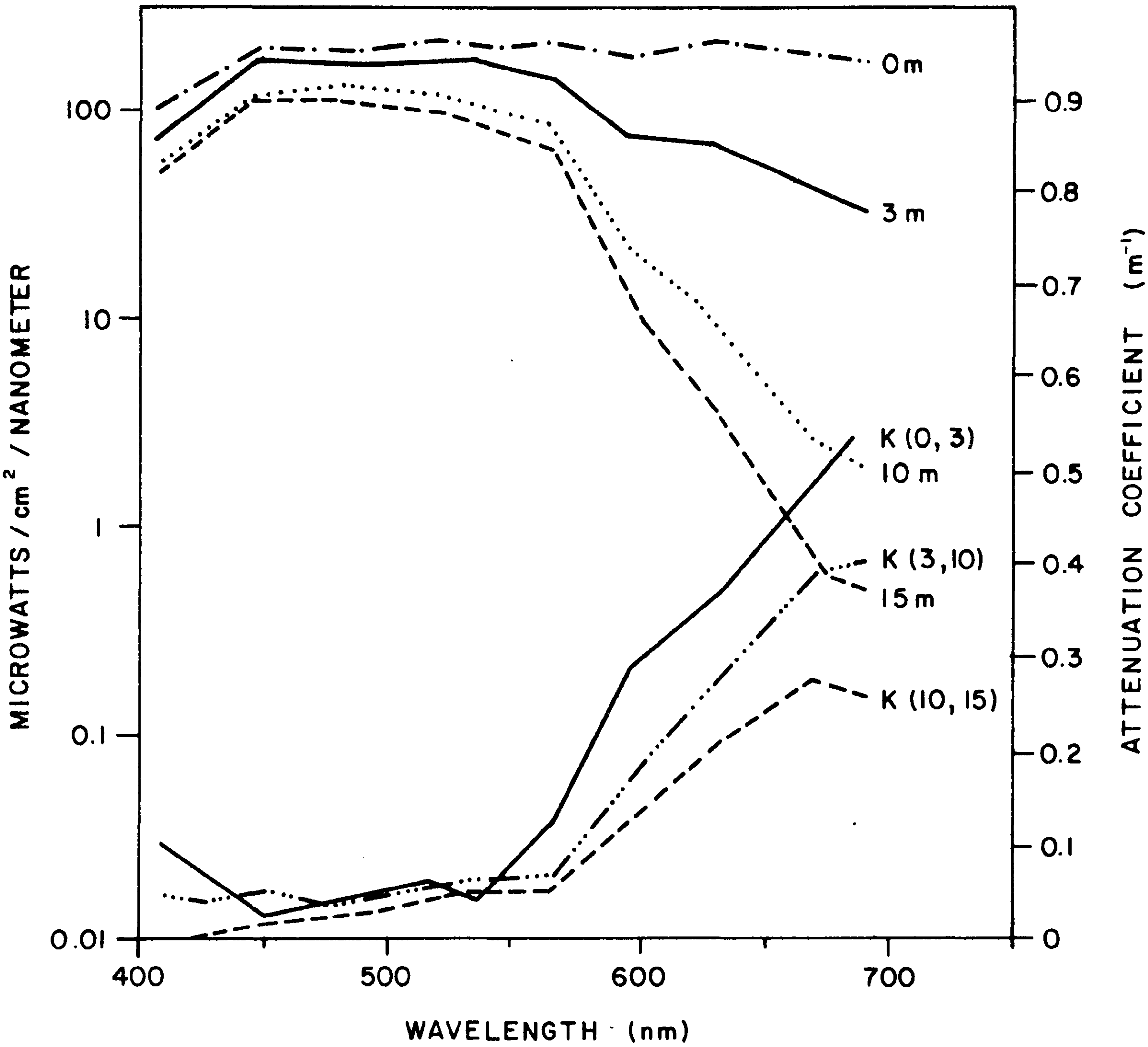

Figure 11. Spectral irradiance and diffuse attenuation coefficients for a different depths at noon on a reef in Jamaica. (After Booth and Dunstan, 1979).

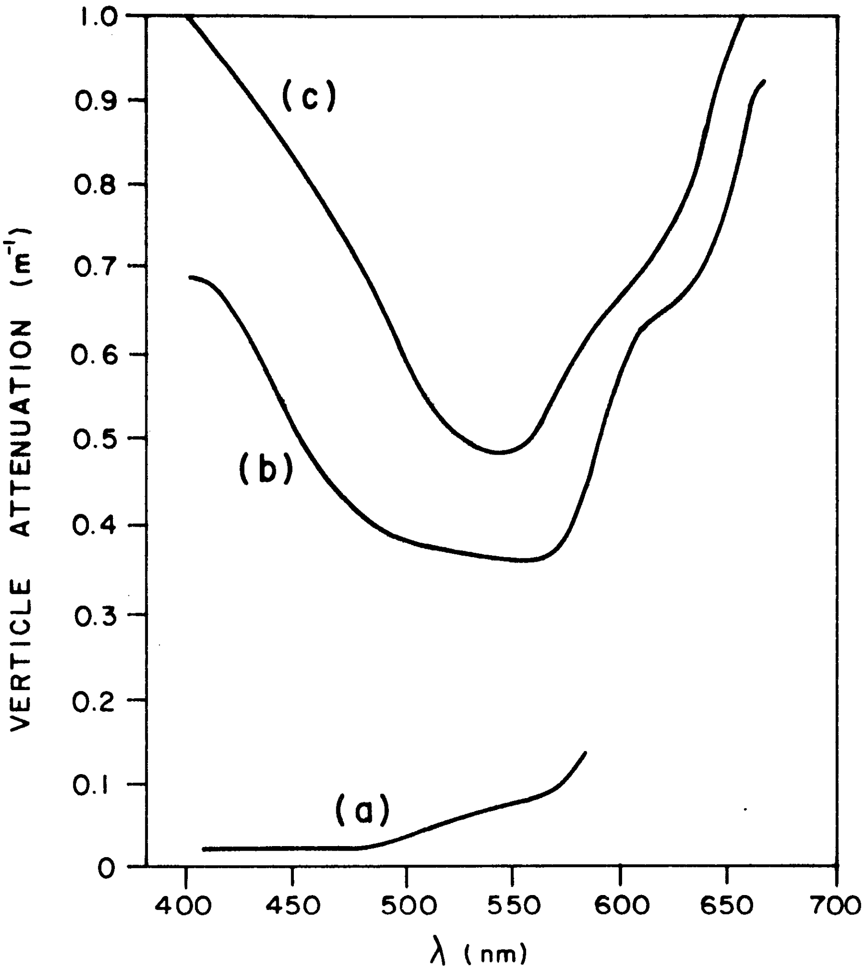

Figure 12. The attenuation coefficient, K_d of downward irradiance. (a = Sargasso Sea, b = African Coast (After Jerlov, 1976), c = clearest Chesapeake Bay).

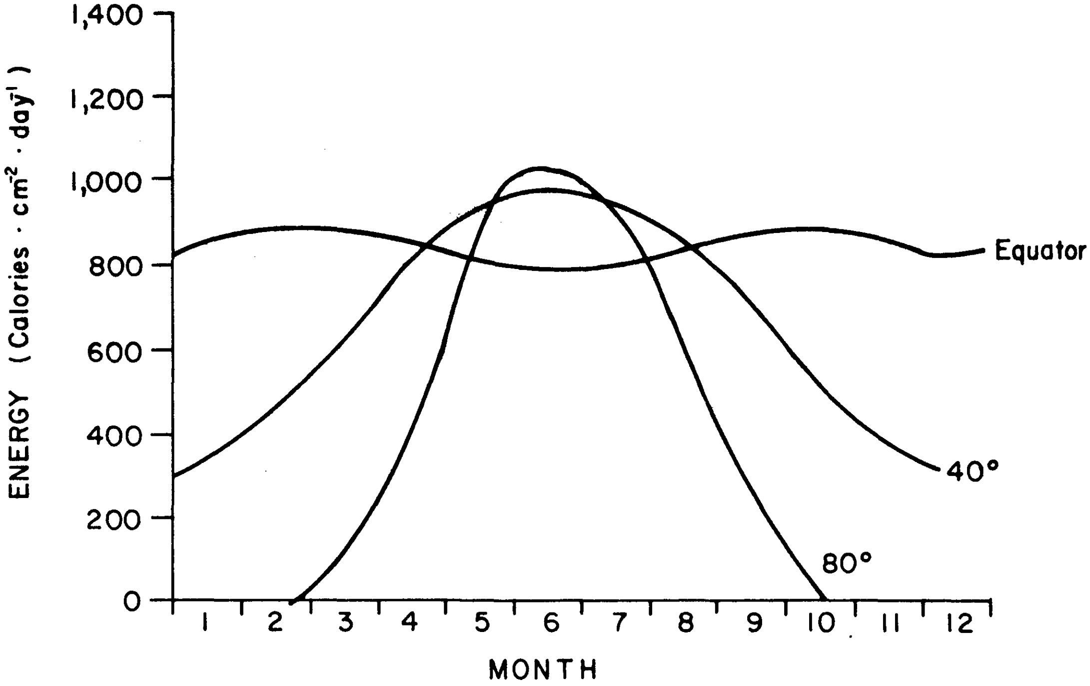

Figure 13. Seasonal variation of solar radiation outside earth's atmosphere for the Equator and latitudes 40 degrees and 80 degrees. (After Gates, 1971).

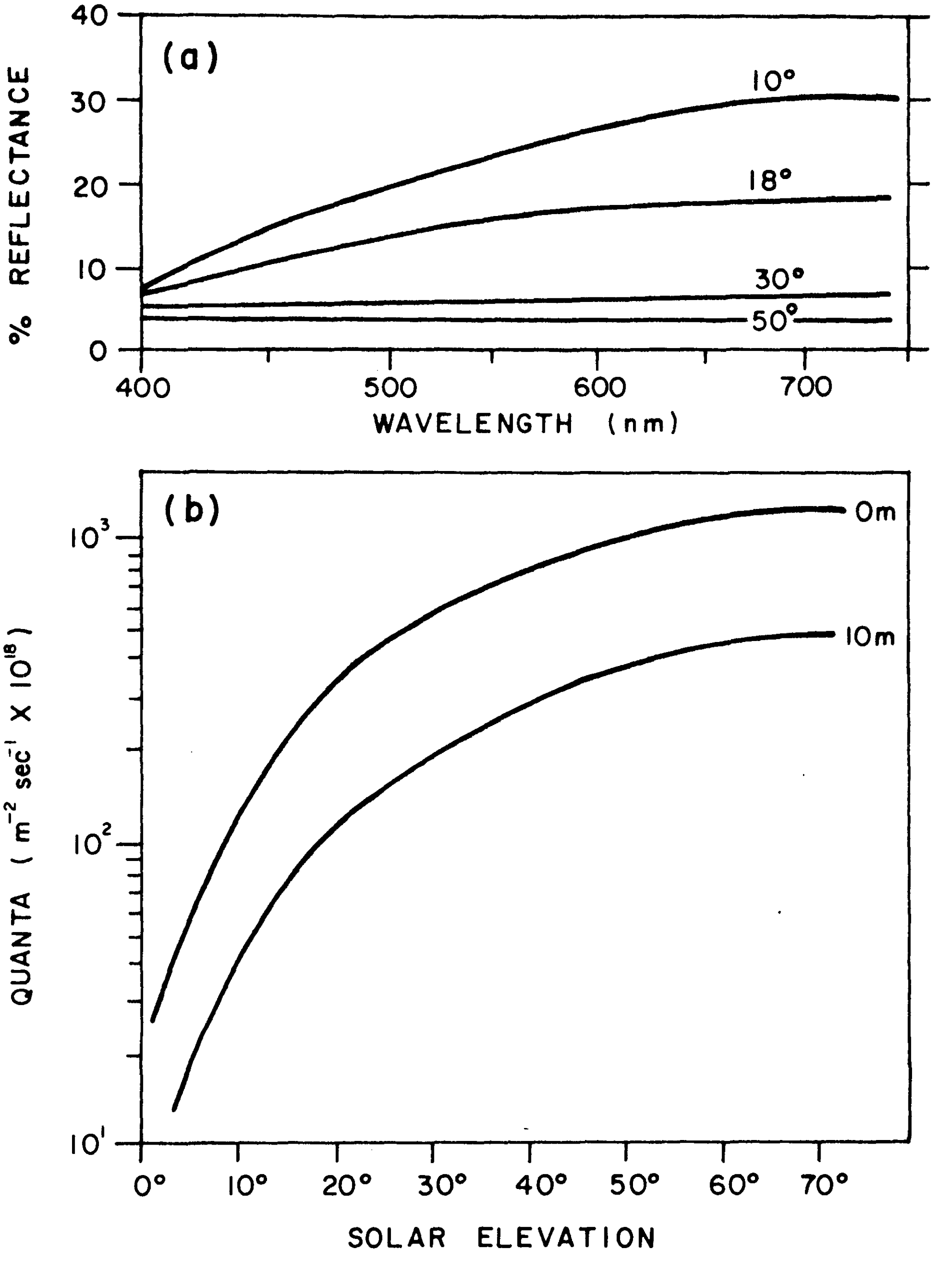

Figure 14. Variation of reflectance and submarine irradiance with solar elevation. (a) Reflectance (%) of global radiation for different solar elevations as a function of wavelength (After Sauberer and Ruttner, 1941). (b) Diurnal variation of quanta (PAR) off Sardinia (After Jerlov, 1976).

more red light is reflected. Wave action reduces the net reflection at low angles because the light is reflected back into the water column. The refractive index (n) of the sea, defined by Snell's Law

$$\frac{\sin i}{\sin j} = n$$

is $\frac{4}{3}$ (where i is the angle of incidence and j is the refracted angle). This means that light coming in parallel to a horizontal sea is refracted into the water at an angle of 48.5° from zenith. As the solar elevation increases more light is able to penetrate the water (Fig. 14b).

Tidal cycles in estuaries cause not only changes in water bodies and their associated seston and dissolved components but also cause resuspension of benthic sediments and changes in the height of the water column. These are of course highly idiosyncratic for each specific systems.

Storm and wind events cause both increased land runoff, with its associated particulate and dissolved load, and increased wind-driven currents and waves. In shallow areas these increase resuspension. Scott (1978) following changes in attenuation in an estuary after a rainstorm found that it took 11 days for the submarine irradiance to return to the pre-storm condition. In near-shore littoral regions the average submarine light conditions may be controlled by the juxtaposition of the local coastal morphology with the prevailing wind patterns.

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Chapter 2

LIGHT AND SUBMERGED MACROPHYTE COMMUNITIES IN THE CHESAPEAKE BAY: A SCIENTIFIC SUMMARY

by

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INTRODUCTION

The initial focus of submerged aquatic vascular plant (SAV) research for the U.S. Environmental Protection Agency, Chesapeake Bay Program (CBP) was evaluation of the structural and functional ecology of these communities. In the upper Bay, *Myriophyllum spicatum* and *Potamogeton perfoliatus* are the dominant species while *Zostera marina* and *Ruppia maritima* are the dominant species in the lower Bay. Studies were centered on various aspects of productivity (both primary and secondary), trophic structure, and resource utilization by both ecologically and economically important species. Much of the initial research was descriptively oriented due to a general lack of information on Chesapeake Bay submerged plant communities. These investigations created the data base necessary for the development of ecologically realistic simulation models of the ecosystem. Following these initial studies, the research programs in both Maryland and Virginia evolved toward more detailed analyses of specific factors that potentially limited or controlled plant growth and productivity. Previous results indicated certain environmental parameters and biological processes that possibly limited and controlled SAV distribution and abundance. Specifically, these included light, nutrients, herbicides and fouling (epibiotic growth). Laboratory and field studies were devoted in the later phases of the CBP-SAV program toward investigating these interactions.

The overall objectives of this later work were to more precisely evaluate environmental and biological factors in relation to submerged aquatic plant community structure and function. Both the published literature and the results of CBP-SAV program studies indicated that the interaction of these environmental parameters together with other physical and biological characteristics of the ecosystem determine the longer term success or failure of SAV communities (den Hartog, 1970, 1975; Williams, 1977; Wetzel et al., 1979; van Tine, 1981).

BACKGROUND

A major goal of the CBP-SAV research was to investigate the response of bay grasses to various environmental variables. Studies centered on the four dominant submerged aquatic plants in the Bay. Understanding the relationship between environmental factors and the productivity and growth of SAV was determined to be the first step necessary in aiding the overall goals of the management program. Natural and man-made changes in environmental quality may favor one species or another, or result in alteration of the entire community. The basic responses of the plants, as well as the community, must be determined before environmental change can be evaluated in terms of specific management criteria.

Studies in the various CBP-SAV research programs that addressed environmental regulation and control of SAV communities focused on nutrient regulation (primarily nitrogen as NH_4^+ and NO_3^-), light and photosynthesis, and other biological and physical-chemical factors influencing light energy distribution.

The results of studies in the lower Bay communities suggested a net positive response to short term nutrient additions and supported the observation by others that these communities are nutrient limited (Orth, 1977). The most consistent positive response was associated with *Ruppia* dominated communities and the most variable associated with the deeper *Zostea* community (Wetzel et al., 1979). In contrast, Kemp et al. (1981) observed that upper Bay SAV communities did not appear nutrient limited but were perhaps limited by suboptimal light conditions. These results, together with community metabolism studies, suggested that light and the environmental factors controlling benthic light availability were key factors governing plant community growth and productivity. The working hypothesis developed that light-temperature-turbidity regimes and their interaction would explain in large part the observed variability in distribution and abundance. Changes in these parameters, governed by either natural or man-induced events and perhaps determined over long time scales, influence variation in distribution and abundance ~~in~~ the Chesapeake Bay ecosystem as a whole.

Throughout the Chesapeake Bay, submerged aquatic plant communities exhibit a distinct zonation pattern from the shallower inshore high-light area to the deeper, low-light area of the beds. These characteristic distribution patterns also suggested different physiological responses to and control by local environmental conditions, principally light.

^{14}C studies were initiated in August, 1979, on lower Bay *Ruppia-Zostera* communities and continued for an annual cycle to investigate the effects of light and temperature on specific rates of seagrass photosynthesis. Plants were removed from the sediment, placed in a set of screened jars and incubated in a running seawater system using ambient sunlight. The plants were exposed to 100, 50, 30, 15, 5 and 1% of ambient light to determine the effect of light quantity on phytosynthesis. Experimental designs comparable to these were also conducted for upper Bay species.

In conjunction with these studies, measures of leaf area index (LAI) were also conducted. The light levels at which SAV can grow and reproduce, i.e., succeed, is determined by the photosynthesis-light relationship. A greater leaf area exposed to light may result in greater productivity, however, light reaching the plants is not only determined by physical factors controlling light penetration through the water column, but by plant self-shading. Maximum plant biomass can in part be related to leaf area. The leaf area index (plant area/sediment surface area) estimates maximum leaf density and thus potential area available to absorb light (Evans, 1972 cited in McRoy and McMillan, 1979). Leaf surface area also provides a substrate for epiphytic growth. Leaf area samples were collected to characterize the three main vegetation zones typical of lower Bay communities. These data were used to provide a more accurate description of light penetration through the plant canopy as well as evaluate potential morphological adaptation of the plants to various light environments. Complimentary field studies were designed to determine the effects of in situ light reduction through artificial shading.

Light reductions of 70 to 20% of ambient were used. The results of these studies supported the hypothesis that total community metabolism was governed and very sensitive to available light. During the course of these investigations, light data collected in the field for various environmental (climatic) conditions indicated that natural light reductions of these magnitudes were common. In order to determine the overall effects of light reduction, specific factors were investigated more thoroughly using both laboratory and in situ experimental approaches for light-photosynthesis relationships as well as studies to determine those environmental variables which controlled light energy distribution and availability to the plant communities.

Studies initiated during the later phases of the CBP-SAV research program, investigated the effects of epiphytic growth and metabolism and the interactive effects of light and acute exposure to the herbicide atrazine. Studies on epiphyte colonization were along two lines: (1) the epiphytic community as a primary producer and food source and (2) as competitors with the vascular plant community for available light. Experiments completed suggested that the epiphyte community at times dominates metabolism of the community and limits the light available for vascular plant photosynthesis[1]. What remained was the determination of which environmental conditions favor colonization and at what point is the vascular plant stressed.

These various research activities provided a data and information base to serve management needs and to identify specific research areas where additional information was required for integration and synthesis. The work proposed in the latter part of the CBP/SAV program centered on filling what were considered major gaps in information and the data base. The synthesis report that follows was based on our current state of understanding of light energy and distribution in Chesapeake Bay and the relation of this information to past and recent knowledge about SAV community growth and survival. Much of it was based on preliminary and incomplete data reports of ongoing research in attempt to be as current as possible.

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[1] See Vol. I for a discussion of this matter.

THE RESEARCH PROGRAM ON LIGHT AND SAV: AN OVERVIEW

It has been the working hypothesis of the Chesapeake Bay Program SAV group that changes in such water quality variables as suspended particulates (both living and non-living), dissolved substances and nutrients alter directly or indirectly underwater light regimes in such a way as to limit benthic macrophytic primary production. Plants absorb light energy for photosynthesis at particular wavelengths determined by their specific pigment complexes. As light penetrates the water column, its energy content and spectral quality are changed by absorption and scattering. Water itself, dissolved substances and particulate materials are responsible for both the absorption (conversion into heat energy) and scattering of light. Selective absorption and scattering by these factors results in the attenuation of the energy of specific light wavelengths causing a "color shift" (Kalle, 1966; Jerlov, 1976, Champ et al., 1980). Scattering, the change in direction of light propogation, returns some of the incident radiation toward the surface and thus further reduces the total light energy available to support photosynthesis. Phytoplankton act as both scattering and selectively absorptive and reflective particles and are in direct competition with benthic primary producers for the same wavelengths of light, i.e. red and blue.

The temporal and spatial distribution of particulate materials and dissolved substances are largely determined by climatic variables. Wind velocity and direction, tidal amplitude and frequency, current velocity, rain and land runoff all interact to induce variations in water quality parameters and subsequently the spectral composition of light in the water column (Dubinsky and Berman, 1979; Kranck, 1980; Anderson, 1980; Thompson et al., 1979; Scott, 1978; Riaux and Douville, 1980).

Based on these general premises, the light research program encompassed four basic facets: (1) description of the submarine light environment, together with measures of various water quality parameters, (2) description of climatic and oceanic forcing functions, (3) detailed studies of photosynthesis-light relations by individual species and for entire SAV communities, and (4) analysis of the relationship/correlations among the above data and other available information. The measurement and collection of light, water qualtiy parameters, climatic and oceanic forcing functions were made simultaneously with the light-photosynthesis investigations. Studies on both shores of the upper and lower Chesapeake Bay in vegetated and non-vegetated regions were undertaken.

Characterization of the light environment was accomplished using a Biospherical Instruments Model MER-1000 Spectroradiometer (Booth and Dunstan, 1979). Specific attenuation in 12 biologically important wavelengths and integrated photosynthetically active radiation (PAR) values were calculated from these data. The spectral irradiance measurements were made in quantum units as suggested for biological studies by the Special Committee on Oceanographic Research (SCOR) of the International Association of Physical Oceanographers (IAPO).

There is a paucity of data on spectral irradiance in marine environments (Jerlov, 1976)--especially for estuarine waters, the Chesapeake Bay being no exception. Burt (1953, 1955a) using a shipboard spectrophotometer analyzed filtered seawater samples from the Chesapeake Bay and concluded that the primary factor in light extinction was the filterable, particulate matter. Seliger and Loftus (1974) studied the spectral distribution of light in shallow water in a subestuary in the upper Bay in July and found a marked reduction of light in the 400-500 nm region of the spectrum. Champ et al. (1980) observed an "orange-shift" in the upper Bay during August 1977 using a submersible solar illuminance meter equipped with optical filters. They suggest, that there is a continuum of spectral shifts toward the penetration of longer wavelengths from oceanic to coastal to estuarine waters. This corroborates and extends Kalle's "yellow shift" theory (Kalle, 1966). Kalle contends that the shift to longer wavelengths is more pronounced as the concentrations of suspended particles increases. These investigations make up in large part the only complementary data base and to our knowledge no data exists for the light environment in and around SAV habitats with the exception of that gathered by the EPA-CBP study.

Various lines of evidence as discussed earlier, suggested light as a major factor controlling the distribution and productivity of seagrasses. Preliminary studies demonstrated both potential nutrient and light quantity effects on plant community metabolism. More quantitative field and laboratory studies were designed and carried out in later phases of the CBP-SAV research program on photosynthesis-light relations in Chesapeake Bay SAV communities.

For the field approaches, the entire SAV community and its interactions were included by the experimental designs. Short-term shading experiments reflected the community response to daily variations in light quantity due to such natural phenomena as cloud cover, tidal stage, and storm events. Long-term shading studies reflected community response to situations where light penetration is reduced. The purpose was to estimate minimum light quantities necessary to keep the SAV community alive. For the latter effort sets of neutral density, mesh canopies were placed in selected SAV areas for long term studies. Shaded and control areas were studied at regular intervals over the course of these experiments (1-2 months). Community metabolism and various plant community parameters (e.g., leaf area index, chlorophyll *a* and *b*, biomass and other plant meristic characters) were measured. Studies were carried out in spring, summer, and early fall 1981 to include the major growth and die-back periods.

Past research programs in the CBP-SAV program resulted in several hypotheses that might explain both the short and longer term survival of Bay grasses. Among these, the potential for light, including those variables influencing light-energy distribution, as a major environmental variable controlling SAV distribution, growth and survival was postulated. The intent of the remaining sections of this chapter are to: (1) provide in an overview fashion, the general characterisitcs of light in natural aquatic systems with emphasis on Chesapeake Bay, (2) summarize the research results throughout the Bay relative to light and Bay grasses, and (3) discuss the potential for light or light related causality of Bay grass declines.

LIGHT IN THE CHESAPEAKE BAY

General Characteristics of Estuarine Optical Properties[2]

The study of the interaction of solar energy with estuarine waters necessitates not only an understanding of the propeties of light and H_2O but also must take into account the myriad living and non-living entities, both dissolved and suspended, which affect the propagation of light in aquatic environments.

The sun emits electromagnetic radiation in discrete packets of quanta (Q) of energy termed photons. The energy content (ε) of each quantum is directly proportional to the frequency (ν),

$$\varepsilon = h\nu$$

and indirectly proportional to the wavelength (λ),

$$\varepsilon = \frac{hc}{\lambda}$$

where h is Planck's universal constant and c is the speed of light in a vacuum. This means that the quanta of shorter wavelengths contain more energy than quanta of longer wavelengths.

The complete spectrum of downward irradiance for incoming solar radiation at the top of the atmosphere, at sea level, and at several water depths in the open ocean is illustrated in Fig. 1a. Most of the energy reaching the earth's surface is contained within the shorter wavelengths [.4-10 μ or 400-1000 nanometers[3](nm]. Not surprisingly, this region includes the wavelengths of greatest biological importance, i.e. 400-700 nm, the photosynthetically active region of the spectrum termed PAR or PHAR. There is almost no energy outside the PAR at a depth of 1 m. Most of the "missing" energy has been converted to heat via absorption. Only 4-11% of incident irradiance between 300-700 nm is reflected from the surface or backscattered out of the open ocean water column (Clark and Ewing, 1974). Slightly more may be backscattered from estuarine waters.

The properties and concepts of optical oceanography are usually divided into two mutually exclusive classes: (1) inherent and (2) apparent. Inherent

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[2] See Chapter 1 for a more detailed treatment.

[3] $1\text{nm} = 10^{-3}\ \text{m} = 10^{-9}\ \text{m}$

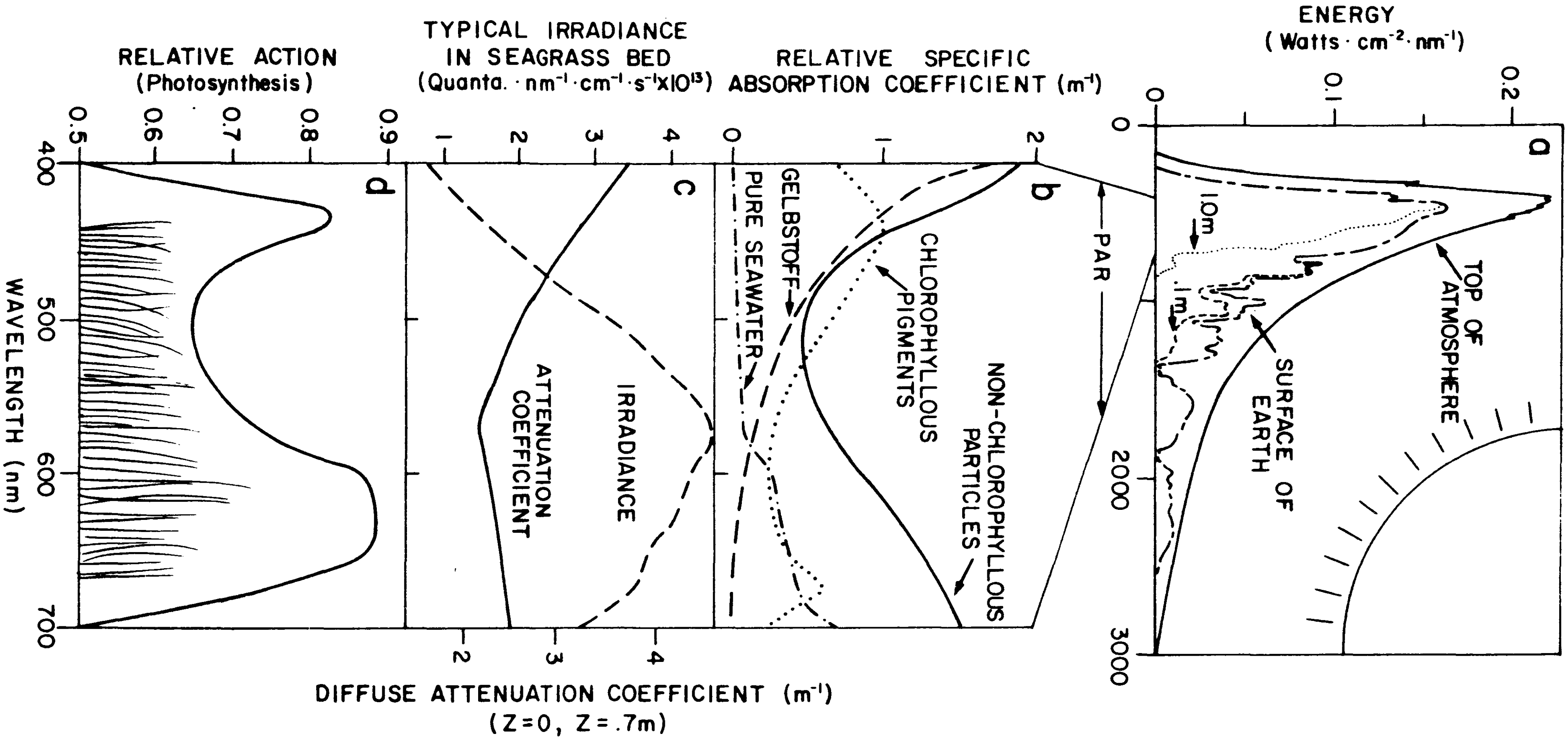

Figure 1. Theoretical path of light from top of atmosphere to benthic estuarine macrophytes. (a) Spectral energy distribution of light at top of atmosphere, at the surface of earth, and at two depths in the ocean on a clear day (Redrawn from: Jerlov, 1976 and Gates, 1971). (b) Relative spectral absorption of various constituents of esturine waters (Redrawn from Prieur and Sathyendranath, 1981). (c) Typical spectral irradiance and attenuation in a Chesapeake Bay seagrass bed. (van Tine and Wetzel, 1983), (d) Mean quantum action spectrum for higher plants (Redrawn from Inada, 1976).

properties, such as absorption and scattering are independent of changes in insolation (incoming light), whereas apparent properties, such as underwater irradiance, vary with changing solar and atmospheric conditions.

As light passes through the water column its energy content and spectral quality are changed by absorption and scattering due to the water itself, dissolved substances, and suspended particles. The combined effect of these processes is termed attenuation. The spectral distribution of the total attenuation coefficient (α or c), measured with the beam transmissometer, generally shows high attenuance at both ends of the PAR. Since "c" is an aggregated coefficient, it is informative to consider the component parameters which cause the observed attenuance.

Scattering is the change in direction of light propagation caused by diffraction, refraction, and reflection due to particles, water molecules, and dissolved substances. Backscattering results in the loss of energy from the water. Lateral scattering and forward scattering increase the path length of the light thus exposing it to further absorption. The fine particles - clays and silts - characteristic of estuaries may differentially scatter shorter wavelengths (blue) causing increased attenuation. Scattering is wavelength dependent, but in an irregular and complex manner. Absorption is a thermodynamically irreversible process wherein photons are converted to thermal, kinetic, or chemical energy; photosynthesis is an example. Much of the attenuance of the energy of the long wavelengths is due to the water itself, as shown by James and Birge (1938) for pure water and by Clarke and James (1939) for filtered seawater (see Fig. 1). The effect of sea salts on attenuance is relatively insignificant in the PAR. Of course, natural water bodies (particularly estuaries) are not pure, but contain constantly varying particulate and dissolved substances. Burt (1958), using uncontaminated filtered seawater samples, was able to determine the attenuance due to dissolved substances. By subtracting this from the total attenuation coefficient of non-filtered seawater he was able to calculate the light attenuance due to particulate matter. The energy of blue and red wavelengths are selectively absorbed by particles, as shown in the example given by Prieur and Sathyendranath (1981) (Fig. 1b). The shorter wavelengths are also attenuated by yellow substance or Gelbstoff (see Fig. 1b), the collective name given to a complex mixture of organic compounds by Kalle (1966). Gelbstoff is formed from carbohydrates resulting from organic matter decomposition. Sources are both allocthonous (swamps, marshes, land runoff) and autocthonous (planktonic and benthic organisms). Flocculation of fine suspended and colloidal materials in estuaries probably promotes the reaction, as does the presence of amino acids (Kalle, 1966).

The apparent optical properties of a body of water result from the measurement of natural light fields underwater, i.e. the measurement of in situ radiant flux. Irradiance (E), the flux of light reaching a defined area, is usually collected with a flat circular opal glass (or plastic) diffuser (2 π collector). The diffuser is designed so that light received from all angles is transmitted to the sensor according to Lambert's cosine law, i.e., the irradiance transmitted is proportional to the incident radiant intensity multiplied by the cosine of the angle of incidence. Jerlov (1976) reports that the ratio of cosine collection of downwelling irradiance (E_d) to equal hemispherical collection (E_o) is generally in the range of .75 to .85 downwelling. 2 ¶ irradiance is the apparent property of water bodies most commonly measured for biological purposes, and was the measure used in CBP-SAV research. Of course, irradiance can be expressed as either energy or quanta and measured in broad spectral regions, such as the PAR, or at discrete wavelengths, i.e., spectral irradiance. A family of downwelling spectral irradiance curves by depth, in quanta, is shown in Figure 2 for a Zostera marina bed on the Eastern Shore of the Chesapeake Bay.

Primary producers or autotrophs contain light-capturing pigments to carry out photosynthesis. Most phytoplankton possess a pigment complex similar to that of seagrasses and other higher plants. These pigment systems absorb strongly in the blue and red regions. Figure 1b illustrates how combinations of water column constituents may cause specific spectral attenuation patterns. As these constituents change both temporally and spatially, the resultant spectral absorption pattern changes. Prieur and Sathyendranath (1981) have attempted to classify water bodies based on combinations of these factors.

The diffuse downwelling (or vertical) attenuation coefficient[4] (K_d) expresses the decay of irradiance as an exponential function,

$$K_d = \frac{-\ell n \frac{E_2}{E_1}}{(Z_2 - Z_1)}$$

where E_2 is the irradiance at depth Z_2, E_1 is the irradiance at depth Z_1, and (Z_2-Z_1) is the distance between the two measured depths in meters. The units of K_d are m^{-1}. The reciprocal of K_d is termed attenuation length and is considered by some to be more intuitively understandable then K.

If (Z_2-Z_1) brackets the air-water interface, it will include the effects of reflection and inflate the estimate of K_d. K_d calculated between depths within the water column measures the effects of the inherent properties of the layer of water on the propagation of light through that distance. Since this distinction is not always specified in the literature it is sometimes difficult to compare attenuation values. The well-defined spectral attenuation coefficient $[K_d\ (\lambda)]$ is a particularly useful parameter for comparing underwater irradiance between water bodies, seasons, and wavelengths and as such can be considered a quasi-inherent property (Baker and Smith, 1980). Since K_d is inconsistant at different depths in shallow water (<10 m), comparisons should be made at the same depths. Figure 1c shows a typical spectral distribution of both E_d and K_d over the PAR in a Chesapeake Bay seagrass bed. The distribution is a result of the additive effects of the attenuations and scattering of seawater, dissolved substances, non-chlorophyllous particles, and phystoplankton (see Fig. 1b). Pierce et al. (1981) have determined by step-wise multiple linear regression that chlorophylls

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[4] Often termed extinction coefficient

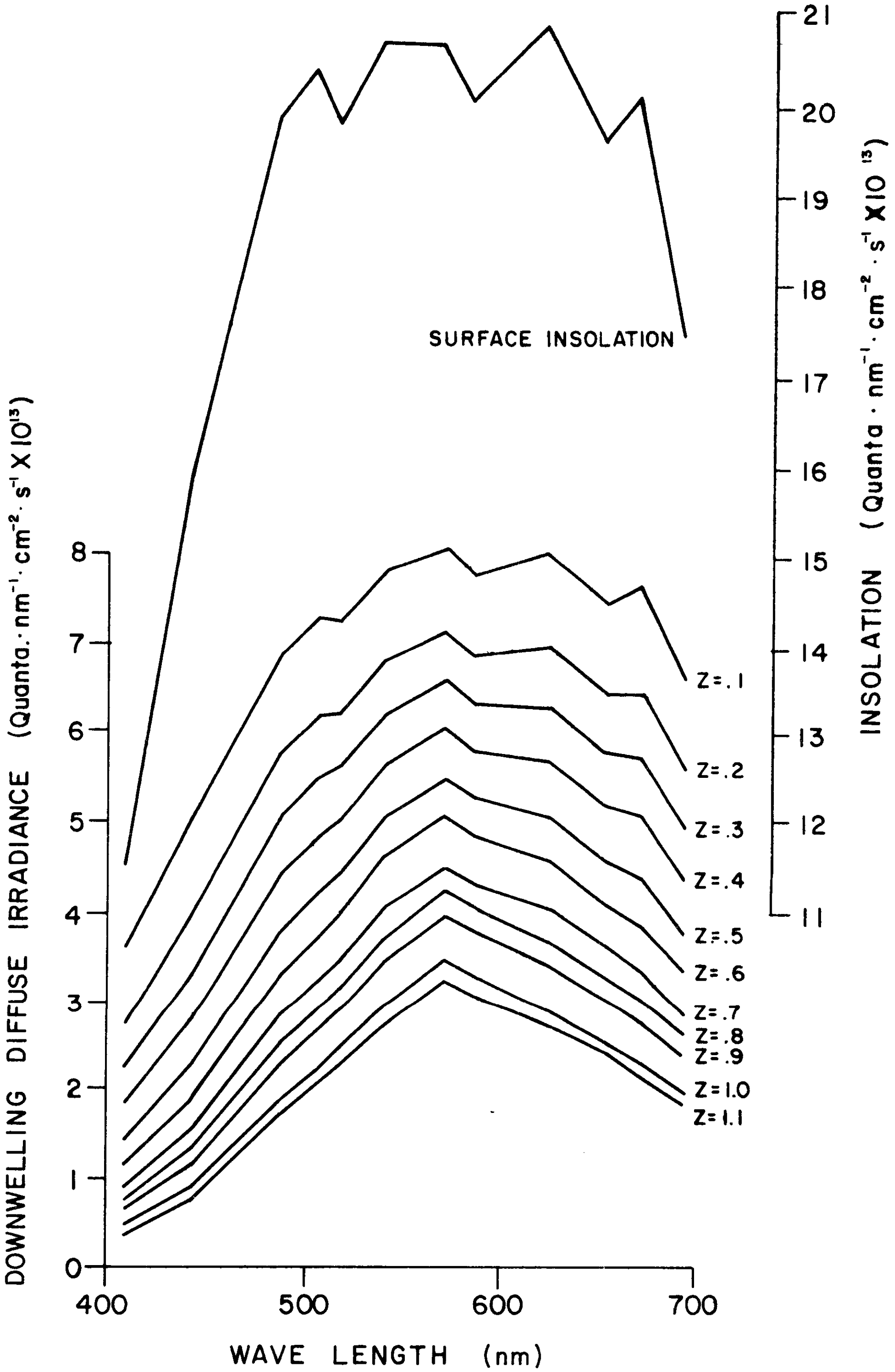

Figure 2. Downwelling spectral quanta irradiance at the surface and at several depths above the canopy of a Zostera marina bed on the Eastern Shore of the lower Chesapeake Bay (Vaucluse Shores) at 1230 E.S.T. on a cloudy April day. The scale for the insolation is on the right.

a and c and inorganic particles explain most of the observed variation in spectral attenuation in the Rhode River Estuary (upper Chesapeake Bay).

The diffuse attenuation coefficient (K_d) and the total attenuation coefficient (c or) derived from the beam transmissometer measure two different properties with no simple relatedness. Calculation of c is based on a spectrally defined and emission-controlled collimated light source which is designed to eliminate diffuse (scattered) light. K_d, however, is based on the natural diffuse submarine light field. Secchi disk readings (D_s) are actually attempts to measure K_d. According to Idso and Gilbert (1974), the relationship

$$K = \frac{1.7}{D_s}$$

is valid for depths between 1.9 and 35 meters, but without consideration of other factors, including c, (Williams, 1970) it will give unrealistic values of K.

The light energy reaching the benthic plants of an estuary is usually reduced in both the blue and red portions of the spectrum, exactly those portions to which higher plants such as seagrasses respond the most efficiently. The mean quantum action spectrum for 50 species of higher plants is presented in Figure 1d (Inada, 1976). A photosynthetic action spectrum is produced by exposing a plant to controlled amounts of energy (or quanta) at discrete wavelengths and measuring its photosynthetic response. The action spectrum in this figure is normalized to the highest photosynthetic rates for red light observed by Inada. The curve presented here is an approximation of the likely action spectrum for seagrasses. A major peak falls in the 400-500 nm (blue) range, a region in estuarine waters where very little light is available due to scattering and absorption by inorganic particles, phytoplankton, and Gelbstoff.

Temporal variations in light distribution, both in the atmosphere and underwater, are due directly and indirectly to the relative motions of the earth, moon and sun. The distance between the earth and sun and between the earth and moon determines not only the amount of energy received by the earth but also the depth of water through which it must travel to reach the seagrasses. The seasonal distribution of nutrients and the resultant planktonic blooms, and runoff (with particulate and dissolved loads and changed salinity regimes) also cause temporal variations in estuarine underwater optical properties. Storms and wind increase not only land runoff, but currents and waves. In shallow areas this action increases resuspension. For example, Scott (1978) found that it took 11 days for the submarine irradiance to return to pre-storm levels in an estuary in Australia. In littoral regions the average submarine light conditions may be partially controlled by the interaction of the local coastal morphology with prevailing wind patterns.

Diurnal variations have two components: solar elevation and tidal variation (amplitude and frequency). Solar elevation determines the angle of incidence of light striking the surface. Since the interface between water and air is a boundary between media of different optical densities, an electromagnetic wave striking it splits into a reflected and a refracted wave. Reflection of combined sun and skylight from a horizontal, flat surface varies asymptotically with solar elevation, i.e., between 3-6% at angles greater than 30° from the horizon. Below 30°, the reflectance increases dramatically up to 40% at 5°. Reflection below 30° is wavelength dependent. The longer waves are reflected more due to the changing quantity of diffuse atmospheric light at low sun angles (Sauberer and Ruttner, 1941). Wave action, on the other hand, reduces reflection at low angles.

Tidal cycles in estuaries not only change water bodies and their associated seston and dissolved components, but also cause resuspension of sediments and cause changes in depth. These are, of course, highly idosyncratic for specific systems. (Burt, 1955b; Scott, 1978).

Light Attenuation in the Chesapeake Bay

A comparison of diffuse downwelling spectral attenuation coefficients reported for the Chesapeake Bay and its tributaries is presented in Figure 3 along with Jerlov's (1976) standard curve (Type 9) for most turbid coastal water. For the Chesapeake Bay, the earliest measurements of $K_d(\lambda)$ were made by Hurlburt (1945) (Fig. 3a). His values fall in the lower range of more recent in situ measurements. The shaded areas in Fig. 3 represent the range of values measured by us (see Chpt. 3) from March through July, 1981 in shallow regions of the lower Bay (<3 m). Jerlov's curve falls in these observed ranges. Champ et al. (1980) conducted a light characterization survey of the Chesapeake Bay during August, 1977. Their mean values are shown in Fig. 3a and their specific site measurements in and near the mouths of the Sassafrass, Patuxent, Potomac and Chester Rivers in Fig. 3c. Their reported means fall within the upper ranges measured by us (van Tine and Wetzel, 1983) in the lower Bay. Pierce et al. (1981) intensively monitored the Rhode River during 1980 and 1981. Their annual mean attenuation values for an upriver station and for one at the River mouth are plotted in Fig. 3b. The upriver station was found to be consistently more turbid; presumably due to its proximity to autocthonous sources. Attenuation at both stations was higher for green, yellow and red wavelengths than observed in the lower Bay, however attenuations in the shorter wavelengths (violet, blue) were in the same range. Maximum penetration was at 575 nm and minima at 775 and 425 nm. Lower Bay maxima were similar and minimum measured was at 410 (775 was not measured in the lower Bay). Curves derived from Seliger and Loftus (1974) from 4 ¶ irradiance measurements in the Rhode River generally agree with the measurements of Pierce et al. (1981) except in the region 500-700 nm. Their measures fall within our observations made in the lower Bay. The differences noted in the 500-700 nm range may be due to upwelling irradiance measured by the spherical collector. Results of the August, 1977 survey by Champ et al. (1980) are shown in Figure 3c. Their attenuation measurements in the turbidity maximum zone at the mouth of the Sassafras River are the highest reported for the Bay. As noted, there is nearly no available light below 500-600 nm. We have also observed very high attenuations in the blue region (400-500 nm) at lower Bay sites during a spring runoff event following a major rain storm. The attenuation of green wavelengths (∿500-550 nm) in the summer

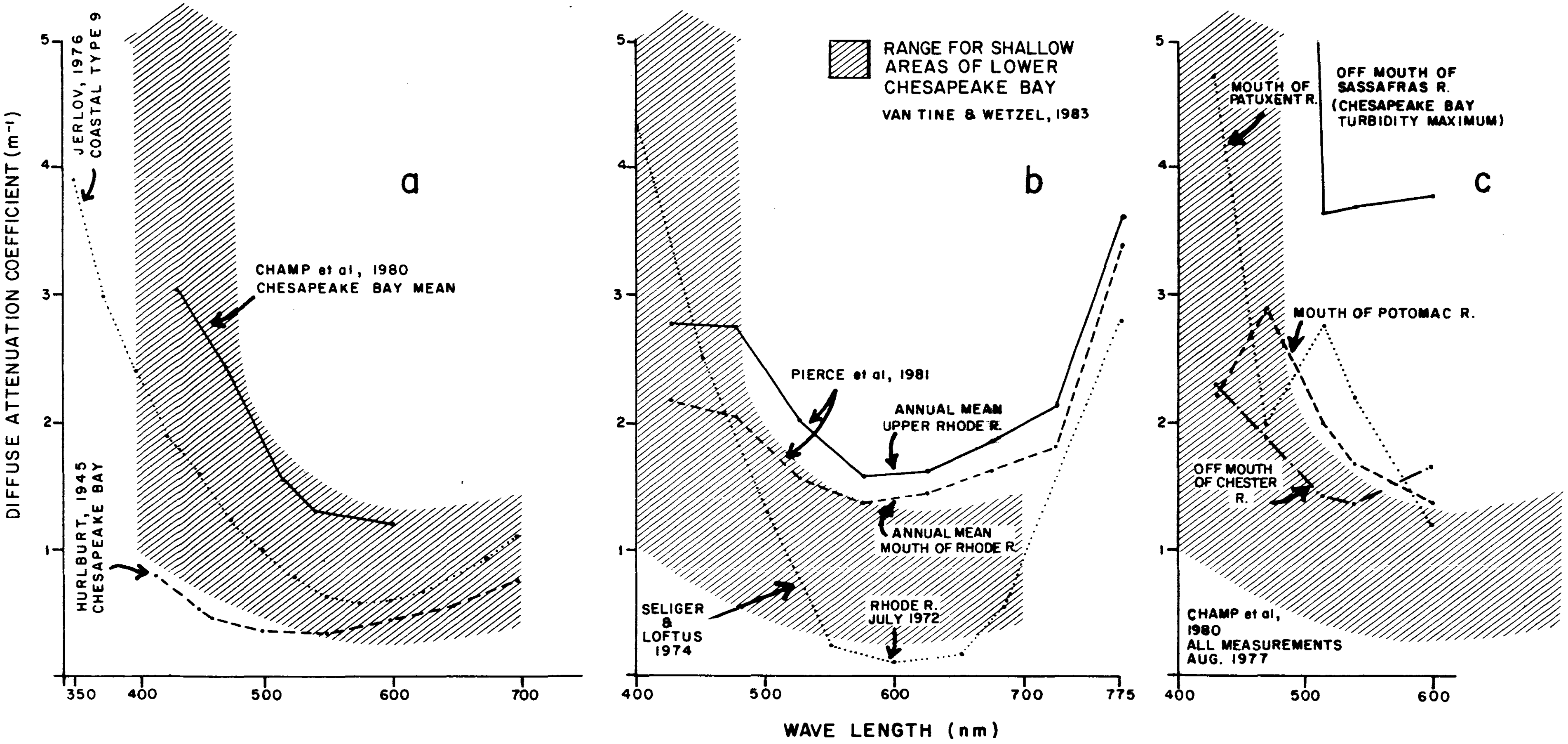

Figure 3. Comparison of diffuse downwelling spectral attenuation coefficients for Chesapeake Bay with Jerlov's most turbid coastal classification. (a) Plotted from tables in Jerlov, 1976; Hurlburt, 1945; Champ et al., 1980 (b) Plotted from table in Pierce et al., 1981 and calculated from 4 irradiance curves in Seliger and Loftus, 1974 (c) Plotted from tables in Champ et al., 1980. Shaded area represents ranges of attenuation found by van Tine and Wetzel (1983) in shallow lower Bay waters.

was much higher at the mouths of the Patuxent and Potomac Rivers (upper Bay) than at the mouths of the York, Severn and Ware Rivers (lower Bay). Fig. 4 locates the lower Bay sampling stations.

This brief summary of the recent available Chesapeake Bay data on diffuse downwelling 2 irradiance attenuation indicates a severe attenuation of light energy in the photosynthetically important 400-500 nm (violet-blue) and 650-775 nm, (red and near infrared) regions of the spectrum. Attenuation in the short wavelengths was particularly marked in the turbidity maximum region of the Bay at the mouth of the Sassafras River, and at the mouth of the Patuxent River during August (Champ et al., 1980) and at the lower Bay sites during spring runoffs (Fig. 5, and see Chpt. 3). The mean attenuation coefficients calculated for the Bay by Champ et al. (1980) are about 1.0 m^{-1} higher than Jerlov's (1976) most turbid coastal water classification but are close to those calculated by ourselves (see Fig. 7, Chpt. 3; van Tine and Wetzel, 1983).

Comparison of Light Attenuation in Vegetated and unvegetated Sites of the Bay: Preliminary Analysis[5]

An analysis of the spectral attenuation coefficients at shallow sites in the lower Chesapeake was undertaken to determine if correlations existed between the presence or absence of benthic macrophytes (*Zostera marina* and *Ruppia maritima*) and specific spectral patterns. The specific question addressed was -- What are the light quality differences between vegetated and unvegetated sites? The sites (Fig. 4) were chosen because of their varied vegetational histories (Orth et al., 1979). The Mumfort Island (York River) and Severn River sites are presently unvegetated. The Guinea Marsh and Four Point Marsh (Ware River) sites have seagrass beds. Both the Severn River and Four Point Marsh sites are impacted by agricultural runoff (C. Hershner, pers. comm.). Twelve wavelengths, (410, 441, 488, 507, 520, 540, 570, 589, 625, 656, 671, 694 nm ± 5 nm), and total PAR were analyzed at depths of 0.1 and 0.5 m. Downwelling irradiance (E_d) was measured as quanta nm^{-1} cm^{-2} s^{-1}, each reading representing the mean of at least 250 scans. Diffuse downwelling spectal attenuation was calculated between 0.1 and 0.5 m.

The mean spectral attenuation values ranged from about 0.2 to 9.0 m^{-1}. Integrated PAR attenuation varied from about 0.5 to 1.6 m^{-1} (Fig. 6). A clear seasonal pattern of extreme attenuation of the blue wavelengths was evident at all sites beginning in May. This was probably due to a combination of increased particulates associated with runoff events and seasonal plankton blooms.

Mean PAR attenuation coefficients were found to be significantly lower (mean difference of 0.47 m^{-1}) *in vegetated than in unvegetated sites during May, 1981* (Fig. 6). This was due to a lower attenuation in the 500-700 nm

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[5] See Chapter 3, this volume, for a more complete analysis

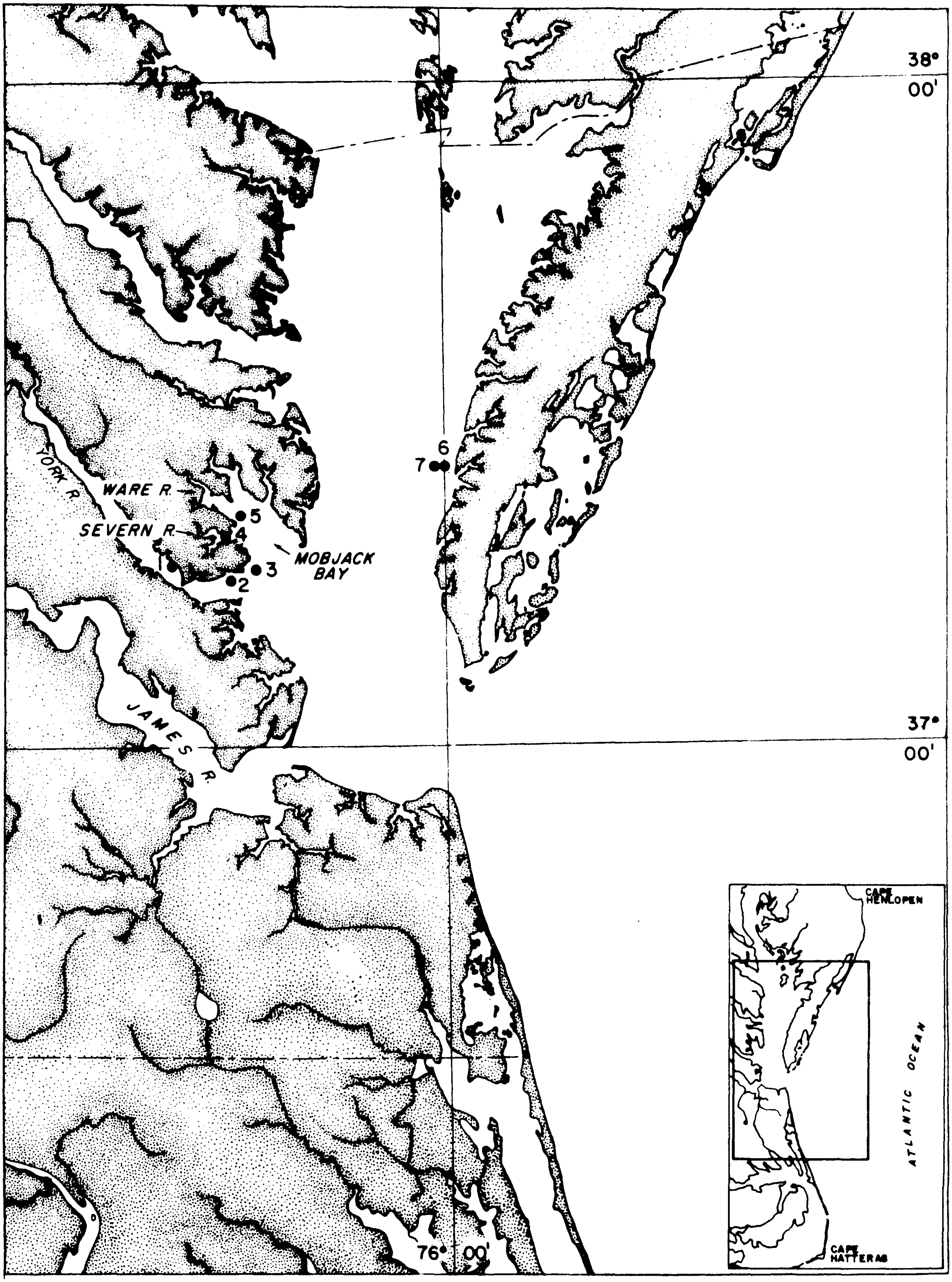

Figure 4. Locations of lower Bay stations (1) Mumfort Is., York R., (2) Allen's Is., York R., (3) Guinea Marshes, (4) Mouth of Severn R., Mobjack Bay, (5) Four Point Marsh, Ware R., Mobjack Bay, (6) Vaucluse Shores off Hungars Creek, (7) deep station.

region of the spectrum at the vegetated sites (Fig. 5), despite the effects of high blue attenuation due to runoff. A significant difference among sites based on PAR attenuation coefficients was also observed in July; however, one vegetated site (Four Point Marsh) had attenuation coefficients as high as the unvegetated sites (Fig. 6). This was due to the increased attenuation of wavelengths above 500 nm at the Four Point Marsh site during July. The only general light quality differences between vegetated and unvegetated sites that was evident from these preliminary analyses was the reduced attenuation in the 500-700 nm region at vegetated sites during May.[6]

Kaumeyer et al. (1981) measured a significant difference in PAR attenuation coefficient inside and outside SAV beds at Todd's Cove, Md. during July, August, and September, 1980. K_d (PAR) for the vegetated areas was from 0.4 m^{-1} to approximately 2 m^{-1} lower. Significant differences were not found in attenuation inside and outside grassbeds at their Parson's Island study site. Table 1 summarizes the results of their studies.

Historical Data Bases and Optical Properties of the Chesapeake Bay

Most of the historical light data for the Chesapeake Bay has been collected by Secchi disc. This method is not ideal but can be used to indicate trends. Heinle et al. (1980) reviewed Secchi disc light data for both mid-Bay and the Patuxent River, which was chosen because of the extensive data base (Fig. 7). Transparency has decreased since the 1930's, especially during the winter in the mid-Bay (Fig. 7a). An increase in turbidity, as estimated by Secchi disc measures, has been quite dramatic in the Patuxent (Figs. 7b, 7c). Mid-1970's Secchi disc data for rivers in the upper Chesapeake Bay are reported in Table II from Stevenson and Confer (1978). The values are generally low (<1.0 m) and are similar to those reported for the Patuxent during the 1960's and 1970's (Figs. 7b, 7c).

Increases in chlorophyllous pigments due to phytoplankton blooms (which can be caused by increased nutrients) may have a severe effect on light attenuation in the photosynthetically critical blue and red spectral regions (Fig. 1b, 1d). Historical chlorophyll data for the Chesapeake Bay and Patuxent River are summarized in Figures 8 and 9. Chlorophyll concentrations have increased dramatically in the upper and mid-Bay since the early 1950's. Concentrations as high as 100 to 200 $\mu g \cdot l^{-1}$ are not unusual. In contrast, lower Bay -- main stem -- concentrations have not significantly changed (Fig. 8b). Concentrations in the Patuxent River have inceased significantly in both the upper and lower portions (Fig. 9), especially during late spring and early summer (Fig. 9b). Levels in excess of 100 $\mu g \cdot l^{-1}$ were common in the summer throughout the 1970's, these are TWICE the concentrations measured during the previous decade.

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[6] Subsequent measurements and analysis extend and corroborate this conclusion: not only is the mean violet and blue attenuation lower at vegetated sites but the variation is also less. (see Chapter 3, this volume).

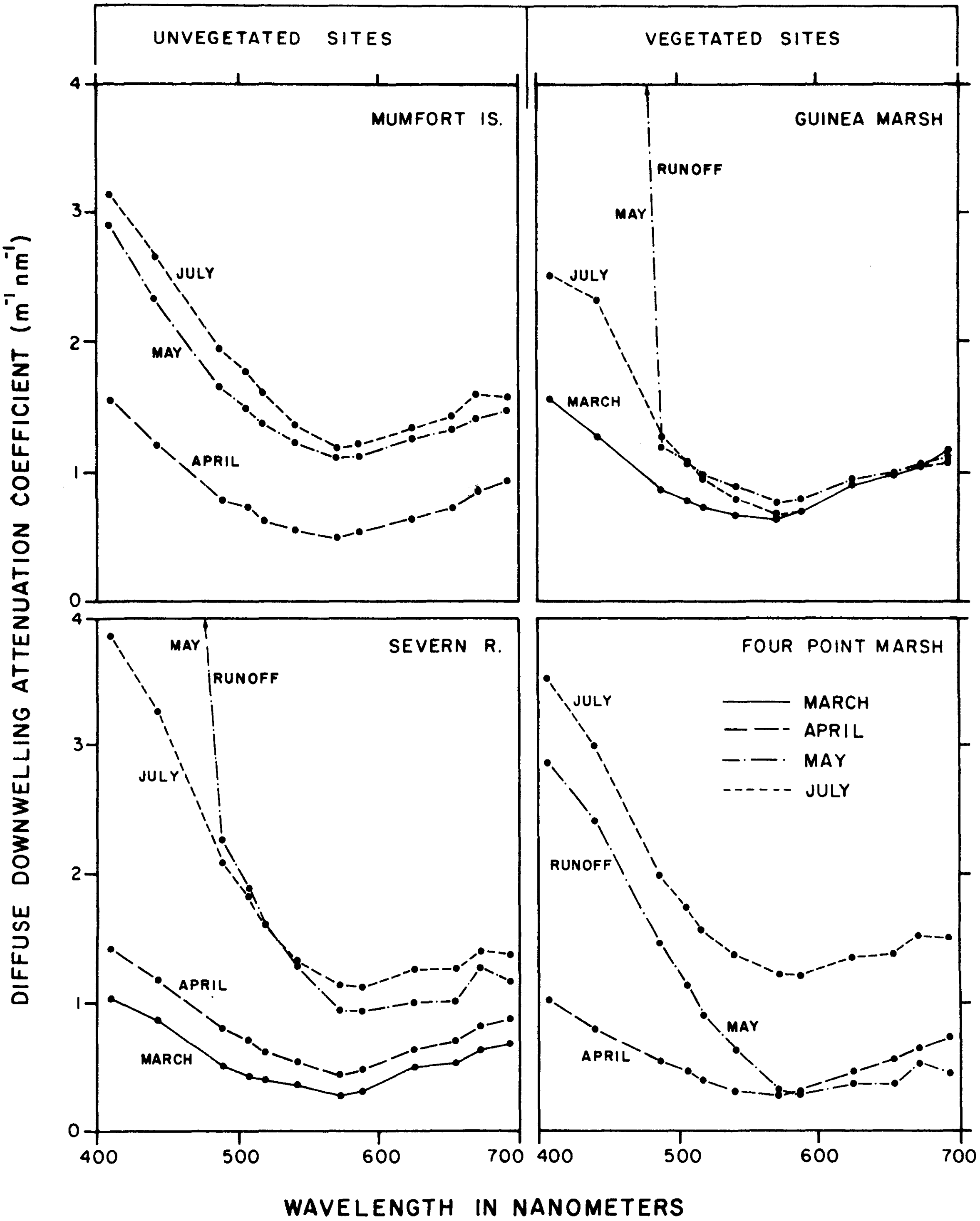

Figure 5. Mean monthly diffuse downwelling spectral attenuation coefficients for vegetated and unvegetated sites in the lower Chesapeake (March-July, 1981). All coefficients calculated for the depth interval 0.1 to 0.5 m. Mumfort Island (York River) and Severn River sites: unvegetated. Guinea Marsh and Four Point Marsh (Ware River) sites: vegetated.

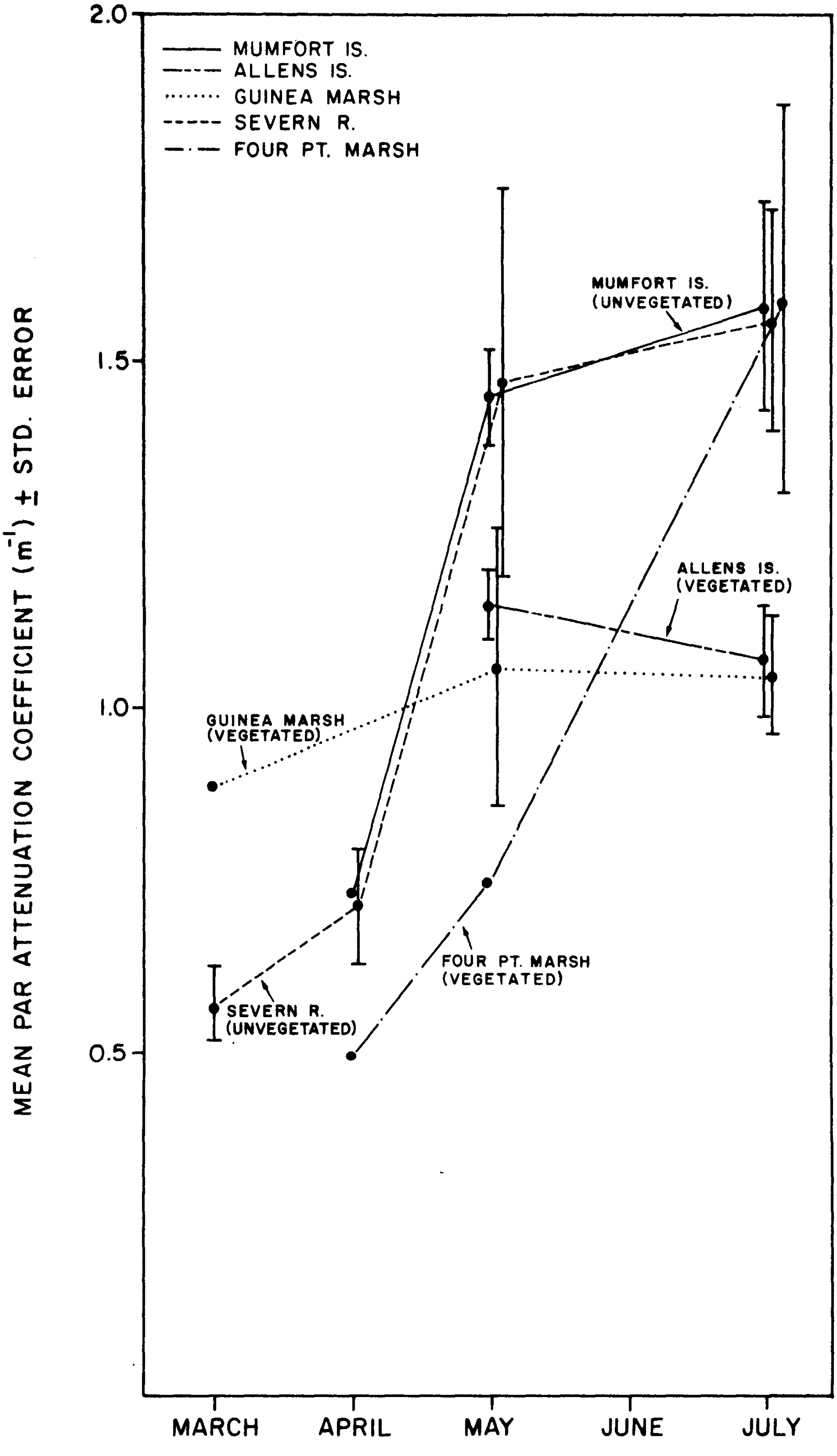

Figure 6. Mean monthly downwelling PAR attenuation coefficient ± 1 standard error of the mean for vegetated and unvegetated sites in the lower Chesapeake Bay.

TABLE I. COMPARISON OF MEAN PAR ATTENUATION COEFFICIENTS INSIDE AND OUTSIDE OF VEGETATED AREAS AT TODD'S COVE, MD. 1980 (KAUMEYER et al., 1981)

Month	Location	$K_{PAR}(m^{-1})$
June	SAV	2.6 ± 0.20
	Reference	2.5 ± 0.75
July	SAV	2.5 ± 0.30
	Reference	2.9 ± 0.70
August	SAV	1.8 ± 0.56
	Reference	3.1 ± 0.33
September	SAV	1.9 ± 0.34
	Reference	3.8 ± 0.96

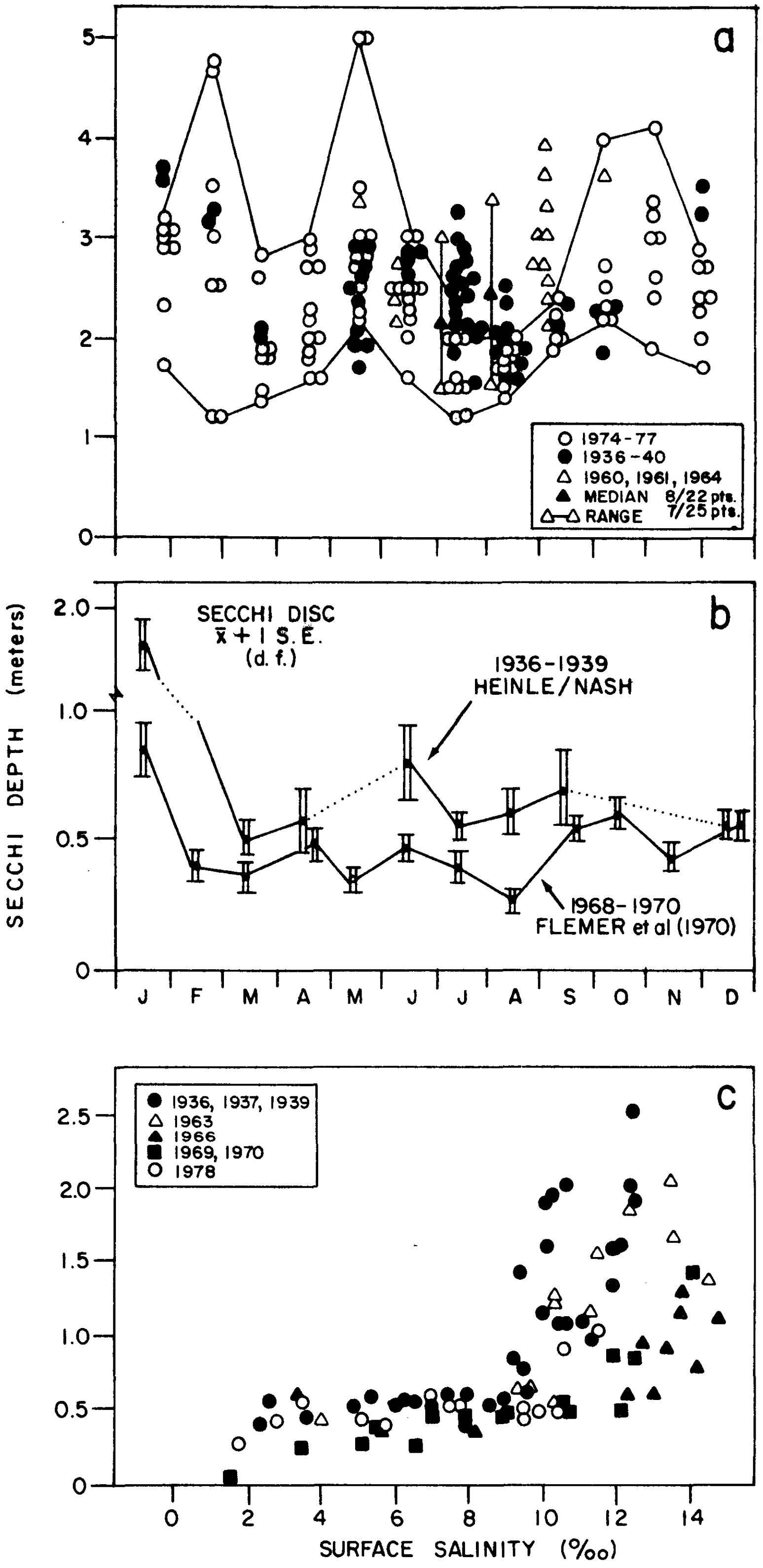

Figure 7. Historical Chesapeake Bay Secchi disc values (after Heinle et al., 1980 and references therein). (a) monthly mid-Bay means. (b) monthly means Patuxent River estuary. (c) Patuxent River Secchi depth vs. salinity, July (after Mihursky and Boynton, 1978).

TABLE II. AVERAGE SECCHI DISC DATA (cm) BY RIVER SYSTEM, MARYLAND CHESAPEAKE BAY, 1972-1976a, (as reported in Stevenson & Confer, 1978).

River System	1972	1973	1974	1975	1976
Elk & Bohemia	33.0	35.1	-	25.7	36.3
Sassafras	34.3	52.3	-	29.2	51.
Howell & Swan Points	33.8	75.4	-	61.2	57.7
Eastern Bay	67.3	62.5	76.5	54.6	75.9
Choptank	60.7	62.5	84.3	61.5	64.3
Little Choptank	64.5	59.4	66.8	63.8	78.5
James Island & Honga	70.1	64.0	74.2	67.1	73.4
Honga River	78.2	67.3	72.6	68.8	67.8
Bloodsworth Island	73.7	87.6	94.7	177.0	83.3
Susquehanna Flats	64.5	65.5	82.6	33.8	76.5
Fishing Bay	49.5	77.0	85.6	75.7	54.1
Nanticoke & Wicomico	55.4	58.9	65.8	61.0	58.9
Manokin	94.2	94.7	101.3	107.4	81.0
Patapsco	73.7	80.0	67.8	-	70.1
Big & Little Annemessex	109.7	92.7	96.3	88.1	85.1
Gunpowder & Bush Headwaters	42.9	38.3	46.7	-	53.8
Pocomoke Sound, MD	101.6	82.0	-	96.8	85.9
Magothy	83.8	97.3	73.4	-	74.4
Severn	97.3	70.4	79.5	-	86.4
Patuxent	80.3	80.8	61.5	66.8	62.7
Back, Middle & Gunpowder	79.5	75.7	73.2	75.4	61.2
Curtis & Cove Point	45.2	77.0	81.8	58.9	73.7
South, West & Rhode	74.7	66.0	61.2	48.5	67.1
Chester	76.2	73.4	100.1	87.9	85.1
Love & Kent Points	89.7	74.7	117.6	72.1	89.9
Smith Island, MD	78.5	76.2	89.7	139.4	87.6
AVERAGE	70.1	71.1	79.5	76.2	71.4

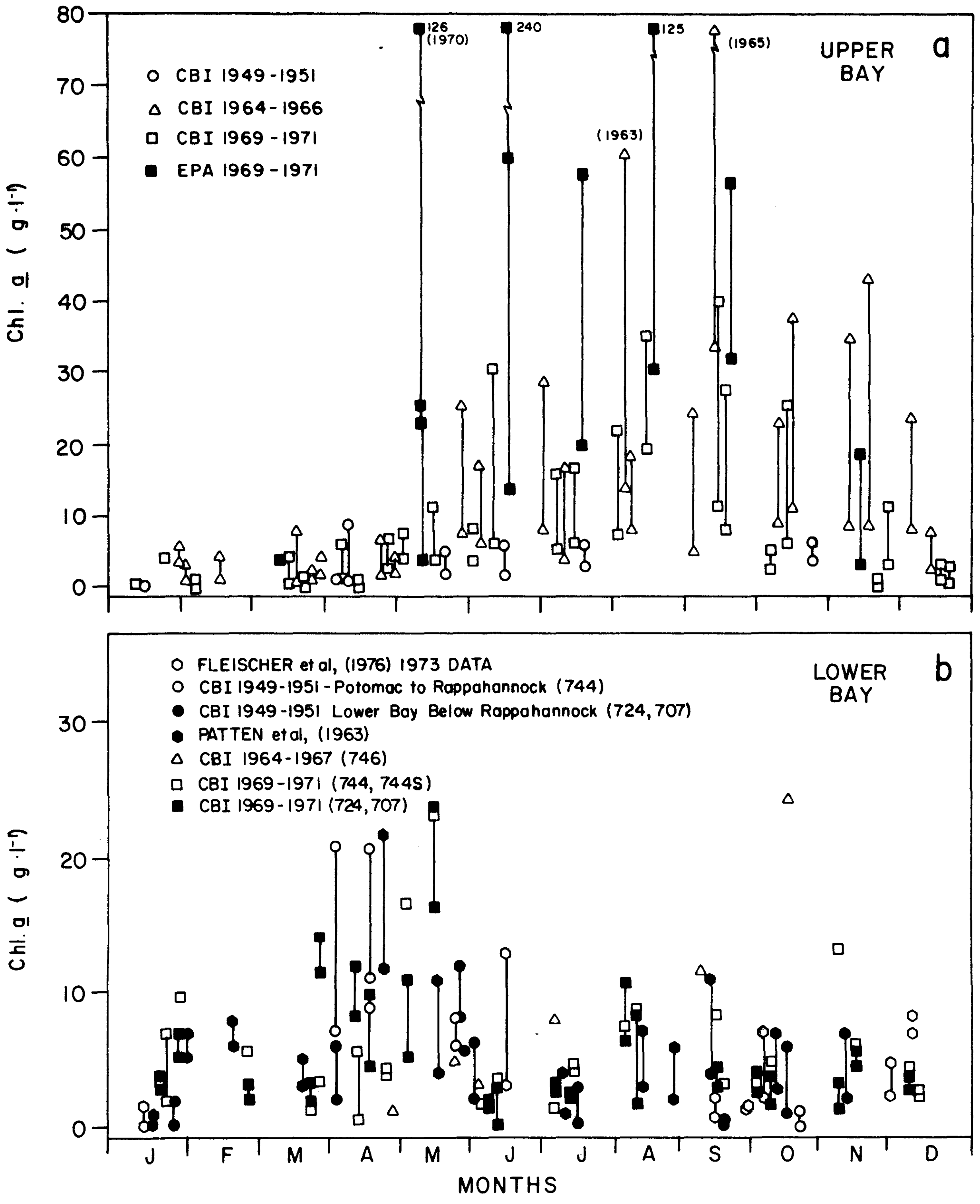

Figure 8. Summary of historical chlorophyll a data for the main stem of the Chesapeake Bay. (a) upper Bay. (b) lower Bay (after Heinle et al., 1980).

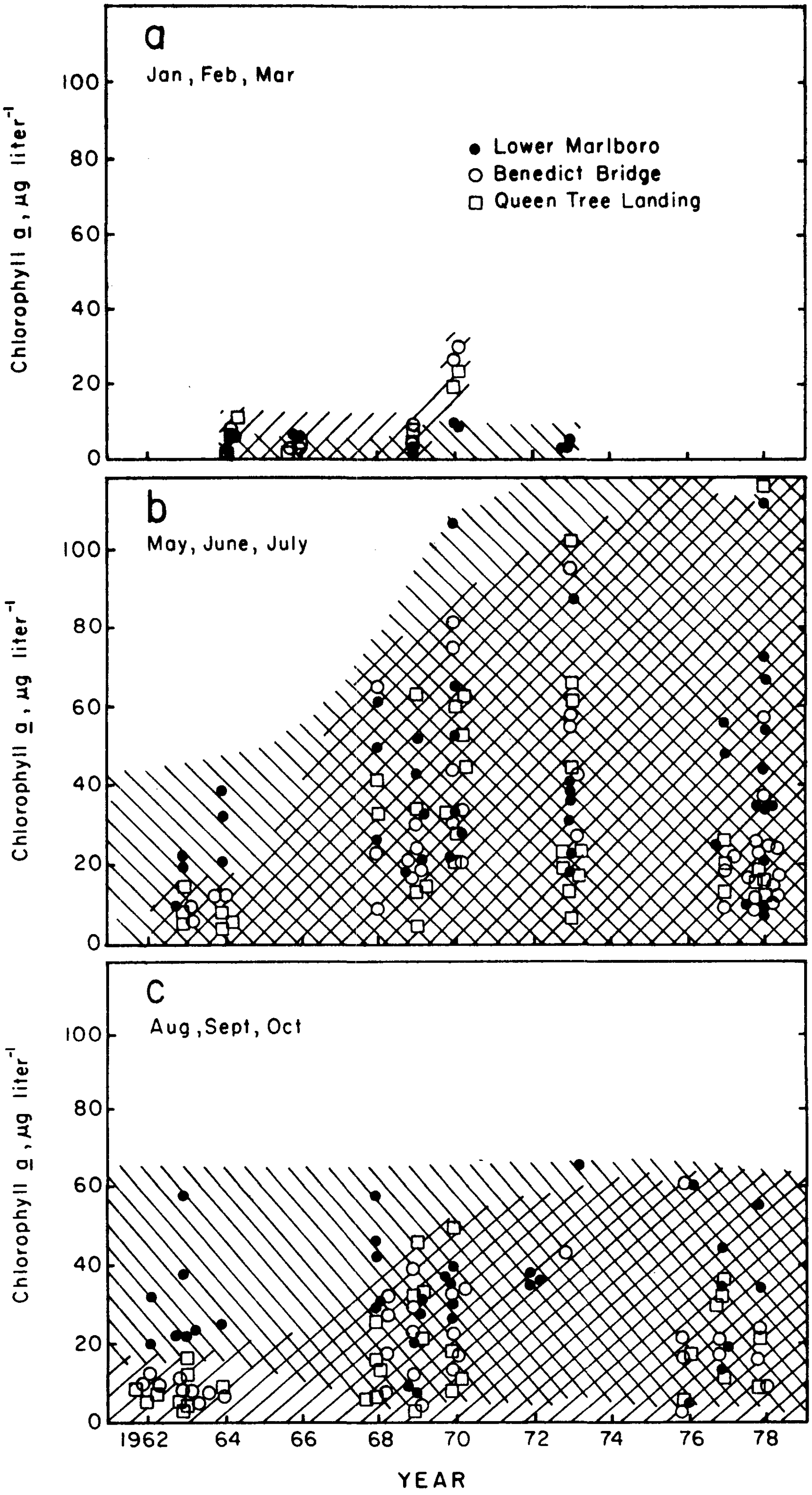

Figure 9. Summary of historical chlorophyll a data for three regions of the surface waters of the Patuxent R., Md. (a) January-March (b) May-July (c) August-October (after Heinle et al., 1980).

In addition to the thoroughly documented increased chlorophyll-*a* concentration in the Patuxent, there have also been increases in most of the other tributaries of the Bay. Chlorophyll-*a* concentrations in the Choptank, Chester, and Miles Rivers of the Middle Eastern Shore are 1.5 to 2 times higher presently than earliest data showed. There have also been upstream increases in the Magothy, Severn (Md.) and South Rivers. In the upper Potomac concentrations up to 100 $\mu g \cdot l^{-1}$ were measured in the mid-1960's. Concentrations in the lower Potomac were generally higher in the 1960's than 1950, except during March and April (Heinle et al., 1980) (see Table III). Increased chlorophyll *a* concentrations have also been measured in the Rappahannock and York rivers during the last few years. The upper James has had high concentrations similar to the upper Potomac since the mid-1960's but the lower River still does not. Dense algal blooms have been noted in the Elizabeth, Back, and Poquoson Rivers of the lower Bay.

Heinle et al. (1980) summarized the state of the Bay graphically in terms of enrichment--which they defined as "deviations in concentrations of chlorophyll *a* from historic, natural periods of stability or steady state concentrations." Figure 10 depicts the regions of the Bay which they categorized as moderately or heavily enriched. Significantly, most of these same areas have experienced declines in Bay grasses on a time scale overlapping the enrichment (Orth and Moore, 1982).

Suspended particulates and dissolved materials also impede the amount and quality of light reaching the benthos. Amounts of dissolved organic materials, inorganic particulate matter and allochthonous organic particulate matter in the Bay are mainly determined by input (runoff) of freshwater to the tributaries. Dramatic increases can result from storm events. Table IV summarizes annual mean freshwater flow to the entire Bay and major storms during the period, 1951-1979. In addition to adding large amounts of sediment to the water column, major storm events increase nutrient loads originating from agricultural fertilizers and other sources thus stimulating phytoplankton blooms. There is also an apparent wet-year, dry-year cycle imposed on the data. The five year flow averages suggest a mid-1960's depression followed by an increase through the 1970's. Although these data have not been rigorously analyzed, it is apparent that long term changes and or cycles in climatic conditions (rainfall, temperature and major storms) influence water quality and therefore the optical properties of Bay waters.

Suspended sediment transport and discharge of the Susquehanna River, the major source of freshwater to the Bay, is given in Table V. Gross et al. (1978) suggest that one-half to two-thirds of the suspended sediment discharge of the Susquehanna is deposited behind the dams or in lower reaches of the river during years of low flow and no major flooding. However, during major floods these deposits are eroded and transported into the Bay. Thus, the dams effectively increase the amount and variability of sediment discharged under flood conditions possibly contributing to periodic stressing of the Bay.

TABLE III. RANGES OF CONCENTRATIONS OF CHLORPHYLL a (μg l^{-1}) AT SURFACE AND BOTTOM DEPTHS IN THE LOWER POTOMAC RIVER DURING 1949-1951, AND 1965-1966 (after, Heinle et al., 1980).

	1949-1951		1965-1966	
Month	Surface	Bottom	Surface	Bottom
January	1-2	1-2	3.2-4.7	3.1-5.0
March-April	10-21	12-27+	1.1-20.0	1.1-9.5
May	3-6	9-24+	5.8-13.2	4.3-9.8
July	3-5	1-2+	9.0-13.8	1.0-1.8
October-November	1-9+	1-7	9.3-24.0	3.6-11.0

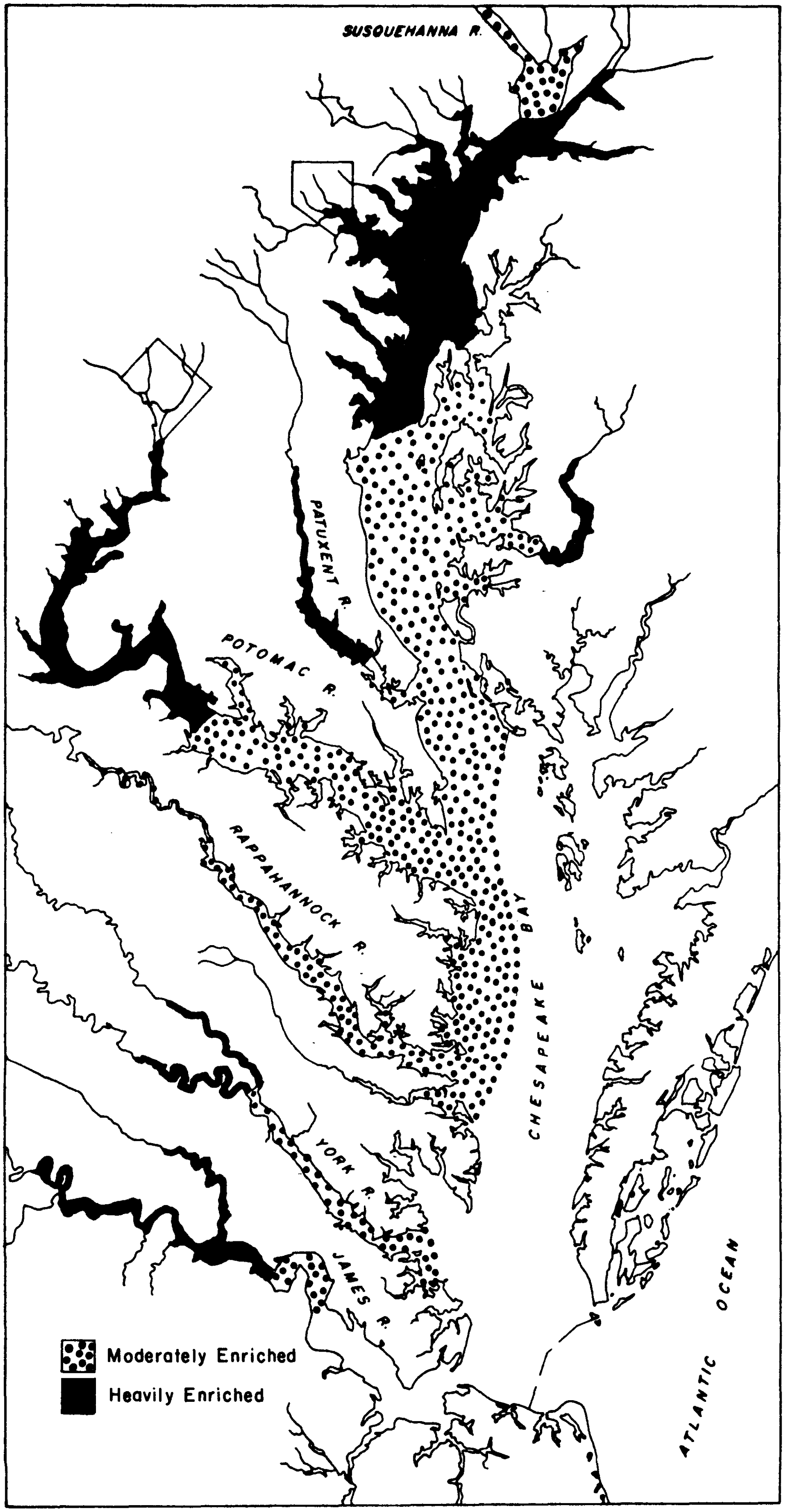

Figure 10. Enriched sections of the Chesapeake Bay. Enrichment is defined as an increase in chlorophyll a levels from historic, natural periods of stability (after Heinle et al., 1980).

TABLE IV. TOTAL ANNUAL MEAN FRESHWATER FLOWS TO THE CHESAPEAKE BAY AND OCCURRENCE OF HURRICANES, 1951-1979 (after Heinle et al., 1980).

Year	Bay Annual Average ($ft^3 \cdot s^{-1}$)	5-Year Average
1951	82,100	
1952	94,300	
1953	72,800	
1954 Hurricane	58,700	
1955 (2) Hurricanes	73,400	76,260
1956	76,000	
1957	64,400	
1958	81,400	
1959	66,400	
1960	77,300	73,100
1961	78,000	
1962	64,800	
1963	52,400	
1964	61,900	
1965	49,000	61,220
1971	79,000	
1972 Hurricane	131,800	
1973	95,200	
1974	76,900	
1975	103,100	97,180
1976	84,400	
1977	80,100	
1978	91,300	
1979 Hurricane	113,800	92,400

TABLE V. SUSPENDED SEDIMENT TRANSPORT AND DISCHARGES OF SUSQUEHANNA RIVER TO THE CHESAPEAKE BAY (after Gross et al., 1978).

Calendar Year	Annual suspended sediment discharged (10^6 metric tons/yr.) Above Dam	Below Dam
1966	1.5	0.7 (60%)*
1967	1.7	>0.3**
1968	>1.7**	nd
1969	nd	0.32 (60%)*
1970	>2.0	>1.1**
1971	>1.4**	1.0
1972	11.3	33
Agnes, 24-30 June 1972	7.6	30
1973	3.2	1.2 (54%)*
1974	1.7	0.8 (53%)*
1975	>3.8	11
Eloise, 26-30 Sept. 1975	1.6	9.9
1976	nd	1.2

nd = no data
* Percent discharged during annual spring flood
**Records incomplete for the year

LIGHT AND PHOTOSYNTHESIS IN CHESAPEAKE BAY SAV COMMUNITIES

General Review of Photosynthesis

Photosynthesis is the process by which light is used as the energy source for the synthesis of organic compounds. Three basic steps are involved in the process: 1) absorption of light energy by photosynthetic pigments; 2) processing the captured light energy to produce the compounds ATP and NADPH; and 3) the reduction of CO_2 using ATP and NADPH and the production of carbohydrates. The first two steps are light-dependent and collectively referred to as the "light reaction." The third step is light-independent and termed the "dark reaction."

Photosynthetic pigments have characteristic light energy absorption peaks within the photosynthetically active region of the spectrum. Chlorophyll a absorbs light more effectively at higher wavelengths (>600 nm) while accessory pigments such as chlorophyll b, carotenoids, and others are more effective absorbs at shorter wavelengths (<600 nm). Chlorophyll a and the accessory pigments transfer the absorbed light energy at varying efficiencies to specialized chlorophyll a molecules (P700) where it is used directly for biochemical reactions.

The photochemical reactions are driven by units of light energy termed photons (quanta). Quantum energy is a function of wavelength; quanta of shorter wavelengths contain more energy than quanta of longer wavelengths. Light energy transferred to P700 is most efficient as it is used directly in the photosynthetic system while light energy transfer via chlorophyll a and accessory pigments is less efficient. Quantum yield, the moles of O_2 produced or CO_2 fixed per photon of light absorbed, may be used to estimate the transfer efficiency.

The light utilization spectrum of a particular species is termed the action spectrum, a characteristic curve obtained by measuring the relative photosynthetic output of intact plant parts at discrete wavelengths. The action spectrum is an important feature since it reflects the ability of a species to adapt to various light quality regimes (Fig. 1d). This is of particular importance when considering photosynthesis of submerged plants. In aquatic environments, spectral shifts in light energy result from the water itself, suspended organic and inorganic materials, dissolved organic compounds and other water column constituents. (See Chpt. 3 for a discussion of the relationship between the light quality environment of the Chesapeake Bay and its potential effect on photosynthesis).

A general approach to the investigation of photosynthesis as related to total PAR radiation is to construct light saturation curves for various species (Fig. 11a). An examination of photosynthesis-light curves (P-I curves) shows that photosynthesis (P) increases with increasing irradiance to an optimal point (I_{opt}) where over a range of irradiance, the photosynthetic

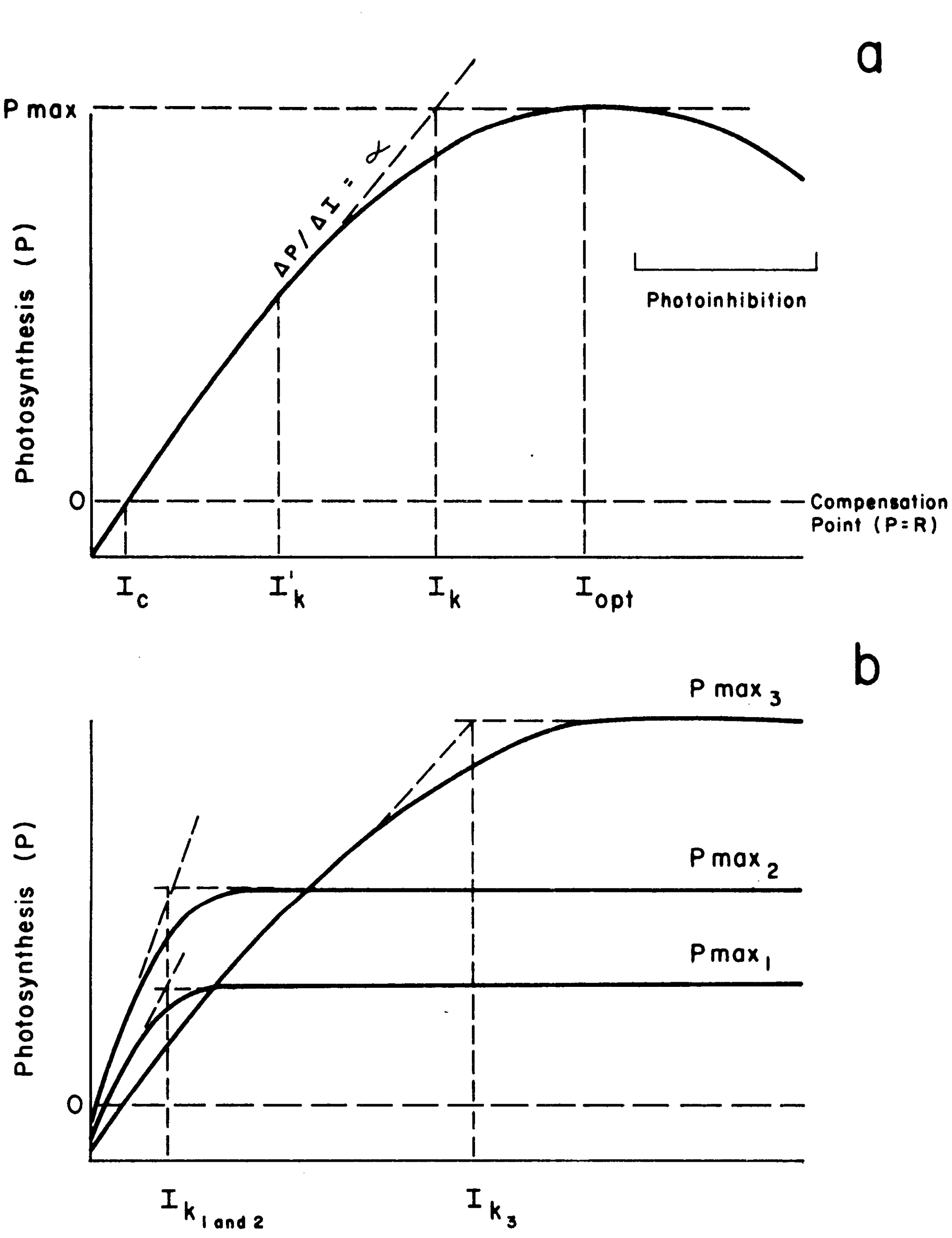

Figure 11. Diagramatic photosynthesis-light relationships (see text for description of parameters).

system is saturated and maximum photosynthesis (P_{max}) occurs. At higher irradiance, there may be a depression in the photosynthetic rate, termed photoinhibition. The initial slope of the curve ($\Delta P/\Delta I$ or α) and P_{max} are the two major parameters used in describing P-I curves (Jassby and Platt, 1976). α is a function of the light reaction of photosynthesis and is an estimator of the quantum yield. P_{max} is a function of the dark reaction and is influenced by environmental factors or the physiological state of the plants (Parsons et al., 1977). The term I_k, proposed by Talling (1957) is the irradiance at which a linear extension of the initial slope intercepts P_{max}. I_k is regarded as indicative of the plant's adaptation to its light regime (Steeman Nielsen, 1975). I'_k is irradiance where $P = 0.5\ P_{max}$ and is similar to the Michalis-Menten half-saturation constant. I_c is the irradiance at the compensation point, where photosynthesis equals respiration ($P = R$).

Characteristic P-I curves are shown in Fig. 11b. Plants adapted to high and low light environments, termed respectively sun and shade species, exhibit different P-I curves. Sun species (curve 3) generally exhibit higher P_{max} values than shade species, which exhibit greater α and lower I_c values (curves 1 and 2). In the aquatic environment, with reduced availability of light, species exhibiting shade type photosynthesis (greater photosynthetic rates at low light intensities) are at an advantage if they are not intertidally exposed to high light levels.

Photosynthesis of Submerged Vascular Plants in Relation to Light and Temperature

In situ studies of submerged angiosperms point to the role of light in seagrass production and distribution (Jacobs, 1979; Mukai et al., 1980). In a study of *Zostera* in Denmark, Sand-Jensen (1975) showed a positive correlation between leaf production and insolation over a nine-month period. Biomass and photosynthetic rates of *Posidonia* declined with depth near Malta (Drew and Jupp, 1976); this probably was due to decreased light penetration with depth. In before and after studies of an estuary that was closed to the sea, Nienhuis and DeBree (1977) reported that the *Zostera* population increased in density and extended to a greater depth; they suggested that this was probably due to an increase in water transparency. van Tine (1977, 1981) found a correlation between reduced light transmission and the biomass and diversity of benthic macrophytes including *Thalassia*, *Halodule* and *Sringodium* in an estuary in the Gulf of Mexico.

In situ light and manipulation experiments have provided evidence of the importance of light to seagrass production. For example, at the end of a nine-month study during which ambient light was reduced by 63%, in situ *Zostera* densities were only 5% of that of the control (Backman and Barilotti, 1976). In similar studies, Congdon and McComb (1979) reported that lower than ambient light levels resulted in lower *Ruppia* biomass; as the shading duration increased, higher light levels were required to sustain a high biomass.

Studies involving the epiphytic community, those organisms directly attached to submerged angiosperm blades, suggest that the epiphytes have a detrimental effect on the seagrass hosts, primarily due to shading of the macrophytes by the epiphytes. Sand-Jensen (1977) reported that *Zostera* photosynthesis was reduced by up to 31% due to a decreased penetration of light and inorganic carbon through the epiphytic community to the seagrass blades. Johnstone (1979) hypothesized that the rapid linear growth of *Enhalus* leaves (up to 2 cm day^{-1}) was related to a shading effect to epiphytes. However, the net community productivity of the seagrass-epiphyte system may not be reduced. It may be that the different pigment complexes of the various epiphytes provide optimum light absorption during seasonally changing aquatic light conditions. Both Kiorbe (1980) and Phillips et al. (1978) provided data to indicate that epiphytic development suppressed macrophyte growth. The data of Penhale and Smith (1977) suggested that an epiphytic community may be beneficial in certain environments. For *Zostera* exposed at low tide, the epiphytes prevented desiccation damage by trapping a film of water and probably reducing the photoinhibitory effect of high light.

In addition to light, temperature also influences submerged macrophyte distribution and productivity rates (Biebl and McRoy, 1971; Drew 1978) van Tine, (1977, 1981) found reduced biomass and diversity of benthic macroalgae and seagrasses in estuarine waters impacted by a lower plant induced thermal plume. The biogeography of marine and brackish water plants points to a temperature effect on world wide distribution; for example, genera such as *Zostera*, *Ruppia*, *Phyllospadix*, and *Posidonia*, occur mainly in temperature zones while genera such as *Thalassia*, *Syringodium*, and *Halophila* occur mainly in subtropical and tropical zones. Drew (1979) reported that the P_{max} of four seagrass species collected near Malta increased in direct proportion to temperature up to temperatures (30-35°C) where tissue damage occurred; decreases were not observed at environmental temperatures. In contrast, Penhale (1977) observed a decline in P_{max} from 22 to 29°C for *Zostera* in North Carolina where environmental temperatures reach 34°C. The co-existence of species such as *Ruppia* and *Zostera* in the lower Chesapeake Bay may be a result of differential responses to both temperature and light as apparently is the case in a *Myriophyllum*-*Vallisneria* association described by Titus and Adams (1979). They reported that a greater for *Vallisneria*, in conjunction with the temperature dependence of photosynthesis, resulted in a temporal partitioning of resources. *Vallisneria* was apparently favored by midsummer conditions and *Myriophyllum* by spring and fall conditions.

Sun and shade species have been described for submerged macrophytes (Spence and Crystal, 1970a, b; Titus and Adams, 1979). Sun species generally exhibit higher P_{max} values than shade species which exhibit greater and lower I_c values and lower dark respiration rates. Certain species can adapt to a wide range of light conditions. Bowes et al. (1977) cultured *Hydrilla* under high and low irradiances; subjecting the plants to high light increased the I_{opt} value four-fold. Plants grown under low light achieved I_c and I_k at lower intensities.

In seagrass systems, pigment relationships generally vary with light quantity or with position within the leaf canopy. The adaptive capability of seagrass pigment systems to the light environment has been shown in various studies. For example, Wiginton and McMillan (1979) reported that the total chlorophyll content was inversely related to light for several Caribbean seagrasses collected at various depths. For seagrasses cultured at several light levels, the total chlorophyll content increased with deceasing quantum flux (McMillan and Phillips, 1979; Wiginton and McMillan, 1979). Within individual meter-long *Zostera* leaves, the chlorophyll *a* to chlorophyll *b* ratio varied significantly, with the lowest ratio at the basal portion of the plant (Stirban, 1968). In a detailed study of chlorophyll relationships in a *Zostera* system, Dennison (1979) observed no substantial variation in total chlorophyll content within the leaves as a function of depth of the leaf canopy in integrated samples along a depth gradient within the bed; however, the chlorophyll *a* to chlorophyll *b* ratio decreased from the apical to basal portion of the leaves.

Although the physiological photosynthesis-light relationship ultimately determines the light levels at which plants grow, the morphology of individual plants and the community canopy structure may play an important role in production and species distribution. In a study of *Myriophyllum* and *Vallisneria*, Titus and Adams (1979) observed that the former had 68% of its foliage within 30 cm of the surface while the latter had 62% of its foliage within 30 cm of the bottom. *Myriophyllum*, an introduced species, has often displaced the native *Vallisneria*; a contributing faactor is probably the ability of *Myriophyllum* to shade *Vallisneria*. In a detailed community structure analysis of a monospecific *Zostera* community across a depth gradient, Dennison (1979) concluded that changing leaf area was a major adaptive mechanism to decreasing light regimes.

PHOTOSYNTHESIS-LIGHT STUDIES IN CHESAPEAKE BAY

Investigations of photosynthesis-light relationships carried out through the Chesapeake Bay Program can be categorized into three general experimental designs. In the first, P-I curves were constructed for the four dominant species in the Chesapeake Bay system, *Myriophyllum spicatum* and *Potamogeton perfoliatus* in the upper Bay (Kemp et al., 1981) and *Zostera marina* and *Ruppia maritima* in the lower Bay (Wetzel et al., 1982). These experiments utilized whole plants or leaves subjected to various light intensities (created through the use of neutral density screens) and various temperatures. Kemp et al. (1981) utilized microcosms in which the effects of various concentrations of phytoplankton and other suspended solids on light penetration and *Potamogeton* photosynthesis were determined. Wetzel et al. (1982) made in situ community metabolism measurements under a wide range of natural light regimes. In certain experiments, neutral density screens were used to shade the community on a short term basis.

P-I Relationship of Major Species

P-I curves were constructed for whole plants of *M. spicatum* and *P. perfoliatus* at 21°C (Kemp et al., 1981) (Fig. 12). Both species exhibited the characteristic photosynthetic response of green plants to light with saturation occurring between 600 and 800 $\mu E\ m^{-2}\ s^{-1}$. *Myriophyllum* exhibited a greater P_{max} and greater I_k than *Potamogeton*; however, the two species exhibited similar α. Although these species occur in the same general locale, they did not form dense, mixed bed stands where they would be in direct competition for light.

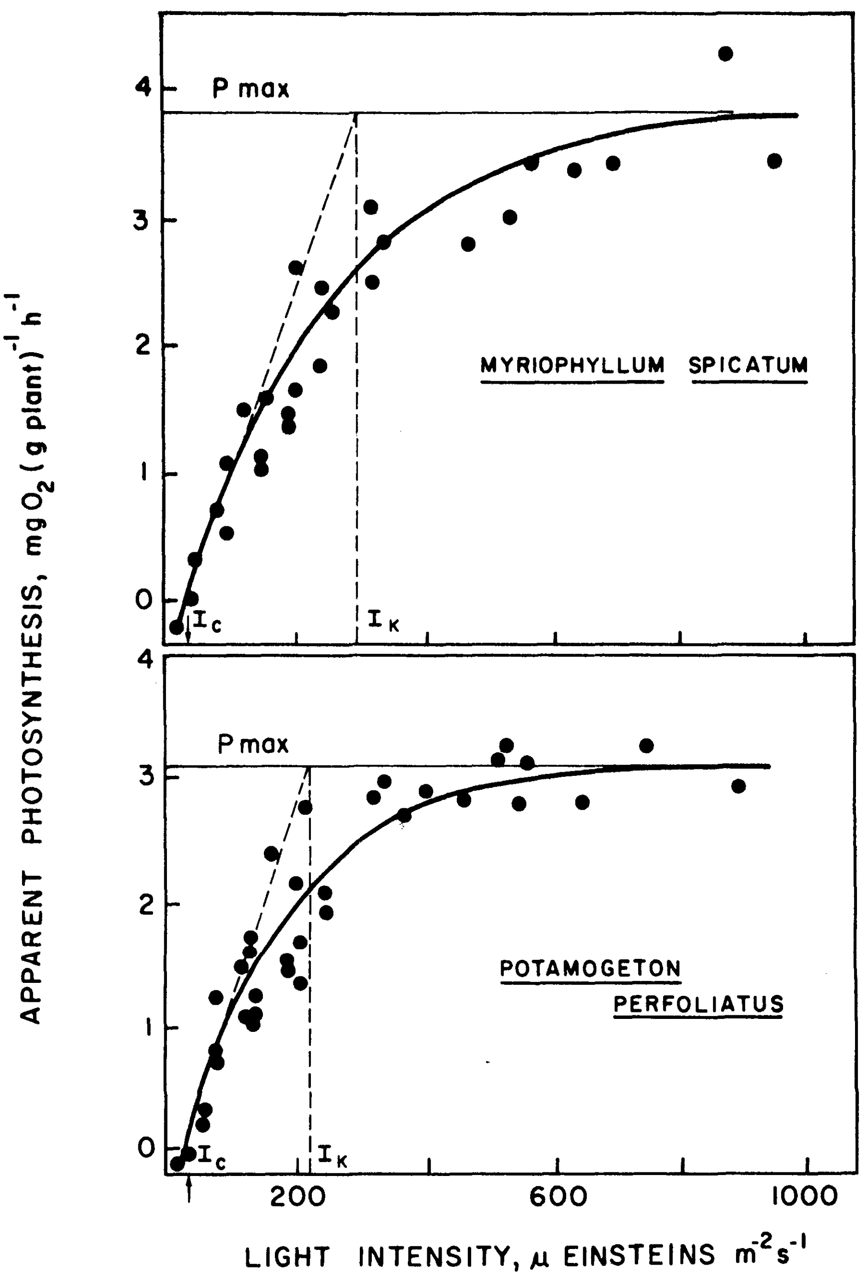

Figure 12. Photosynthesis-light curves for two species of upper Chesapeake Bay submerged vascular plants (after Kemp et al., 1981).

We determined the photosynthetic response to light and temperature for isolated *Z. marina* and *R. maritima* leaves. Since these species co-exist in the lower Chespeake Bay, an evaluation of the photosynthetic parameters of each species might suggest competitive strategies. Experiments carried out at six temperatures and under natural light indicate that light saturation of *Zostera* occurs at about 300 $\mu E\ m^{-2}\ s^{-1}$ while for *Ruppia* light saturation requires about 700 $\mu E\ m^{-2}\ s^{-1}$. Differences in P_{max} between *Zostera* and *Ruppia* were observed and appear related to temperature. At warmer temperatures, *Ruppia* exhibits a higher P_{max} than *Zostera* while the situation is reversed at colder temperatures (e.g. Fig. 13). A summary of the data shows that *Ruppia* exhibits the greater P_{max} at temperature >8°C (Table VI). A comparison between the two species shows that *Zostera* generally exhibits a greater α; this suggests a competitive advantage for *Zostera* at lower light levels.

The data from these experiments suggest mechanisms for the species distribution of *Ruppia* and *Zostera* in the lower Chesapeake Bay: *Ruppia* forms single species stands in shallow intertidal to shallow subtidal areas where high light and high temperatures are prevalent during the summer. *Ruppia* is generally more efficient at the higher light and temperature regimes in these habitats. *Zostera*, which has the greater depth range, is adapted to much lower light conditions as indicated by the lower light saturation point and greater α. In the mixed bed areas, *Ruppia* is always somewhat shaded by the longer leaved *Zostera*. During the winter periods of greater water clarity, *Ruppia* receives sufficient light to survive. During summer periods, its higher P_{max} probably contributes to its survival capability during the period of greatest light attenuation.

Kemp et al. (1981) compared values of photosynthetic parameters taken from the literature on submerged angiosperms (Table VII). Despite the fact that these parameters were obtained under a wide range of experimental conditions and over a wide range of biogeographical areas, the values are rather similar. P_{max}, which is a function of the dark reaction under optimal environmental conditions or a function of the inhibitor under suboptimal conditions, ranged from 0.9 to 3.7 mg C $g^{-1}\ hr^{-1}$. I'_k ranged from 110 to 225 $\mu E\ m^{-2}\ s^{-1}$ and I'_k from 70 to 350 $\mu E\ m^{-2}\ s^{-1}$.

The fact that submerged angiosperms have similar photosynthetic patterns is useful from the management point of view where decisions often must be based on information from only one or two species. However, to answer detailed questions concerning species competition or species adaptations, it is necessary to determine the interrelationship of photosynthetic patterns, pigment complement, plant morphology and community canopy structure.

Thus, features in addition to photosynthetic parameters help determine plant community photosynthesis. Canopy structure and chlorophyll content were determined for a *Ruppia*-*Zostera* bed in the lower Chesapeake Bay (Wetzel et al., 1982). Both *Ruppia* and *Zostera* showed a concentration of leaf area (surface available for light absorption) at the lower portion of the canopy where less light penetrates (Fig. 14). This probably allows for a greater overall net community photosynthesis than if there were a uniform vertical distribution of leaf area. Highly significant differences were observed between the vertical stratification of leaf area of *Ruppia* and *Zostera*.

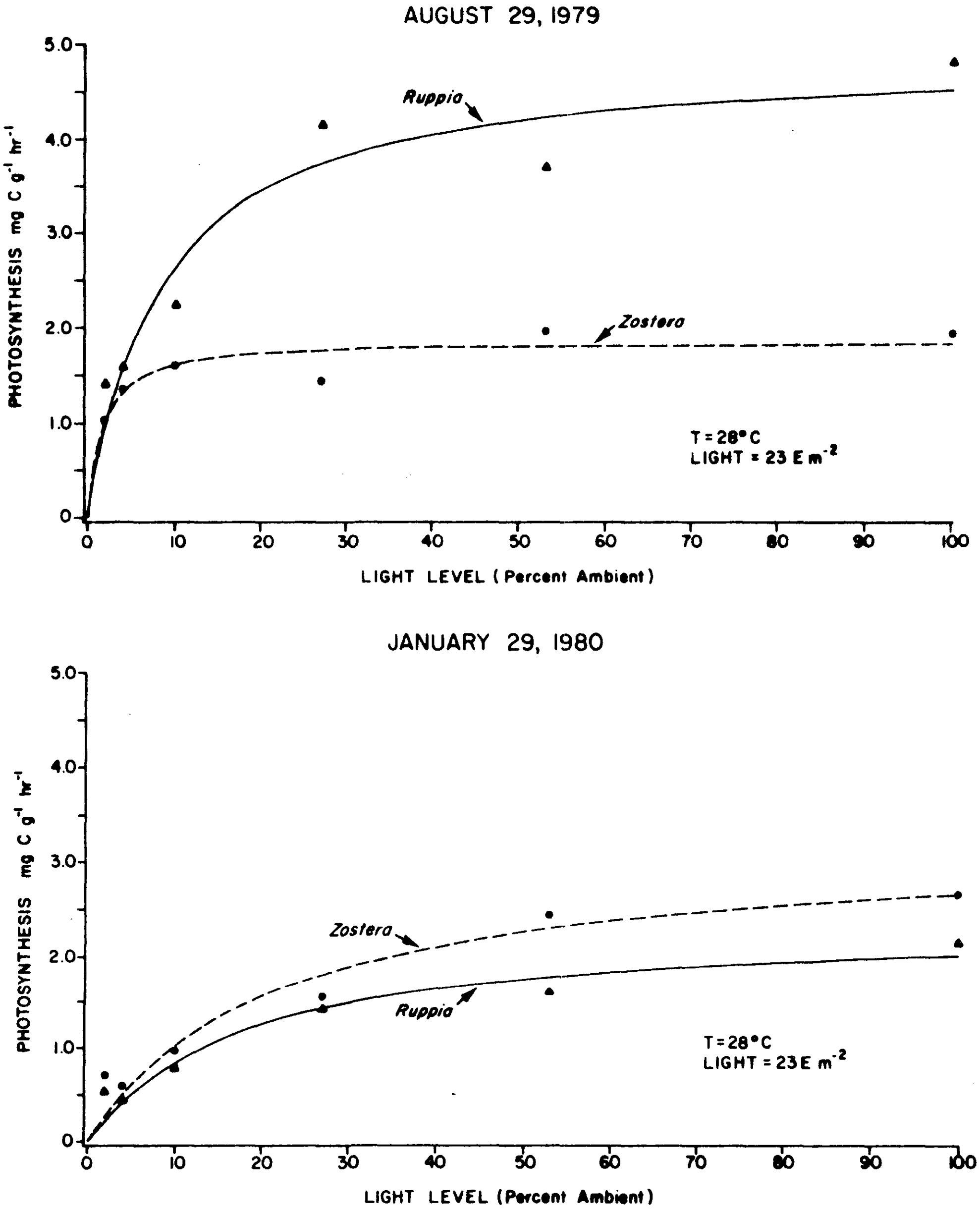

Figure 13. Photosynthesis-light curves for two species of lower Chesapeake Bay submerged vascular plants from A mixed bed (Light is total light flux during 4 h ^{14}C incubations).

TABLE VI. PHOTOSYNTHETIC PARAMETERS OF RUPPIA MARITIMA AND ZOSTERA MARINA LEAVES AT VARIOUS TEMPERATURES. (LIGHT = total light flux during the 4h ^{14}C incubations).

TEMP (°C)	LIGHT ($E\ m^{-2}$)	P_{max} ($mg\ C\ g^{-1}\ h^{-1}$) Ruppia	Zostera	INITIAL SLOPE Ruppia	Zostera
1	5.0	2.15	2.66	0.18	0.70
8	22.1	3.12	3.25	0.41	1.41
12	15.1	3.91	2.15	0.16	0.55
18	21.8	2.60	2.15	0.35	0.34
21	14.5	3.82	3.55	0.27	0.27
28	12.0	2.39	1.31	0.52	0.69

TABLE VII. SUMMARY OF PHOTOSYNTHESIS-LIGHT EXPERIMENTS FOR SELECTED SUBMERGED AQUATIC ANGIOSPERMS[a] (from Kemp et al., 1981).

Plant Species	P_{max}[b]	Light Parameters[c]			Reference
		I'_k	I_k	I_C[d]	
Zostera marina	1.5	140	28		Drew 1979
" "	2.2	170	220	--	Penhale 1977
" "	1.2	167	280	--	McRoy 1974
" "	1.3	184	345	--	Sand-Jensen 1977
Thalassia testudinum	1.7	225	320	145	Buesa 1975
" "	2.5	170	210	--	Capone et al. 1979
Cymodocca nodosa	2.6	140	220	50	Beer & Waisel 1979
" "	1.5	130	175	40	Drew 1978
Halodule uninervis	1.6	140	220	50	Bear & Waisel 1979
Syringodium filiforme	3.7	225	290	120	Buesa 1975
Ruppia maritima	1.9	123	236	30	Nixon & Oviatt 1973
Vallisneria americana	2.2	130	100	--	Titus & Adams 1979
Ceratophyllum demersum	3.2	135	80	30	Van et al. 1976
" "	2.2	130	230	--	Guilizzoni 1977
Ranunculus pseudofluitas	3.3	115	150	20	Westlake 1967
Myriophyllum spicatum	2.8	215	180	--	Titus & Adams 1979
" "	1.9	110	70	25	Van et al. 1976
" "	1.3	200	290	30	Kemp et al. 1981
Potamogeton pectinatus	0.9	195	350	60	Westlake 1967
P. perfoliatus	1.1	140	230	25	Kemp et al. 1981

a. Most of these data were interpolated from graphical relations provided by respective authors.

b. P_{max} is light-saturated photosynthetic rate in mg C g^{-1} h^{-1}, where O_2 production data were converted to C assuming PQ = 1.2.

c. Light variables: I'_k = half-saturation constant; I_k = intersection of initial slope and P_{max}; I_C = light compensation point where apparent production approaches zero. Light data converted to PAR units ($\mu E\ m^{-2}\ s^{-1}$) assuming 1 mW cm^{-2} = 2360 Lux = 0.86 cal cm^{-2} h^{-1} = 46 $\mu E\ m^{-2}\ s^{-1}$ (Hansen & Biggs, 1979).

c. Values of I_C are not available for experiments using the ^{14}C method which cannot measure negative net photosynthesis.

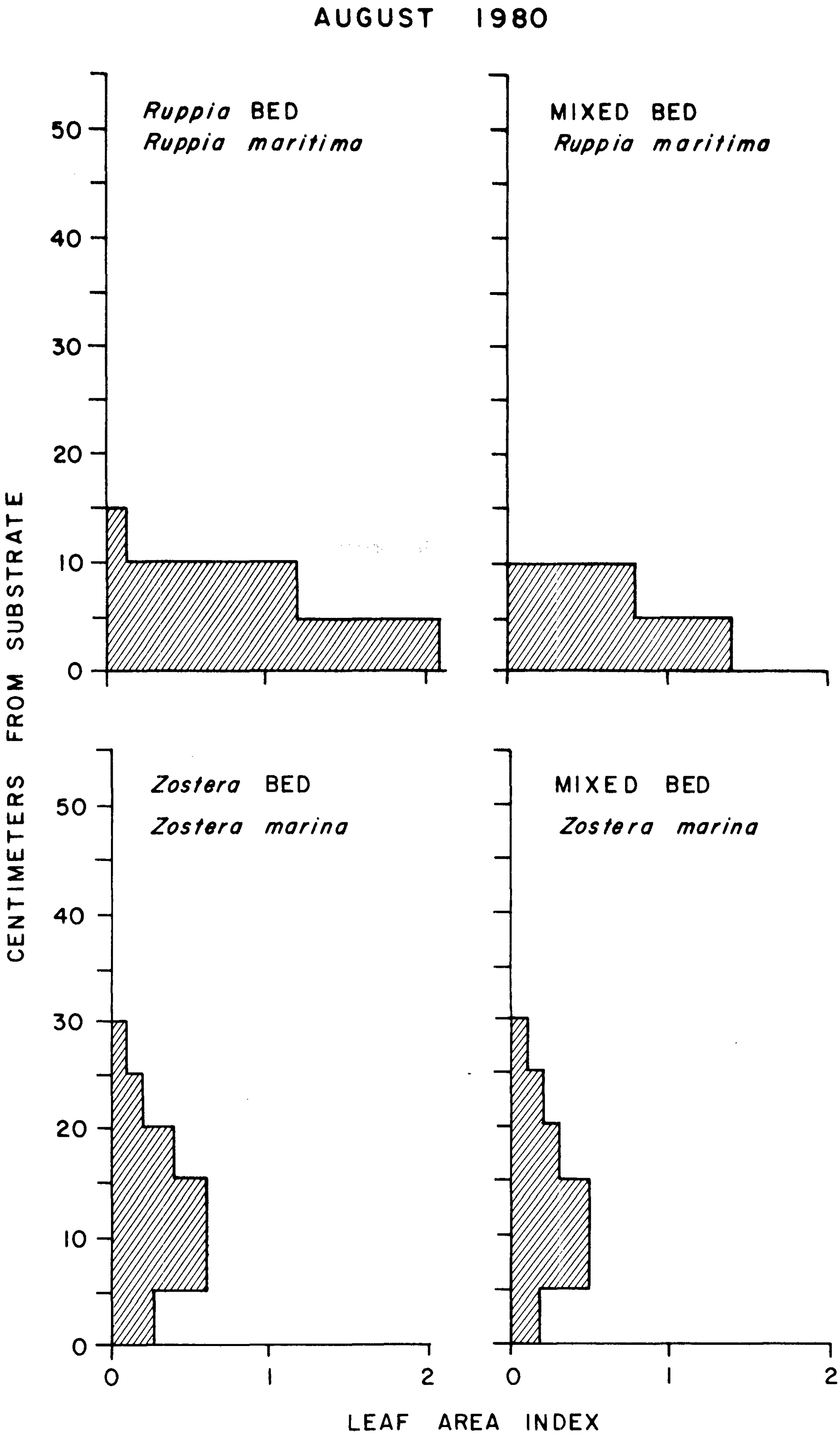

Figure 14. Vertical distribution of one-sided leaf area index (m^{-2} plant m^{-2} substrate) for Ruppia and Zostera at three vegetated sites in the lower Chesapeake Bay.

Ruppia exhibits much greater leaf area than Zostera at the lower canopy (0-10 cm above substrate); this probably contributes to its success in the mixed bed areas where it is shaded by Zostera.

Preliminary estimates of pigment content of Ruppia and Zostera suggest differences between species (Fig. 15). The highest concentrations of chlorophyll were at mid-canopy for Zostera and the top-canopy for Ruppia (Wetzel et al., 1982). Ruppia also showed a higher total chlorophyll concentration than Zostera. This higher chlorophyll concentration in combination with its canopy structure is an adaptation which contribute to Ruppia's success in mixed bed areas.

Microcosm Studies

The microcosm studies of Kemp et al. (1981) showed a negative effect of suspended sediments on Potamogeton photosynthesis (Fig. 16). Two concentrations of fine sediment particles (< 64 μm in diameter), kept in suspension with recirculating pumps, reduced light availability in the two treatments and resulted in significantly lower photosynthesis of Potamogeton compared to a control. Kemp et al. attributed about half the decrease in productivity of treated systems to the accumulation of epiphytic solids on the plant leaves. Further consideration of the microcosm data involved calculating regressions between chlorophyll a or filterable solids and light attenuation coefficients. From these, it was concluded that in the northern Bay, the effect of light attenuation by phytoplankton would be small while the effect of non-chlorophyllous suspended sediments on photosynthesis would be more significant.

In Situ Studies of Community Response to Light

The effect of light on plant community metabolism was investigated in upper and lower Chesapeake Bay grassbeds. In both areas, community metabolism was estimated as oxygen production in large, transparent incubation chambers. During these experiments, detailed measurements of light energy (PAR) reaching the plants were made. In some experiments, neutral density screens were used to decrease available light similar in design to the ^{14}C studies on individual species.

A summary of the upper Bay Potamogeton community response to light is presented in Fig. 17, which includes estimates from both early (May) and late (August) periods in the growing season (Boynton, unpublished data). The I_c of the plant community occurs at about 200 $\mu E\ m^{-2}\ s^{-1}$ and the data suggest that the community is not light-saturated in the ranges of measured in situ light flux. An analysis of the seasonal trends suggested no differences in the regression of light and community metabolism between seasons.

Based on these and other studies, Kemp et al. (1981) concluded that grass communities in the upper Bay are often light limited. For example, actual subsurface light data and three theoretical light extinction coefficients were used to calculate light penetration to a depth of 0.5 m above the substrate; a depth below which Potamogeton grows (Fig. 18a, b). Photosynthetic parameters, I_c, I'_k and P_{max} were calculated from a P-I curve (Fig. 18c). These

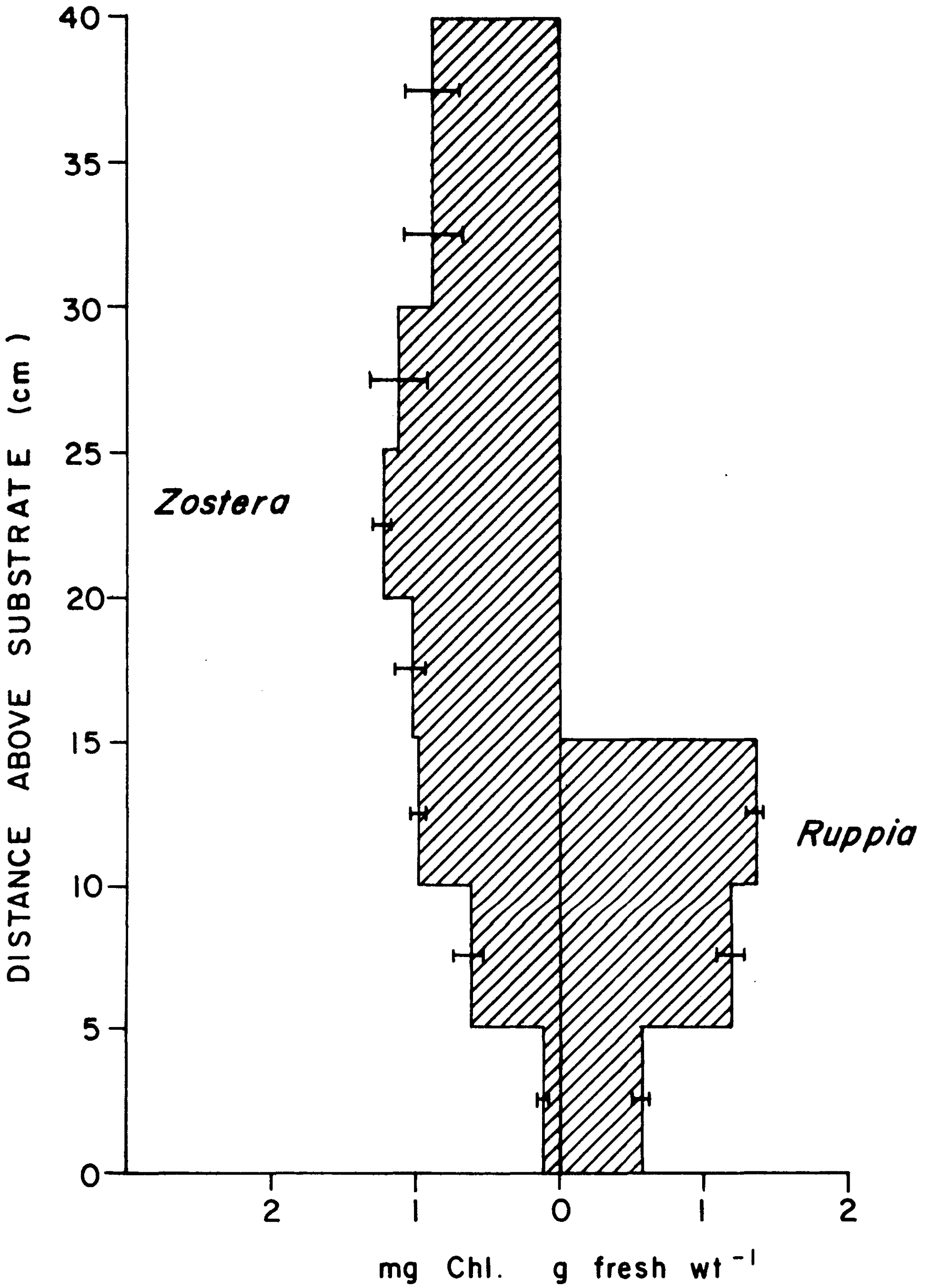

Figure 15. Vertical distribution of total chlorophyll for Ruppia and Zostera from a mixed bed area (Values ± standard error, n = 3.

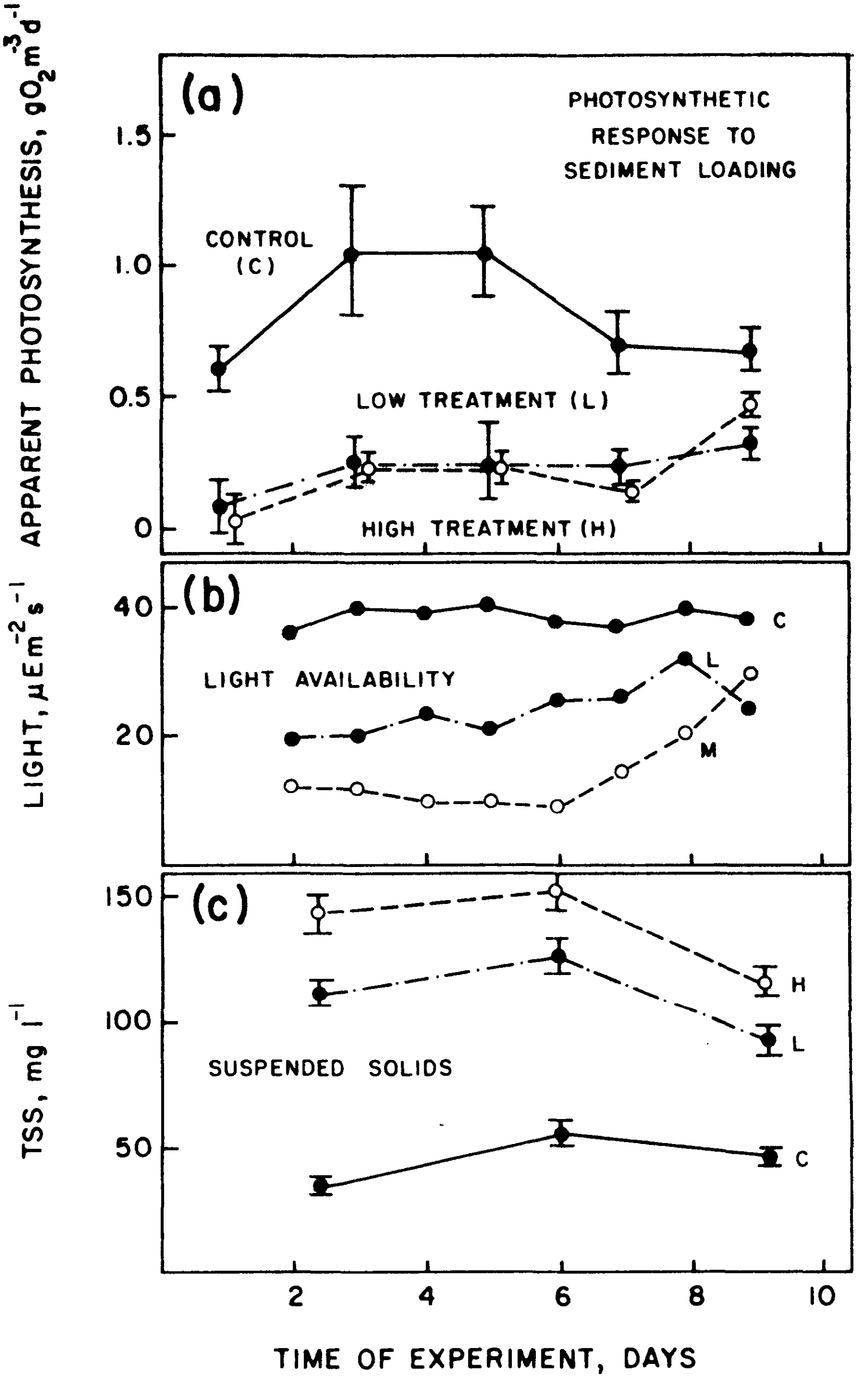

Figure 16. Effect of (c) total suspended solids (TSS) on (b) light availability and (a) rate of photosynthesis of Potamogeton perfoliatus in microcosms (after Kemp et al., 1981).

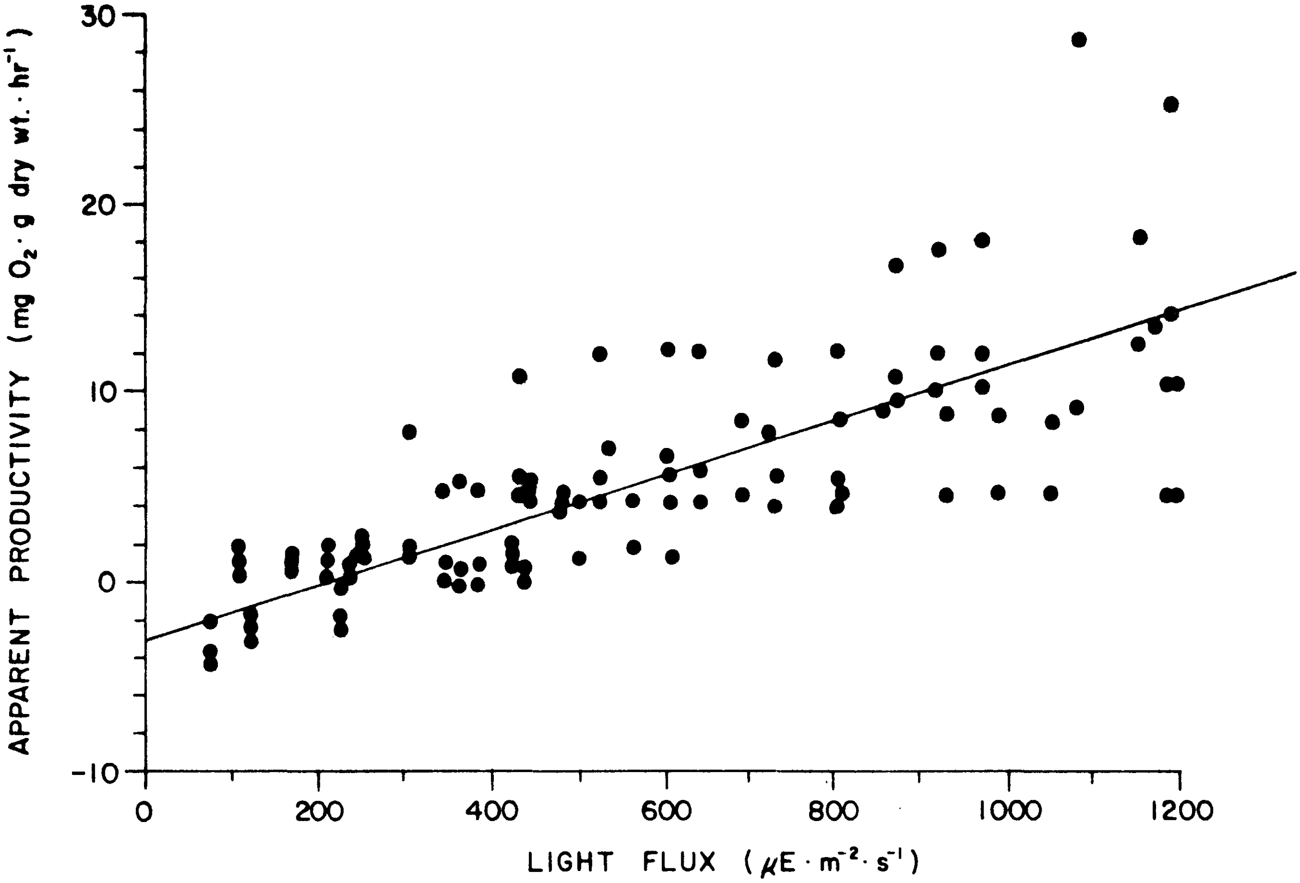

Figure 17. Response of upper Chesapeake Bay submerged vascular plants to light flux (after Boynton, unpublished data).

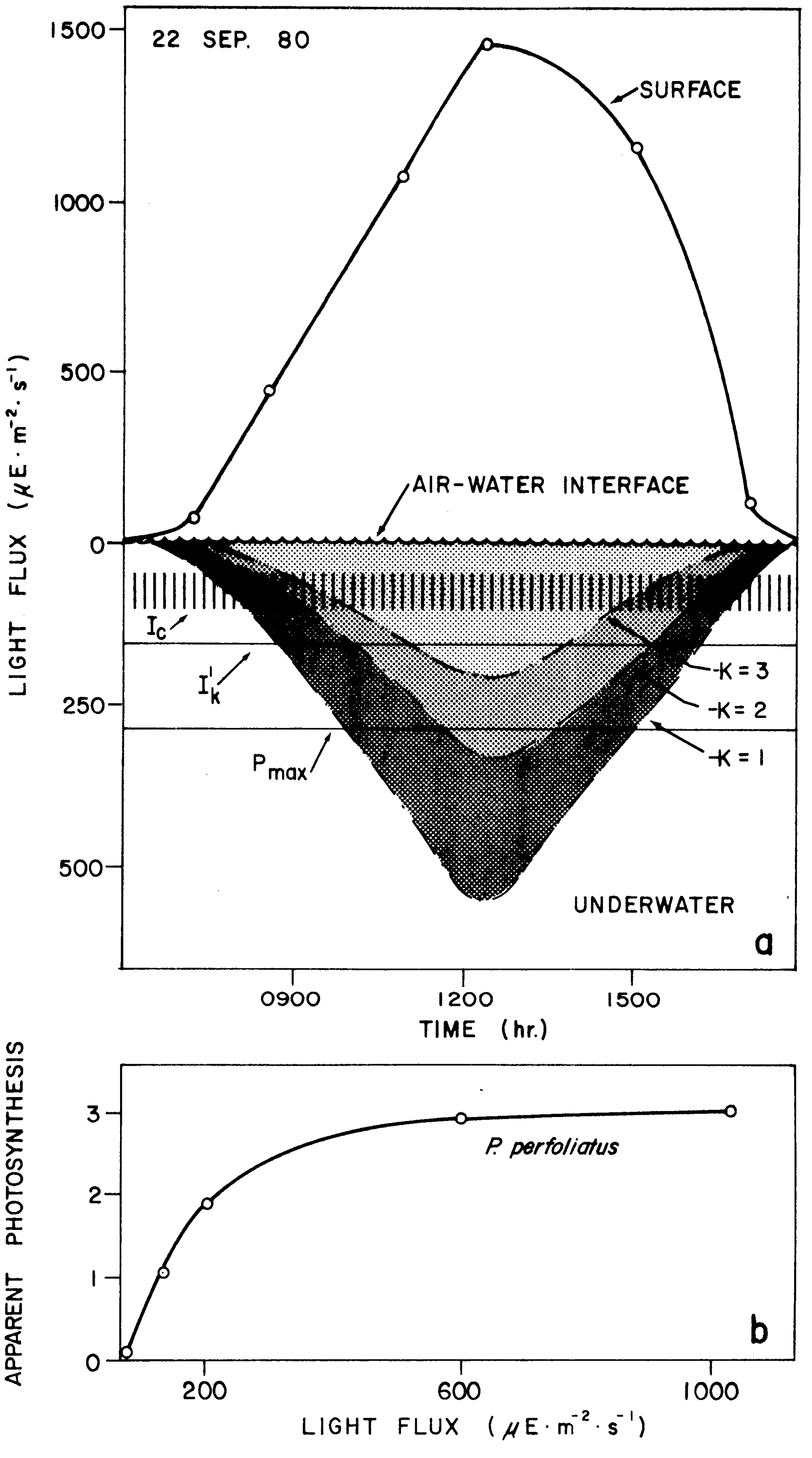

Figure 18. Diagramatic representation of surface (a) and underwater (b) light flux at Todd's Cove, upper Chesapeake Bay calculated for three light extinction (K) coefficients. I_c, I'_k and P_{max} calculated from P - I curve of *Potamogeton perfoliatus* (c) (after Kaumeyer et al., 1981).

parameters are identified for each light penetration curve and suggest that for much of the daylight period, the plant community is light-limited. At the early morning and dusk periods of the day, the community is apparently heterotrophic.

In the lower Bay, community metabolism studies were carried out in three areas: *Ruppia*-dominated, *Zostera*-dominated and a mixed *Ruppia*-*Zostera* area (Wetzel et al., 1982). These studies were conducted under a wide range of in situ light situations and under artificial shading conditions. The shallow *Ruppia* areas exhibit higher light and temperature regimes than the deeper *Zostera* areas; the mixed bed is intermediate between the two.

Short term shading experiments resulted in a general decease in community metabolism for both *Ruppia* and *Zostera* communities. For the *Ruppia* site, apparent productivity increased with increasing light to a midday peak and decreased during the early afternoon (Fig. 19). Based on P-I curves, *Ruppia* was light-saturated during much of the day and would not be photoinhibited. The unexplained afternoon depression, which occurred while light was increasing, may be due to increased community respiration rates under these summer high temperatures. A similar pattern was observed for the *Zostera* site, where shading also resulted in decreased apparent productivity (Fig. 20). In contrast, the afternoon depression in productivity rates was not as dramatic as in the *Ruppia* bed and this trend in *Zostera* seemed to follow the decreasing light availability unlike the trend in *Ruppia*. These results are similar to those found throughout the study and suggest differences between the two communities.

Plots of apparent productivity vs. light flux at the top of the canopy were used to compare all three habitats (Fig. 21). Differences among the three sites were observed for these summer experiments. Both the *Ruppia* and the mixed bed areas showed decreases in apparent productivity at the highest light fluxes. The *Zostera* site, which did not receive the high light that the other sites received, showed no decrease in rates. P-I curves for the seagrass species showed no photoinhibition, even at high summer temperatures, and suggested that the P_{max} of *Ruppia* should be greater than *Zostera* at this time of the year. *Zostera* appears adapted to lower light levels as evidenced by its high apparent productivity rates.

The erratic pattern of data points and greater number of negative rates for *Ruppia* strongly suggest a different community behavior. This pattern may be due to differences in community respiration rates, plant species photorespiration rates or the photosynthetic pattern of other primary producers such as macro- and microalgae. The mixed bed site shows an intermediate pattern, suggesting an interactive effect of the presence of both species of seagrass.

A summary of linear regression analyses of apparent productivity vs. light flux at the top of the canopy for the three areas is presented in Table VIII. At the community level, the correlation coefficient, r, is strongly influenced by season, with the lower values generally observed for the winter months. These are the times of year of clearest water and the specific rate asymptotically approaches P_{max}. Therefore the linear relationship does not

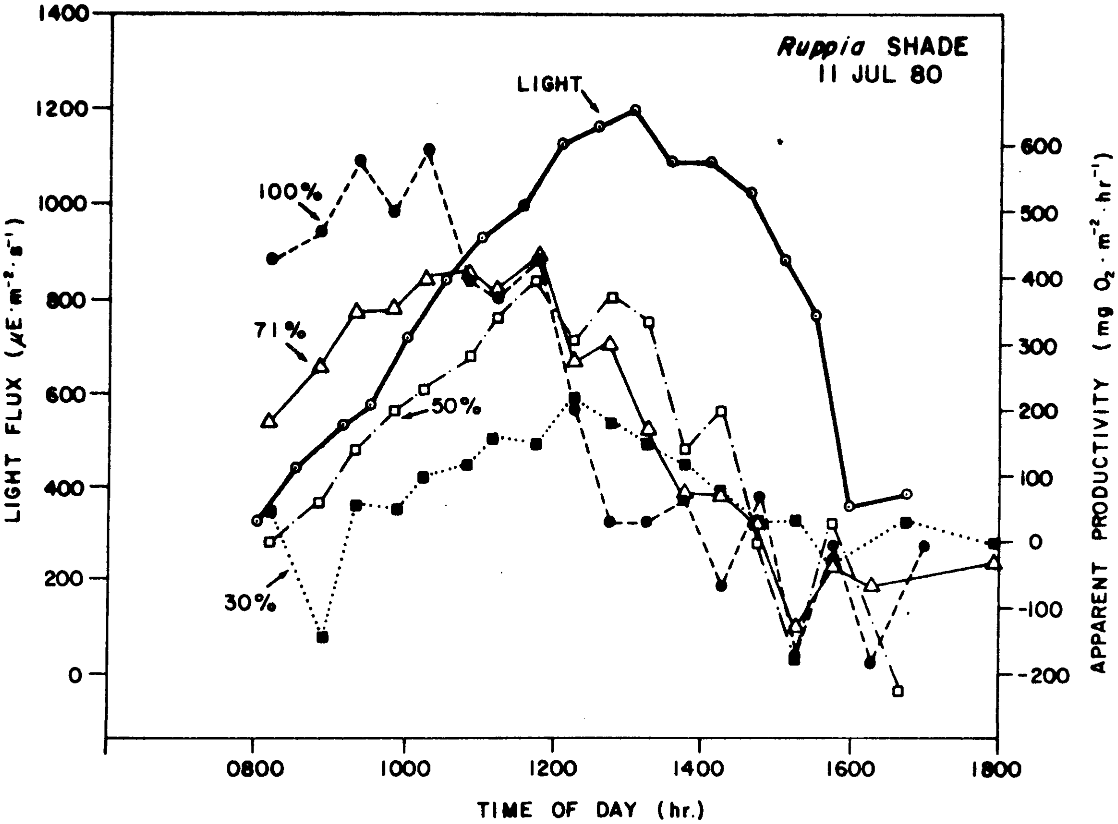

Figure 19. Apparent productivity and light flux at the canopy top vs. time of day for Ruppia experiments at 100, 71, 50 and 30% of ambient light at the canopy top.

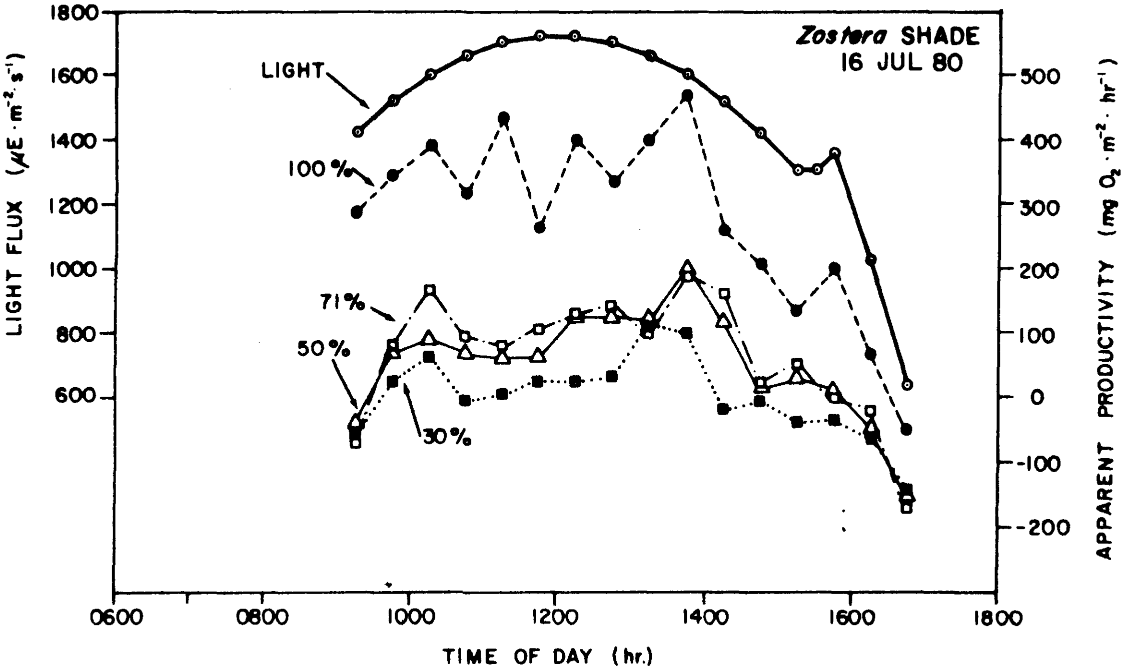

Figure 20. Apparent productivity and light flux at the canopy top vs. time of day for Zostera experiments at 100, 71, 50 and 30% of ambient light at the canopy top.

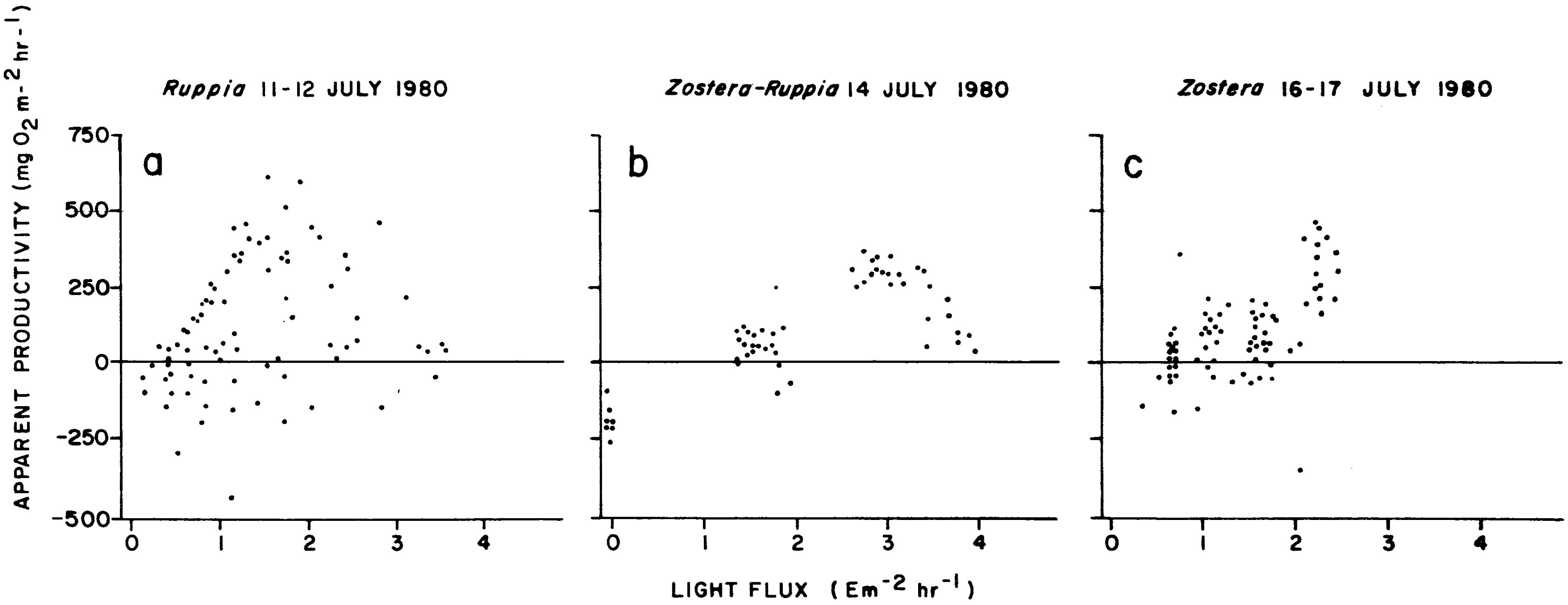

Figure 21. Apparent productivity vs. light flux for Ruppia (a), mixed Ruppia-Zostera (b) and Zostera (c) areas, lower Chesapeake Bay.

TABLE VIII. APPARENT O_2 PRODUCTIVITY AND LIGHT: LINEAR REGRESSION ANALYSIS FOR LOWER BAY STUDIES.

[mg O_2 m^{-2} hr^{-1} vs. E m^{-2} hr^{-1} (at canopy top)]

DATE	AREA	N	m	b	r	I_c	
						E m^{-2} hr^{-1}	E m^{-2} S^{-1}
14 Feb 80	*Zostera*	33	68.1	86.5	0.372	-	-
21 Feb 80	"	36	78.0	157	0.360	-	-
19 Mar 80	"	31	65.4	105	0.210	-	-
29 Apr 80	"	20	280	-183	0.778	0.650	181
2 May 80	"	11	582	-267	0.823	0.459	127
2 Jun 80	"	20	307	-472	0.681	1.54	427
5 Jun 80	"	30	286	-309	0.765	1.08	300
9 Jul 80	"	57	96.5	-147	0.425	1.52	423
16 Jul 80	"	76	124	- 67.1	0.542	0.541	150
19 Aug 80	"	16	89.2	- 84.5	0.793	0.947	203
23 Sep 80	"	27	108.1	-159.8	0.435	1.48	411
7 May 80	*Ruppia*	10	363	-357	0.980	0.983	273
11 Jul 80	"	83	52.5	- 47.2	0.215	0.899	250
21 Aug 80	"	26	385	-434	0.770	1.13	313
25 Sep 80	"	10	242.5	- 79.1	0.806	0.326	90.6
26 Sep 80	"	16	323.2	-194.5	0.532	0.602	167.2
5 May 80	*Mixed*	28	89.7	-189	0.607	2.11	585
14 Jul 80	"	50	77.9	- 48.9	0.553	0.627	174

N = number of observations
m = slope
b = y-intercept
r = correlation coefficient
I_c = estimated light compensation point (x-intercept)

adequately describe the photosynthetic response. This is true for all measures taken at or near P_{max}.

In the Zostera community, maximum rates occur in the spring and early summer. Over this period, the estimated community light compensation point progressively increases, due to increased respiration, to the point that daily community production is negative. This corresponds to the characteristic mid-summer die-off of Zostera in these areas (Wetzel et al., 1982). Except for winter and early spring (February and March), the community as a whole is light-limited.

The Ruppia community dominates the higher light and temperature areas of the bed. Maximum rates of apparent photosynthesis occur during the summer and they corroborate the earlier conclusions that Ruppia has both higher P_{max} and I_c characteristics. Some data suggest that community respiration inceases in early afternoon during high light and temperature conditions. These conditions are prevalent at mid day low tides during July and August. Overall, Ruppia dominated communities in the lower Bay appear adapted to increased light and temperature regimes and do not appear light limited.

For the Chesapeake Bay system as a whole, these data and similar studies completed in upper Bay suggest an extreme sensitivity of Bay grasses to available light. These data also agree very well with information on other geographical areas and species. Our general conclusion is that light and factors governing light energy availability to submerged aquatic vascular plants are principal controlling forces for growth and survival.

SUMMARY

The apparent optical properties of the Chesapeake Bay indicate a light-limited environment for benthic photosynthesis. Water per se, suspended particles and dissolved compounds all interact to selectively absorb those wavelengths most important for autotrophic production. Plant pigment systems are adapted for efficient light energy capture in relatively narrow bands. In many cases, it is precisely these wavelengths that are most rapidly attenuated in the estuarine water column. Diffuse downwelling attenuation coefficients in upper and lower Bay communities indicate a severe attenuation of light energy in the photosynthetically important violet-blue (400 to 500 nm) region of the spectrum. There is a progressive increase in attenuation in these spectral regions during the critical spring growing season for SAV. Comparison of vegetated and non-vegetated areas in the Chesapeake Bay suggests lower attenuation during spring in the vegetated areas (see Chpt. 3 for details). Kaumeyer et al. (1981) also reported significant differences in PAR attenuation for a vegetated site in the upper Bay.

There is a much larger data base on plant response to PAR light energy for the Chesapeake Bay as well as other bodies of water. The dominant plant species in the Bay show the classical, hyperbolic photosynthetic response to increasing PAR. Specific plant response studies suggest physiological differences among species. The dominant upper Bay species, Myriophyllum spicatum and Potamogeton perfoliatus, light-saturate between 600 and 800 μE m^{-2} sec^{-1} but differ in P_{max} and I_k. M. spicatum appears to higher light conditions than *P. perfoliatus*. In a similar manner, the dominant lower Bay species, *Ruppia maritima* and *Zostera marina*, appear physiologically different with regard to light response. *R. maritima* is adapted to high light and temperature while *Z. marina* is adapted to lower light regimes and is stressed at higher, summer temperatures.

In situ studies of entire plant communities in both Maryland and Virginia indicate that the communities generally operate under suboptimal light conditions. There was no apparent light saturation reached for upper Bay communities, i.e., net apparent community productivity did not asymptotically approach a maximum value. Studies in lower Bay communities suggest that *Z. marina* is light-limited during most of its growing season. Only in the shallower *R. maritima* areas did the community photosynthetic response become light-saturated and perhaps photoinhibited at times. These results indicate that at least in terms of total PAR energy and probably because of the extreme attenuation in the 400 to 500 nm region noted earlier, submerged plant communities in Chesapeake Bay are generally light-stressed.

Historical data relative to light (secchi disc, chlorophyll *a* and indirectly nutrients) and the past distribution and abundance of submerged aquatics indicate progressive Bay wide changes in systems structure and function. Heinle et al. (1980) and Orth et al. (1981) discuss these in detail. In terms of Bay grasses and the light environment, two overall conclusions of these reports are particularly important. Heinle et al. (1980) have noted and documented the generalized increase in nutrients (and loadings) and chlorophyll concentrations in major tributaries of the Chesapeake Bay over the past several decades. Orth et al. (1981, 1982) concluded for roughly the same time scale that the general pattern of disappearance of submerged plant communities followed a similar "down-river" pattern. It also appears that upper Bay and western shore lower Bay communities have been the most severely impacted. These conclusions together with our studies on the light environment and photosynthesis-light relations in SAV ecosystems suggest that factors increasing diffuse downwelling attenuation in the 400-500 nm region are critical in controlling plant growth and survival. The specific factors that appear to have the greatest impact are organic and inorganic suspended particles. The presence of these particles is directly related to land runoff and indirectly to nutrient addition.

In summary, it appears that Bay grasses are living in a marginal light environment and that progressive worsening of water quality will further stress the plant communities. To conclude that light has been singularly responsible for recent declines in the vegetation goes beyond the data available. But the data do indicate the extreme sensitivity of the vegetation to changes in available light. The implicit assumption that over the past several decades water quality throughout the Bay and particularly in the tribuaries has progressively declined is a feasible explanation for the corresponding decline of Bay grasses. Further changes in these parameters can only affect Bay grasses in an adverse way.

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Chapter 3

THE UNDERWATER LIGHT ENVIRONMENT OF SHALLOW REGIONS OF THE LOWER CHESAPEAKE BAY, ITS RELATIONSHIP TO SEAGRASSES AND ITS POTENTIAL FOR BENTHIC PRIMARY PRODUCTIVITY

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INTRODUCTION

All plants, whether aquatic or terrestrial, differentially absorb the energy of specific ranges of light of different wavelengths via characteristic complements of photoreactive pigment molecules located within subcellular systems. The energy thus absorbed by quantum amounts is utilized, with varying spectral efficiency, to drive the reactions of photosynthesis-- i.e., the synthesis of complex organic compounds from simple inorganic compounds using the photon energy of sunlight.

Since the driving force of all ecosystems[1] is light, the energetic basis of life, the success or failure of an ecosystem ultimately depends on the ability of its primary producers to utilize efficiently the specific mix of light energies available. Green plants, both terrestrial and marine, photosynthesize most efficiently in the violet-blue (400-500 nm) and orange-red (600-700 nm) regions of the spectrum (Halldal, 1974). Inada (1976) summarized the action spectra literature for a diverse taxonomic group of terrestrial angiosperms and found quite a consistent pattern. The pattern for the common estuarine green alga Ulva is remarkably similar (Levring, 1947, 1966; Haxo and Blinks, 1950; Halldal, 1974). All show the highest rates of photosynthesis in the above mentioned spectral regions. Of course this is no surprise. Green plants appear green because they absorb blue and red light and reflect green light!

Although we are unaware of any reported seagrass action spectra, it seems reasonable to assume that these plants are similar to their terrestrial taxomonic cousins and their marine ecological cousins with similar pigment complexes -- i.e., chlorophyll a, b and accessory pigments β-carotene and xanthophylls. The chlorophylls are solely responsible for the absorption of energy above 600 nm but that below 500 nm is due to both accessory pigments and chlorophylls a and b (Zscheile and Comar, 1941; Zscheile et al., 1942; Govindjee and Govindjee, 1975).

Seagrasses exist in an environment characterized by drastic temporal and spatial fluctuations in light energy. As light passes through the water column it is attenuated by absorption and scattering due to the water itself, dissolved inorganic and organic substances, and suspended particles. Differential spectral attenuation results in light quality shifts -- color changes. These shifts can have profound implications for benthic plants with their genetically determined finite range of usable light energies.

Scattering -- the change in direction of light propagation caused by diffraction, refraction and reflection due to particles, water molecules and dissolved substances -- is wavelength dependent, but in an irregular and

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[1] With the exception of those few driven by chemosynthesis.

complex manner (Jerlov, 1976). Only 4-11% of incident irradiance between 300-700 nm is reflected from the surface or backscattered out of the oceanic water column (Clark and Ewing, 1974). Absorption is a thermodynamically irreversible process wherein photons are converted into thermal, kinetic or chemical energy. Absorption accounts for most of the observed attenuation of light. Forward and lateral scattering effectively increases the path-length of light thereby exposing it to additional absorption. The major particles in estuaries are clays and silts with small diameters which tend to scatter light of the shorter wavelengths of the visible spectrum (blue end) more than the longer wavelengths. Therefore one would expect greater attenuation of blue light than red light in estuaries.[2] Much of the attenuation of the energy contained in the long wavelengths (>600 nm) is due to either the water molecules themselves, as shown by James and Birge (1938) for pure water, or to the water plus its dissolved salts (Clarke and James, 1939). There is little difference in attenuation between pure water and filtered seawater (Yentsch, 1960); the effect of sea salts is insignificant. The energy contained in the lower and upper PAR, violet-blue and orange-red, respectively, is particularly susceptible to absorption by particulate matter (Burt, 1958; Prieur and Sathyendranath, 1981). Chlorophyll pigments in the water column associated with phytoplankton and the breakdown products of plants also absorb most strongly in the blue and red. Dissolved organic compounds ("yellow substance" or Gelbstoff) greatly attenuate the shorter wavelengths (Kalle, 1966). Thus, since estuaries are loaded with a myriad of autochthonous and allochthonous dissolved and suspended substances, the light energy reaching the benthic plants of an estuary is likely to be reduced in both the red and especially the blue regions of the spectrum -- exactly those portions to which green plants respond most efficiently photosynthetically.

The small amount of available Chesapeake Bay data on diffuse downwelling 2 ¶ irradiance attenuation indicates a severe attenuation of light energy in the photosynthetically important 400-500 nm (violet-blue) region of the spectrum. Attenuation in the short wavelengths is particularly marked in the turbidity maximum region of the Bay at the mouth of the Sassafras River, and at the mouth of the Patuxent River during August (Champ et al., 1980). The mean Bay attenuation coefficients calculated by Champ et al. (1980) are about 1.0 m^{-1} higher than Jerlov's (1976) most turbid coastal water classification.

A comparison of attenuation coefficients reported for the Chesapeake Bay and its tributaries is presented in Figure 1 along with Jerlov's (1976) standard k (λ) curve representing his most turbid coastal water classification (Type 9). For the Chesapeake Bay, the earliest measurements of k(λ) were made by Hurlburt (1945) (Fig. 1a). His values fall in the lower range of more recent in situ measurements. Champ et al. (1980) conducted a light characterization survey of the Chesapeake Bay during August, 1977. Their mean values are shown in Fig. 1a. Specific site measurements made by them in and near the mouths of the Sassafrass, Patuxent, Potomac and Chester Rivers appear in Fig. 1c. Their attenuation measurements in the turbidity maximum zone at the mouth of the Sassafras River are the highest reported for the Bay: there

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[2] See Chapter 1 for a more detailed discussion of marine optics.

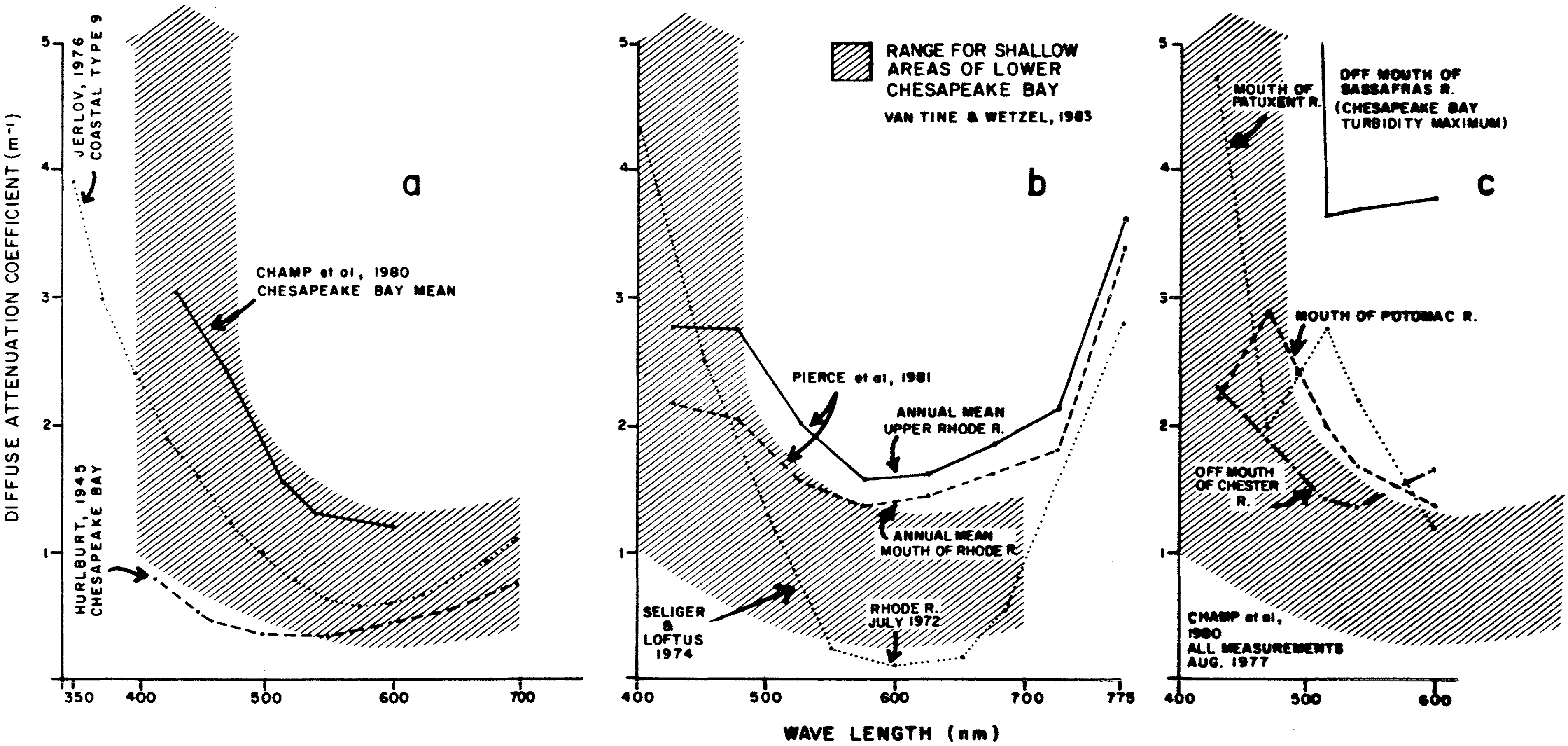

Figure 1. Comparison of spectral attenuation measurements reported for the Chesapeake Bay. Shaded areas represent range of attenuation measured by us in the lower Bay. (a) plotted from tables in Jerlov, 1976; Hurlburt, 1945; Champ et al., 1980 (b) plotted from table in Pierce et al., 1981 and calculated from irradiance curves in Seliger and Loftus, 1974 (c) plotted from tables in Champ et al., 1980.

is nearly no available light below 500 nm. Pierce et al. (1981) intensively monitored the Rhode River during 1980 and 1981. Their annual mean attenuation values for an upriver station and one at the mouth of the river are plotted in Fig. 1b. The upriver station was found to be consistently more turbid, presumably due to its proximity to autochthonous sources. Maximum penetration was at 575 nm and minima at 775 and 425 nm. Attenuation coefficients derived from 4¶ irradiance measurements from the Rhode River (Seliger and Loftus, 1974) are also shown in the figure.

The purposes of the work reported herein were to (1) describe the spectral light environment of shallow areas of the Lower Chesapeake Bay, (2) determine the differences, if any, occurring between vegetated and unvegetated sites, and (3) relate any differences to potential benthic photosynthesis.

METHODS

Downwelling diffuse 2¶ spectral irradiance was measured as quanta·nm^{-1}·cm^{-2}·s^{-1} at 12 biologically significant wavelengths (410, 441,488, 507, 520, 540, 570, 589, 625, 656, 671, 694, nm ± 5 nm). The measurements were made with a Biospherical Labs model Mer-1000 multiwavelength spectroradiometer (Booth and Dustan, 1979), calibrated against U. S. Bureau of Standards lamps every 6 months. Calibration curves changed less than 0.5% indicating an extremely stable system.

Measurements were taken at 6 shallow sites (<2m) and at one relatively deep site in the lower Chesapeake Bay (Fig. 2). The sites were chosen for their vegetational history - all but one having been vegetated by macrophytes in the recent past (Orth, et al., 1979). Five of the sites were located on the western shore of the Lower Chesapeake Bay in the York River and Mobjack Bay. The remaining 2 sites were across the Bay on the eastern shore of Virginia at Vaucluse Shores near Hungar's Creek. The Mumfort Is. (York River) and Severn River (Mobjack Bay) sites were unvegetated but had previously been part of seagrass beds. There were healthy seagrass beds (Zostera marina and Ruppia maritima) at the Guinea Marsh, Four Point Marsh (Mobjack Bay) and Vaucluse Shores sites. Measurements at the later site were made in corroboration with in situ productivity studies (Wetzel et al., 1982; Murray and Wetzel, 1982). The Allen's Is. site (York River) represented a transitional vegetative state - natural populations had disappeared yet Orth and colleagues (Orth, et al., 1979) had successfully transplanted it. Furthermore, it appears that a natural population may be returning to this site (K. Moore, personal communication, 1981). The deep site station was located across a sand bar and about 1 mile west of the Vaucluse Shores vegetated site. It was chosen as a reference station.

The diffuse attenuation coefficient (k_d) for downwelling 2¶ irradiance was chosen as the parameter most suitable for characterizing the light environments at each site due to its quasi-inherent nature. It has been found to be relatively insensitive to changes in solar zenith angle (Baker and Smith, 1979), except for very large angles.

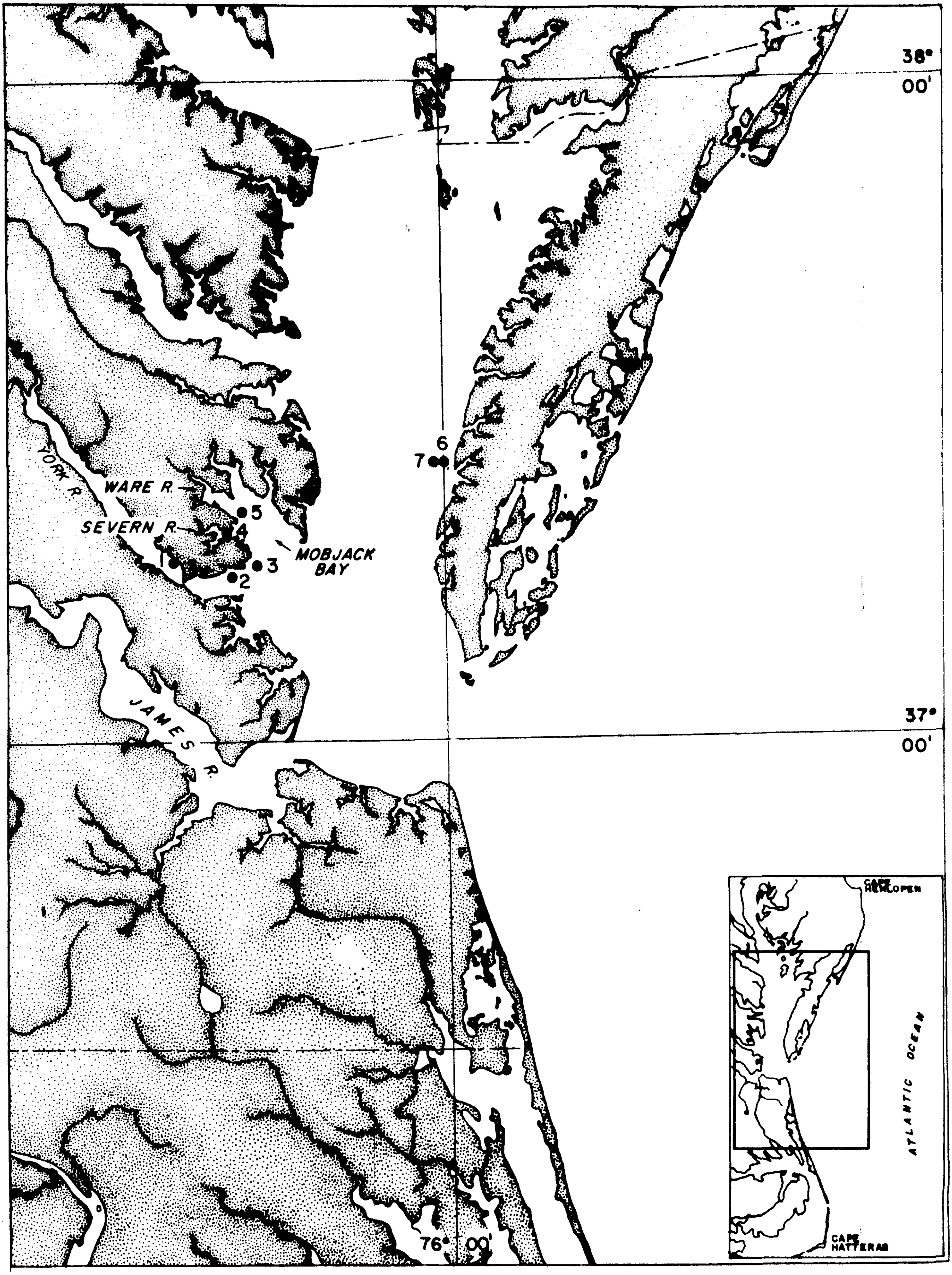

Figure 2. Locations of lower Chesapeake Bay sites. (1) Mumfort Is., York R. (unvegetated), (2) Allen's Is., York R. (transitional), (3) Guinea Marsh (vegetated), (4) Severn R. (unvegetated), (5) Four Point Marsh, Ware R. (vegetated), (6) Vaucluse Shores (vegetated) (7) deep "Bay" Station 1 mi. west of site 6.

The diffuse downwelling attenuation coefficient is defined as

$$k_d(z) = \frac{-1}{E_d(z)} \cdot \frac{dE_d(z)}{dz}$$

or

$$\frac{E_d(z_2)}{E_d(z_1)} = \ell n\ (-k_d(z_2-z_1))$$

where k_d has units of reciprocal length (m^{-1}), and z is the depth at which the downwelling irradiance ($E_d(z)$), is measured. Irradiance at depth z_2 can be estimated for a body of water with known k_d as follows,

$$E_d(z_2) = E_d(z_1) \cdot e^{-k_d(z_2 - z_1)}$$

where e is the base of the natural logs. The attenuation coefficients reported in this work were calculated between depths of 0.1 and 0.5 m as a estimator of water column attenuation not associated with air-water or water-substrate interface phenomena. Hence, these values are a function of the inherent optical properties of the water bodies concerned. Since K_d is not a constant for water bodies less than 10 m deep, all comparisons between sites and seasons were made for the same depth interval, i.e., 0.1 to 0.5 m. All such calculations were based on irradiance measures taken at these depths between 1000 and 1400 e.s.t. Variations in k_d due to sun zenith angle differences at this time of day are less than 5% in the extreme (Baker and Smith, 1979).

Mean monthly attenuation coefficients reported herein include all measurements made during that month. Mean seasonal values were calculated over seasons defined as: Winter--January through March; Spring--April through June; Summer--July through September; and Autumn--October through December.

The total attenuation to a depth of 1.0 m, $k_{(0,1.0)}$ plotted in Figure 36 was estimated as a weighted average between the water column attenuation (z=.1, z=.5) and the air-water interface attenuation $k_{(0,.1)}$ (z=0, z=.1):

$$\frac{9k_{(.1,.5)} + k_{(0,.1)}}{10}$$

where $k_{(.1,.5)}$ is a conservative estimator of $k_{(.1,1.0)}$ since water column-substrate interactions are not considered. The air-water interface attenuation coefficient, $k_{(0,.1)}$ was calculated as the seasonal mean for calm sunny days at 1200 ± 30 e.s.t.

The relative potential photosynthetically storable radiation (PSR) was calculated as the product of the irradiance distribution and the theoretical photosynthetic action spectrum. The PSR is defined by Morel (1978) and Smith (1979) as that portion of absorbed energy actually transferred into stored chemical energy in the form of organic matter through photosynthesis. The relative potential PSR thus expresses the relative potential efficiency of photosynthesis given a specific irradiance distribution and a specific absorption complex (set of pigments).

All irradiance measurements were taken on the sunny side of the boat well away from the boat shadow. Each measurement recorded represented the mean of from 250 to 500 scans taken over approximately 30-60 secs. This was done to smooth out the effects of water waves, patchy clouds, and patchiness of suspended particulates.

The western shore stations were monitored several times each season on paired dates approximately 1 week apart selected to coincide with the confluences of high tide with solar noon and low tide with solar noon. The Vaucluse Shore site was monitored at least every other month at times chosen to accommodate productivity studies being made there (Wetzel et al., 1982; Murray and Wetzel, 1982).

RESULTS

In order to facilitate an understanding of the possible trends in the spectral distribution of underwater light in the shallow Lower Bay, the data for the seven Stations monitored has been summarized variously by month, season, site and vegetational state. All mention of attenuation coefficients, unless otherwise noted, refers to $k_d(\lambda)_{(0.1,\ 0.5)}$, i.e. the diffuse downwelling spectral attenuation coefficient (m^{-1}) for the upper water column (the depth interval 0.1 to 0.5 m). This is a purposefully conservative measure of attenuation intended to characterize specific water bodies.

Mean Seasonal $k(\lambda)$

A comparison of the distribution of the mean seasonal spectral attenuation coefficients (Figs. 3 thru 6 and Table I) reveals a seasonal pattern and some significant differences between vegetated and unvegetated sites. The season of least attenuation was winter and of greatest attenuation was summer. Spring and autumn were intermediate. The seasonal means for all sites combined for both 1981 and 1982 is presented in Figure 7.

There was essentially no difference in mean $k(\lambda)$ between the average vegetated and unvegetated sites during the seasons of maximum and minimum attenuation, i.e. summer and winter. The winter values ranged from lows of about 0.3 m^{-1} at 570 nm to highs of about 1.1 m^{-1} at 410 nm. The highest winter mean red attenuation was calculated as .834 m^{-1} for the vegetated sites and .679 m^{-1} for the unvegetated sites, both at 694 nm, the longest wavelength measured.

The summer values were the highest mean seasonal coefficients calculated, ranging from over 3.0 m^{-1} at 410 nm to about 1 at 570 nm. (If 1.0 unit of irradiance were attenuated over a distance of 1.0 meter at a rate of 3.0 m^{-1} only 0.05 units of irradiance would remain. Over a path of 2.0 m of water the unit would be reduced to about 0.0025 units). The mean seasonal coefficients for vegetated and unvegetated sites were almost identical but there was a

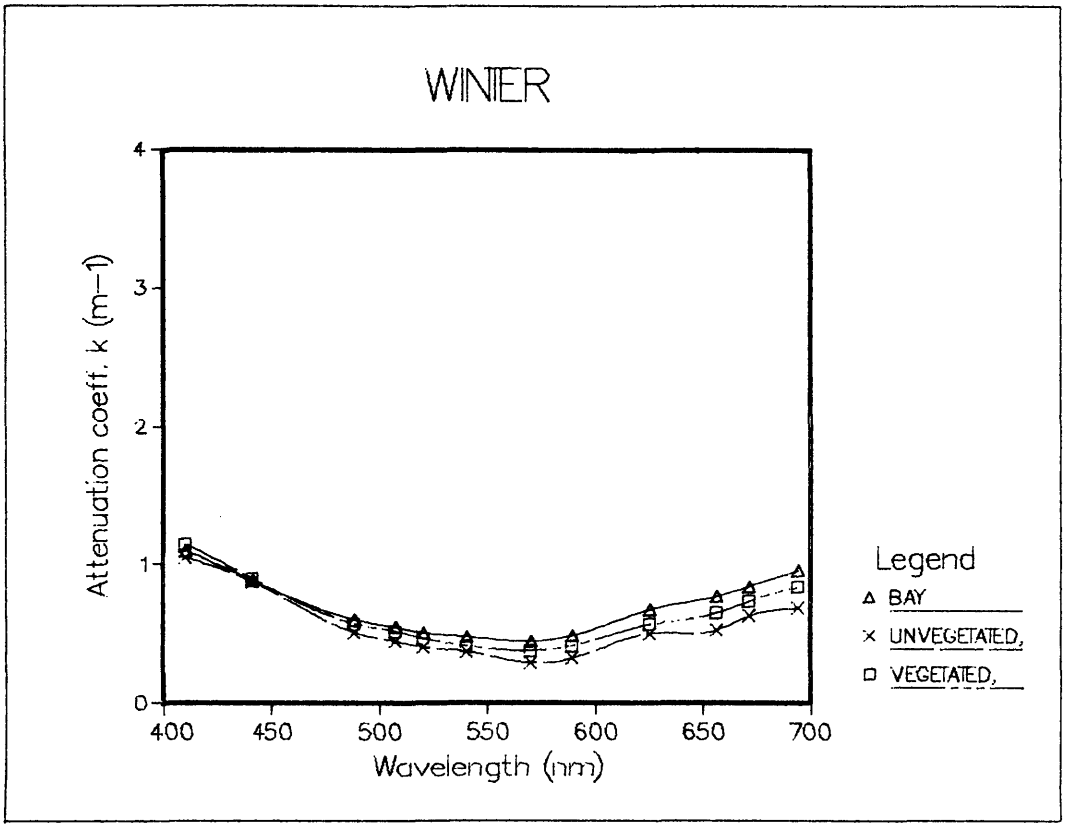

Figure 3. Mean winter spectral attenuation at vegetated and unvegetated sites in the lower Chesapeake Bay. (Bay = Deep water station).

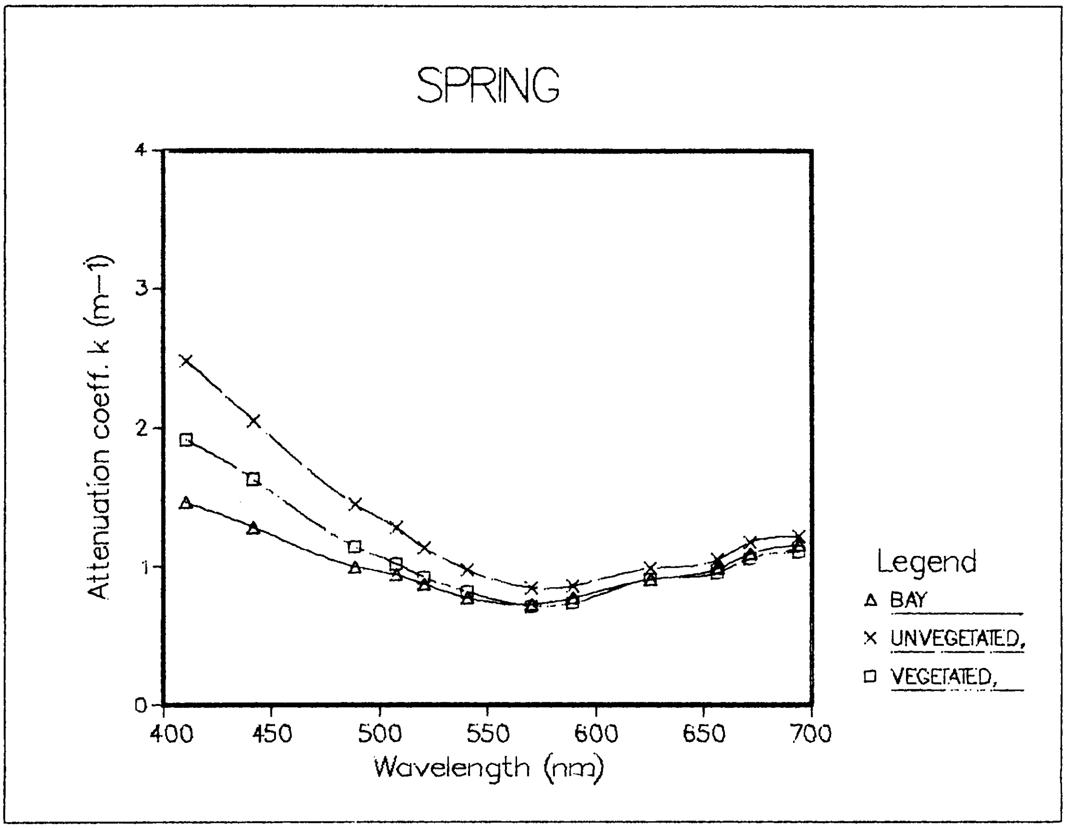

Figure 4. Mean spring 1981 spectral attenuation at vegetated and unvegetated sites in the lower Chesapeake Bay. (Bay = deep water station).

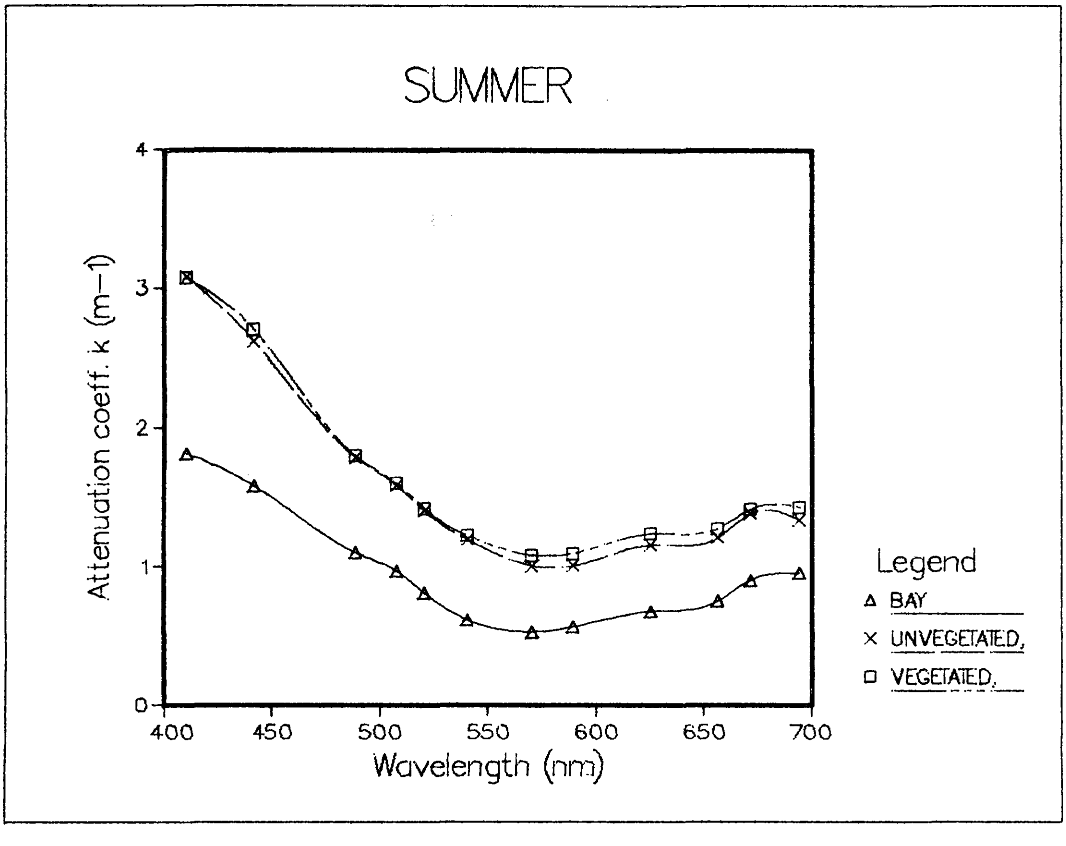

Figure 5. Mean summer 1981 spectral attenuation at vegetated and unvegetated sites in the lower Chesapeake Bay. (Bay = deep water station).

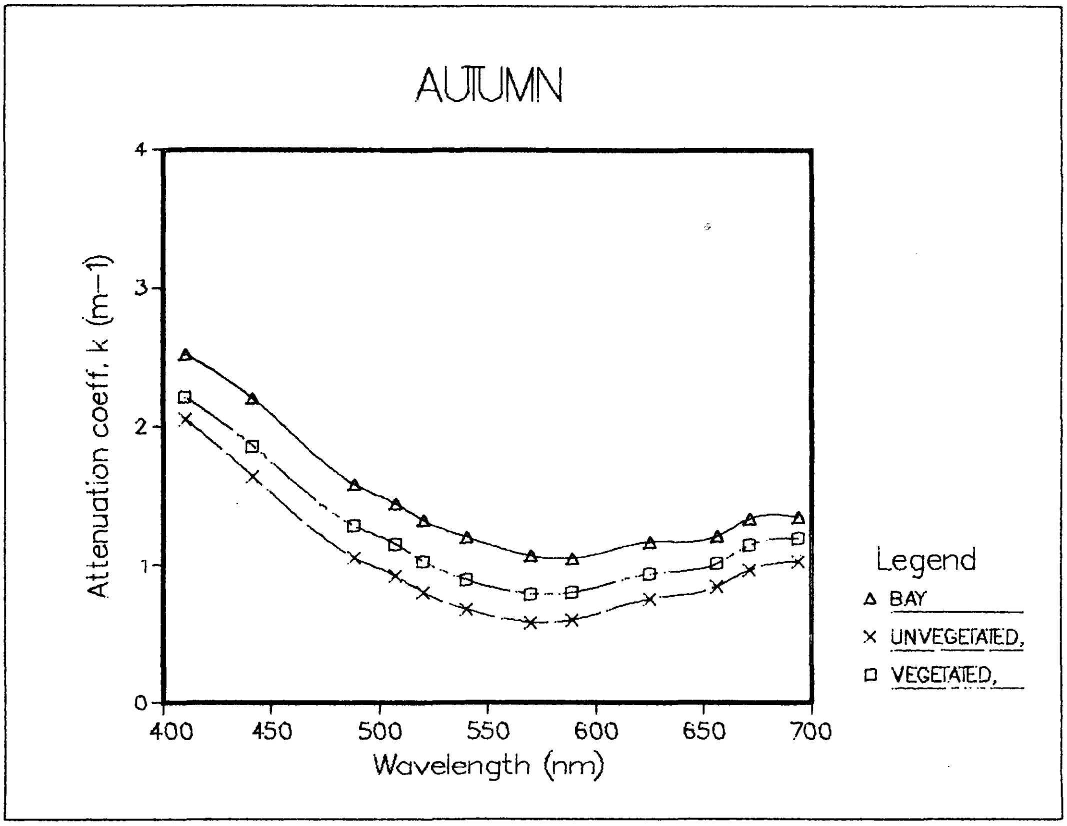

Figure 6. Mean autumn 1981 spectral attenuation at vegetated and unvegetated sites in the Lower Chesapeake Bay. (Bay = Deep water station).

TABLE I. MEAN SEASONAL SHALLOW WATER SPECTRAL ATTENUATION (m^{-1}) LOWER CHESAPEAKE BAY, 1981 (z = .1, .5 m)

	Winter		Spring		Summer		Fall		
(nm)	Veg.	Unveg.	Veg.	Unveg.	Veg.	Unveg.	Veg.	Unveg.	
410	1.14	1.04	1.91	2.48	3.07	3.08	2.21	2.04	
441	.892	.868	1.[illegible]2	2.04	2.70	2.62	1.85	1.64	
488	.566	.503	1.14	1.45	1.79	1.78	1.28	1.05	→ Y
507	.510	.435	1.02	1.28	1.60	1.58	1.15	.918	
520	.460	.397	.919	1.14	1.41	1.40	1.03	.802	
540	.404	.364	.813	.973	1.22	1.19	.887	.674	→ O
570	.371	.283	.711	.841	1.08	1.00	.787	.581	→ R
589	.407	.317	.735	.858	1.09	1.01	.798	.599	
625	.563	.497	.907	.987	1.24	1.15	.935	.754	
656	.644	.522	.956	1.05	1.28	1.21	1.01	.842	
671	.731	.623	1.06	1.18	1.41	1.38	1.14	.961	
694	.834	.679	1.11	1.22	1.43	1.34	1.19	1.02	→ Y → O → R

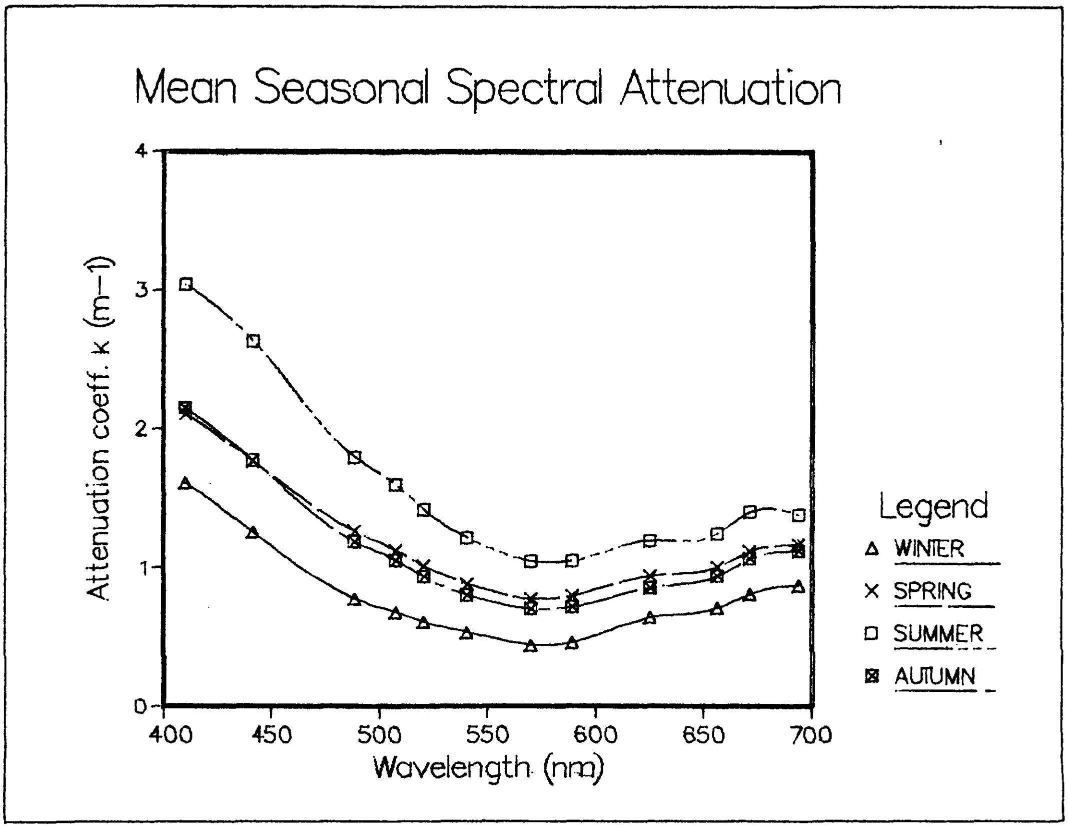

Figure 7. Mean seasonal spectral attenuation for shallow waters of the lower Chesapeake Bay. (All sites combined).

large difference between the mean deep-water (bay site) coefficients and the shallow water coefficients possibly due to lesser resuspension of particulates in the deep site.

The mean autumnal values were similar to those of the spring mean coefficients for the vegetated sites, ranging from about 0.79 m^{-1} at 570 nm to about 2.2 m^{-1} at 410 nm and the unvegetated mean from 0.58 m^{-1} to 2 m^{-1} at the same wavelengths.

A significant difference between the mean spectral attenuation coefficients for vegetated and unvegetated sites was found for spring (Fig. 4). The mean spring violet-blue (500 nm) unvegetated $k(\lambda)$ is more than 1 standard deviation higher than the mean $k(\lambda)$ for violet-blue light at vegetated sites (cf. Figs. 8, 9). Both shallow water vegetated and unvegetated means were higher than that for the deep water (bay site). Mean spring vegetated $k(\lambda)$ ranged from 0.71 m^{-1} at 570 nm to 1.9 m^{-1} at 410 nm. Corresponding values for the unvegetated sites were 0.84 and 2.5 m^{-1}, respectively. That is, violet light of 410 nm was reduced 85% per meter at the average vegetated site and over 92% per meter at the average unvegetated site during spring. There was little or no mean difference for wavelengths greater than 550 nm (yellow, orange, red). The deep water station ranged from about 1 to 1.5 m^{-1}.

Monthly Mean $k(\lambda)$

If one compares the monthly mean spectral attenuation for vegetated sites (Figs. 10, 11, 12) with that for unvegetated sites (Figs. 13, 14, 15) the most obvious difference to be found, as discussed above, is the higher attenuation of the shorter wavelengths at the unvegetated sites during the spring of the year. The unvegetated sites are characterized by elevated attenuation over the entire spectrum from May through October, whereas the vegetated sites do not show consistently elevated attenuation coefficients over the same time period. Attenuation of the violet and blue wavelengths (400-500 nm) at the vegetated sites increases gradually, reaching the maximum during September. Minor peaks occur during April and July. The attenuation coefficient for the remainder of the spectrum (500-700 nm) also exhibits these minor peaks but there is no increase towards the September maximum.

There does however appear to be a strong seasonal pattern to the attenuation coefficient at both vegetated and unvegetated sites, differing mainly in the timing of commencement of high values. The onset of high attenuation, especially of short wavelengths, appears to differ from year to year, as can be seen by comparing the March 1982 values (month 15 on graphs) with the March and May 1981 values (Figs. 10, 13). The correspondences at each type of site between the March 1982 (month 15 on the figures) short wavelength attenuation coefficients and those for the preceeding May (month 5) are quite striking. The relationship between the vegetated and unvegetated sites for the March 1982 attenuation coefficients is also analagous to their relationship in May, 1981. That is, at the average vegetated site the mean violet coefficients (410, 441) for May 1981 and for March 1982 were both between about 1.5 and 2.0 m^{-1} whereas those for the average unvegetated site were between 2 and 3 m^{-1} for both months.

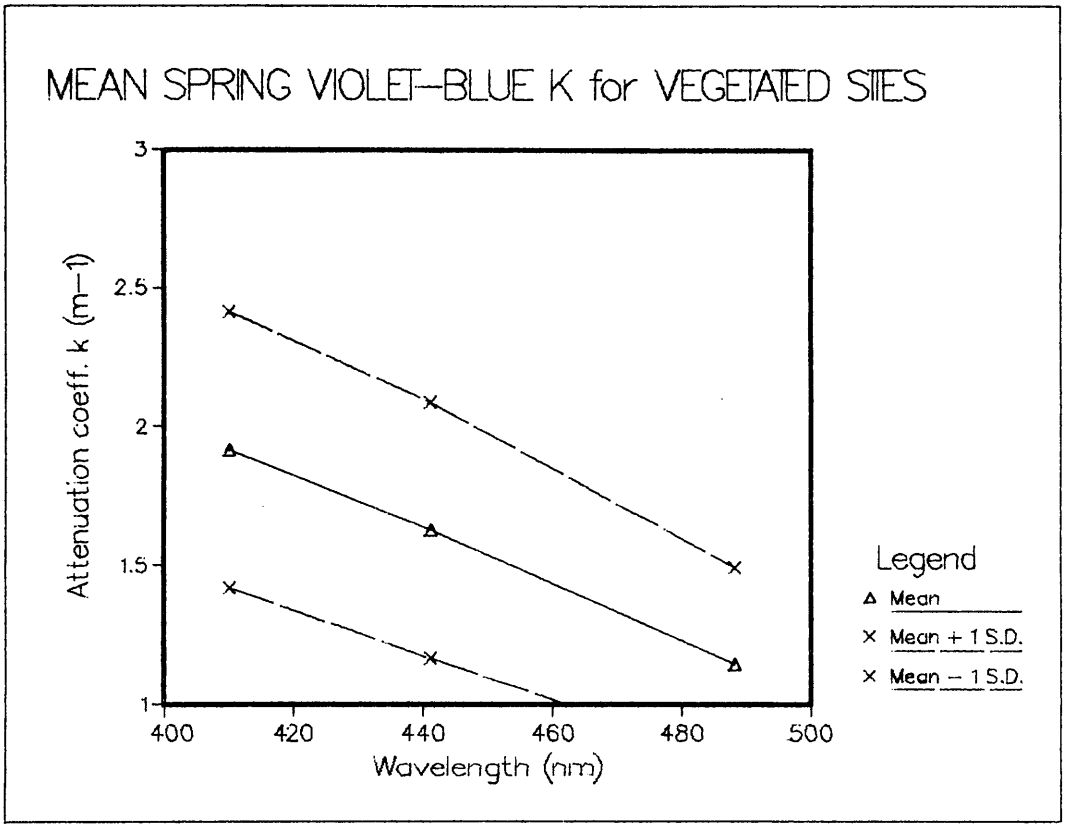

Figure 8. Mean spring 1981 violet-blue attenuation ± 1 S. D. at vegetated sites.

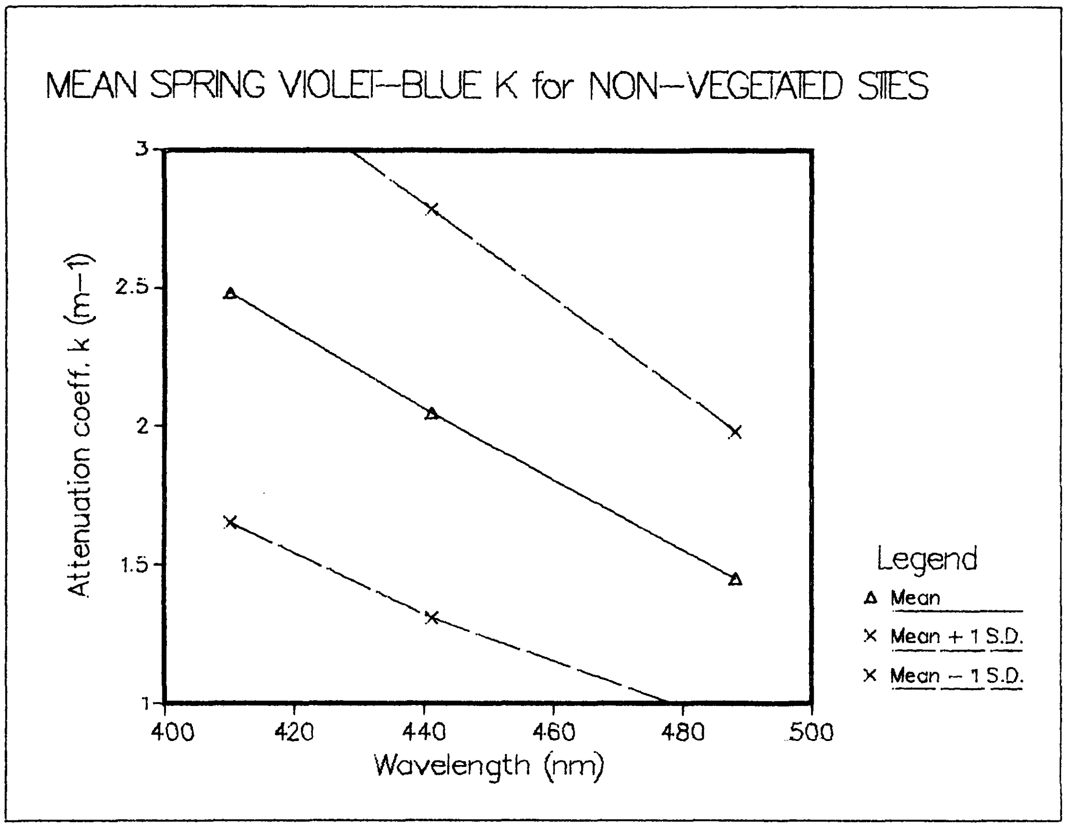

Figure 9. Mean spring 1981 violet-blue attenuation ± 1 S. D. at unvegetated sites.

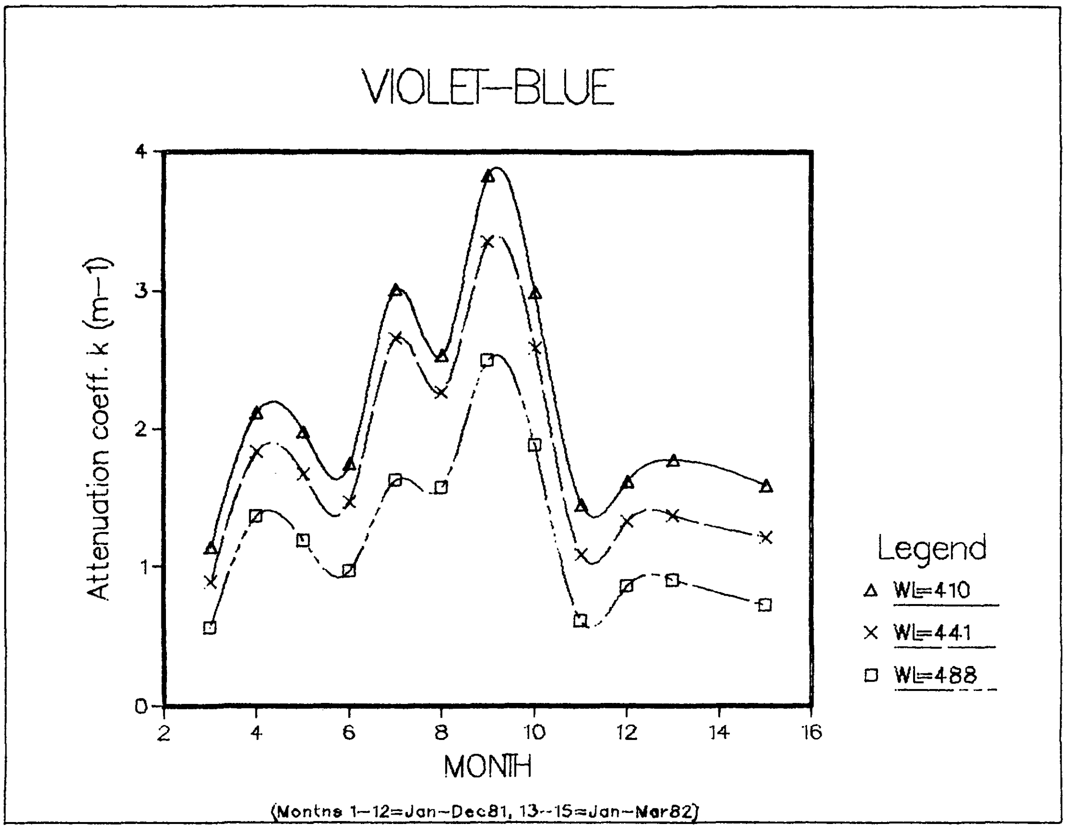

Figure 10. Mean monthly violet-blue attenuation at vegetated sites.

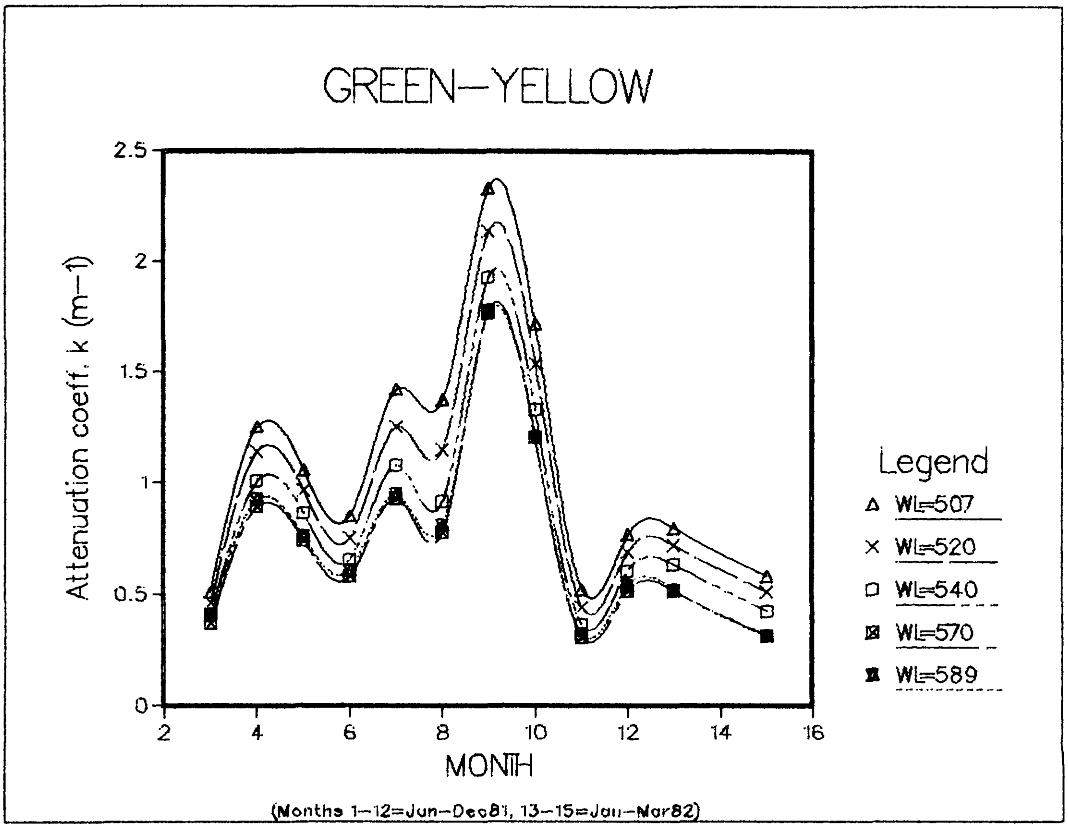

Figure 11. Mean monthly green-yellow attenuation at vegetated sites.

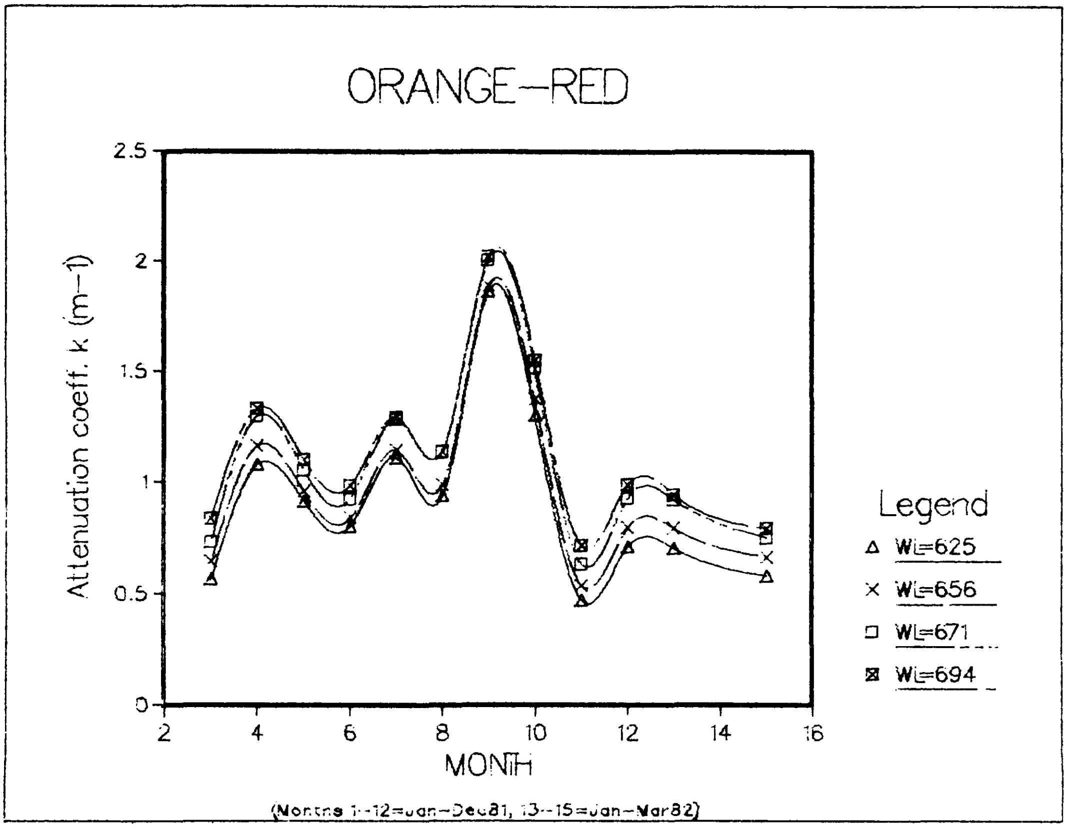

Figure 12. Mean monthly orange-red attenuation at vegetated sites.

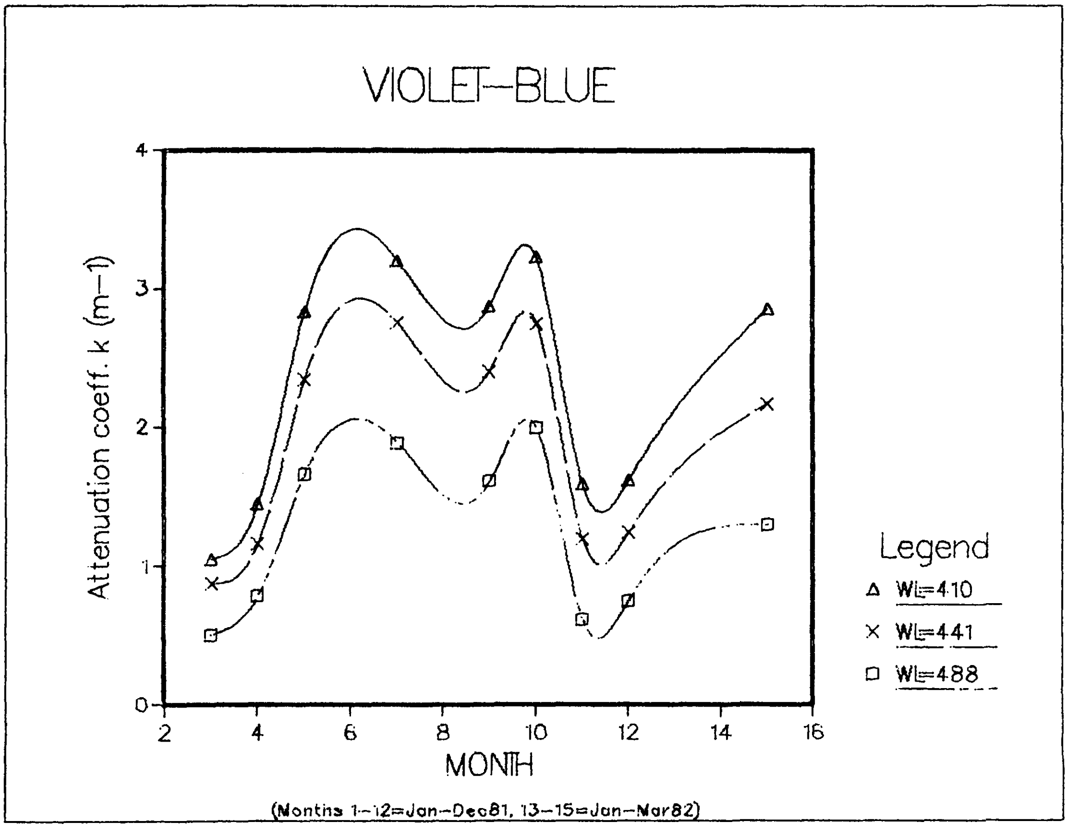

Figure 13. Mean monthly violet-blue attenuation at unvegetated sites.

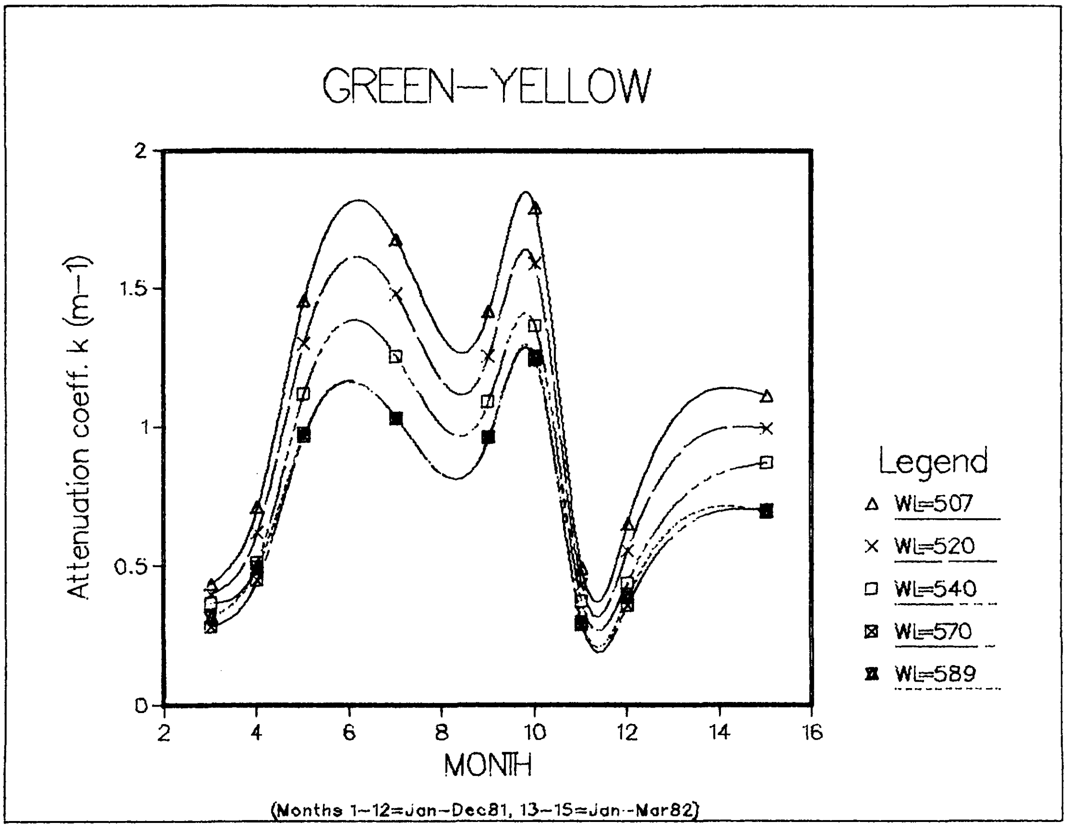

Figure 14. Mean monthly green-yellow attenuation at unvegetated sites.

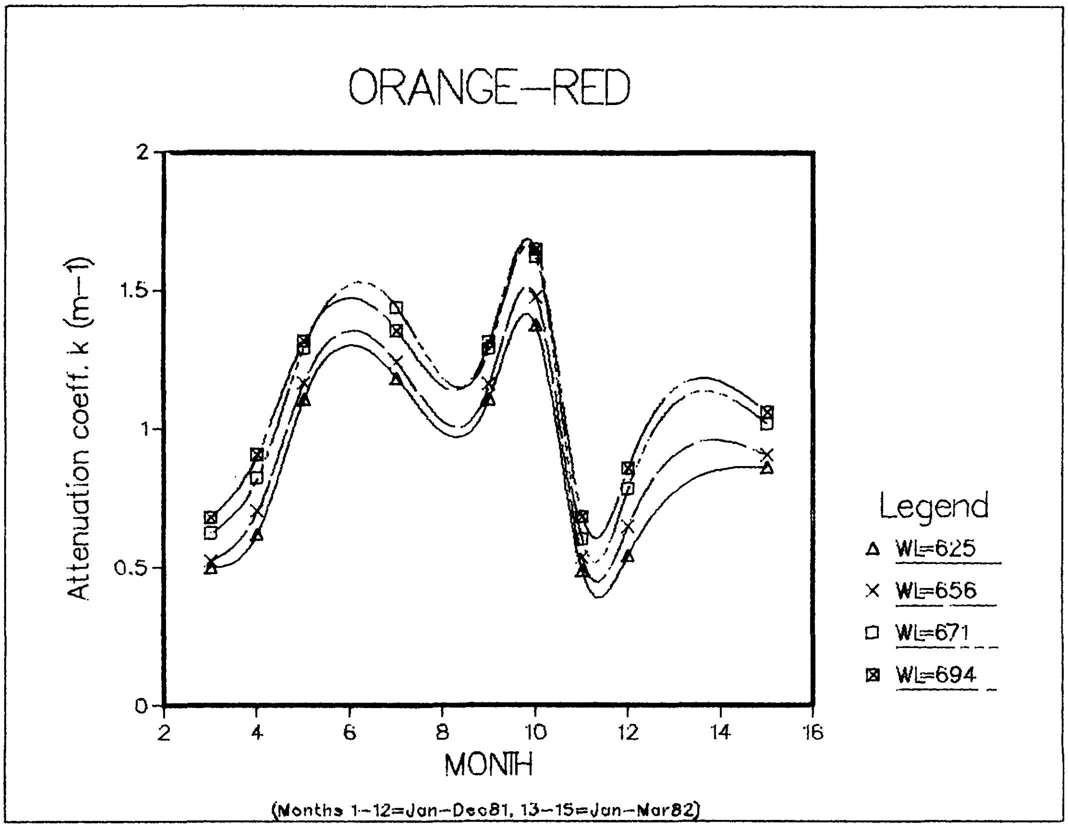

Figure 15. Mean monthly orange-red attenuation at unvegetated sites.

For unvegetated sites the year 1981 was broken up into two distinct light environments with little transition, while in the vegetated sites there was a shorter high attenuation period with a more gradual transition from low to high values.

The variability (expressed as ±1 standard deviation) of the monthly mean attenuation for vegetated and unvegetated sites is shown for wavelengths of 441 nm and 671 nm in Figures 16, 17, 18 and 19. These wavelengths are near the photosynthetic action peaks for marine green plants (Halldal, 1974). The variation in violet attenuation (441 nm) is consistently greater during the high turbidity season (May through October, 1981) for unvegetated sites than for vegetated sites (c.f. Figs. 16, 17). A comparison of the variability of red attenuation between vegetated and unvegetated sites yields much less difference. (The high variability during September for both wavelengths at the "average" vegetated site is mathematically due to the high attenuation at the Vaucluse Shore site, included in the mean, compared to the relatively low attenuation at the vegetated western shore sites). Nonetheless, constancy of light quality may be of consequence to benthic plants.

Since May 1981 seems to have been not only a pivotal month for the relative light environment in the unvegetated sites of the Lower Bay, but is also the month with the highest observed net seagrass community productivity (Murray and Wetzel, 1982) let us look more closely at the radiant energy attenuation calculations for that month. The mean vegetated and unvegetated k(λ) for May are shown in Fig. 20. The unvegetated mean is significantly higher at all wavelengths. There is a difference of more than 1.0 m^{-1} at 410 nm, and a difference of about 1.0 m^{-1} at 441 nm. The difference decreases to about 0.5 at 520 nm. Below 540 nm there is a constant difference of less than 0.4 m^{-1}. A 1.0 m^{-1} difference in attenuation coefficients represents a relative irradiance reduction of 63% over a 1.0 m path. That is, during May approximately 63% less violet light was able to pass through a meter of water at the "average" unvegetated site than at the "average" vegetated site. Over a 2.0 meter path the relative reduction would be 88%.

Individual sites

A comparison of the mean May k(λ) for each site is presented in Fig. 21. The two definitely unvegetated sites (Mumfort Is. in the York R. and the site in the mouth of the Severn R.) had the highest attenuation at all wavelengths. The Severn R. site was especially high below 500 nm. The mean k(λ) for the violet wavelengths (410, 441 nm) was between 3.5 and 4.0 m^{-1} for this site. A unit of radiant energy would be reduced 97-98% passing through a meter of water with an attenuation coefficient between 3.5 and 4.0 m^{-1}. A reduction of greater than 99% would result from the passage of light through two meters of water with an attenuation coefficient greater than 3.5 m^{-1}. That is, there was essentially no violet light below the surface of the water at the Severn R. site during the average May sampling period. Blue light (488 nm) was also greatly attenuated at this site (reduced about 90% per meter). Mean attenuation at the Mumfort Is. site ranged from a high of about 3.0 m^{-1} at 410 nm about 1.5 m^{-1} at 507 nm and no higher than that for the remainder of the spectrum. The red end of the spectrum was even more attenuated at the Mumfort Is. site than in the Severn R.

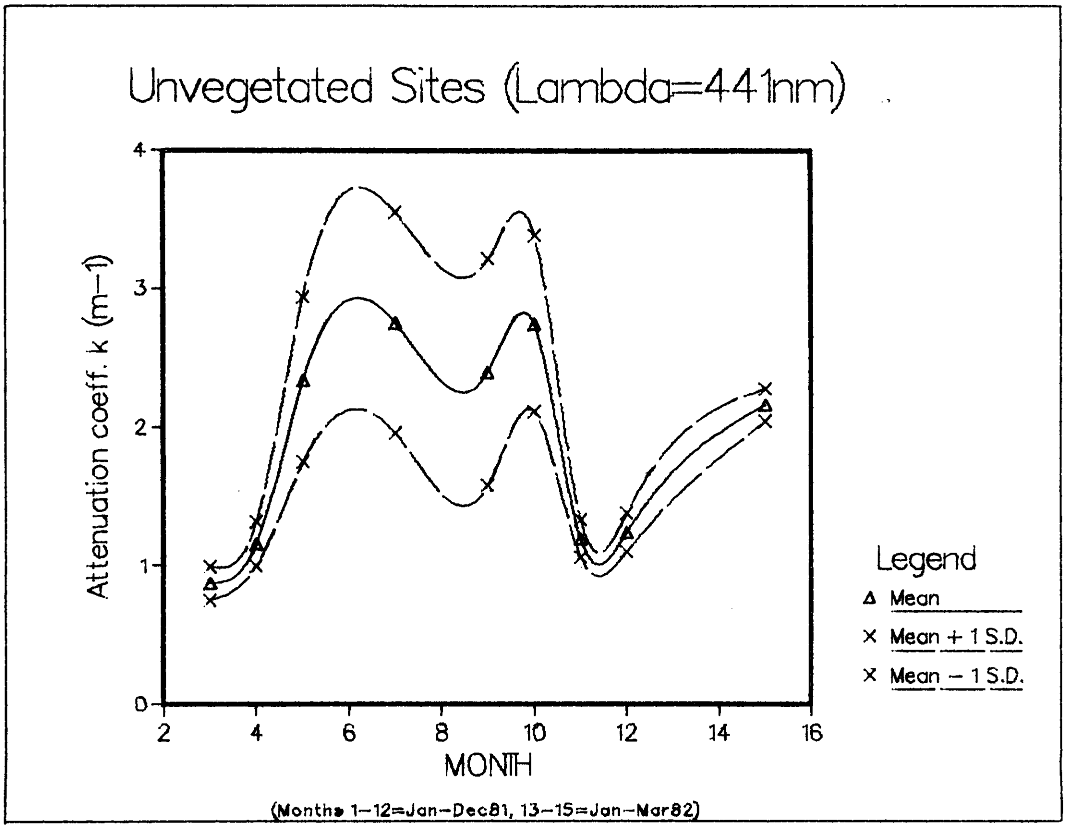

Figure 16. Mean monthly variability of attenuation of light of 441 nm at unvegetated sites.

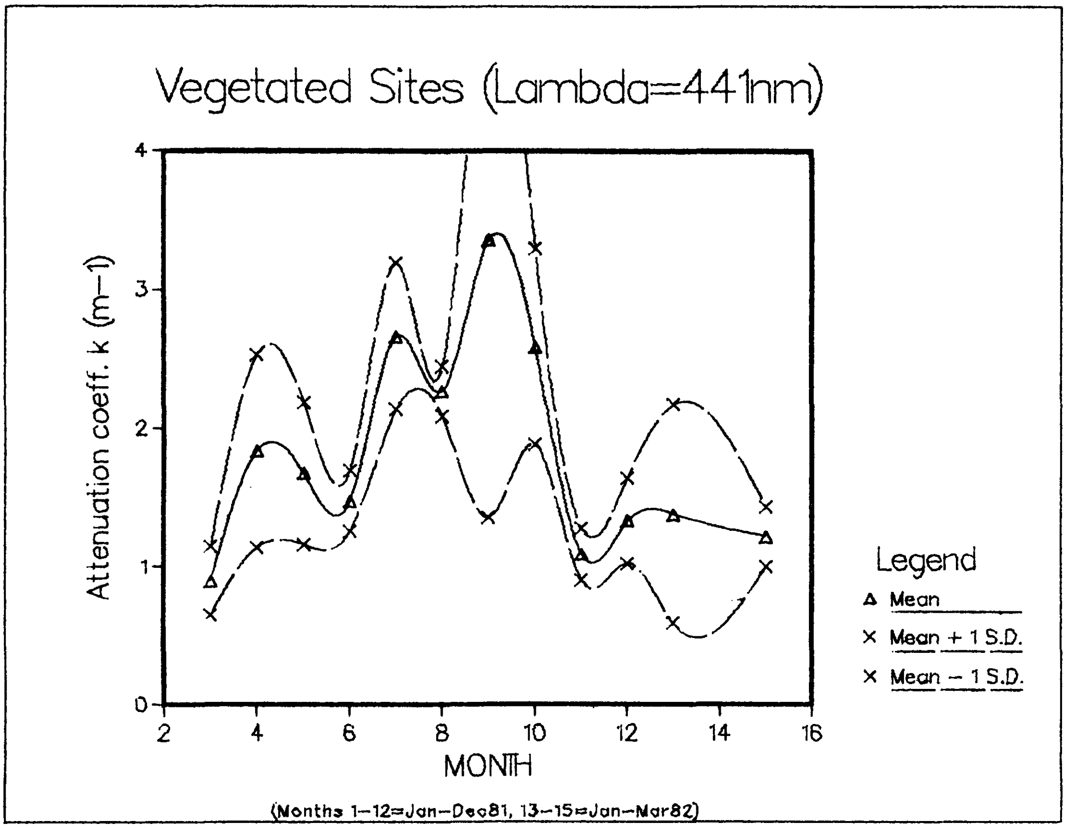

Figure 17. Mean monthly variability of attenuation of light of 441 nm at vegetated sites.

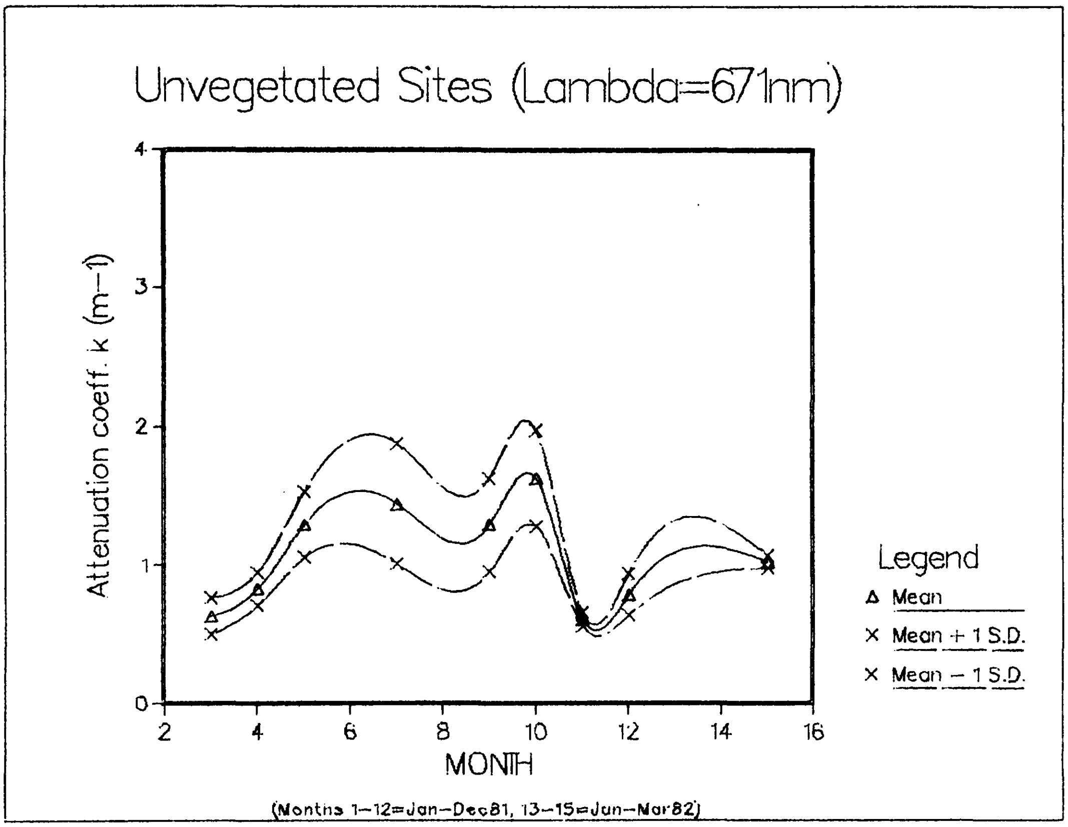

Figure 18. Mean monthly variability of attenuation of light of 671 nm at unvegetated sites.

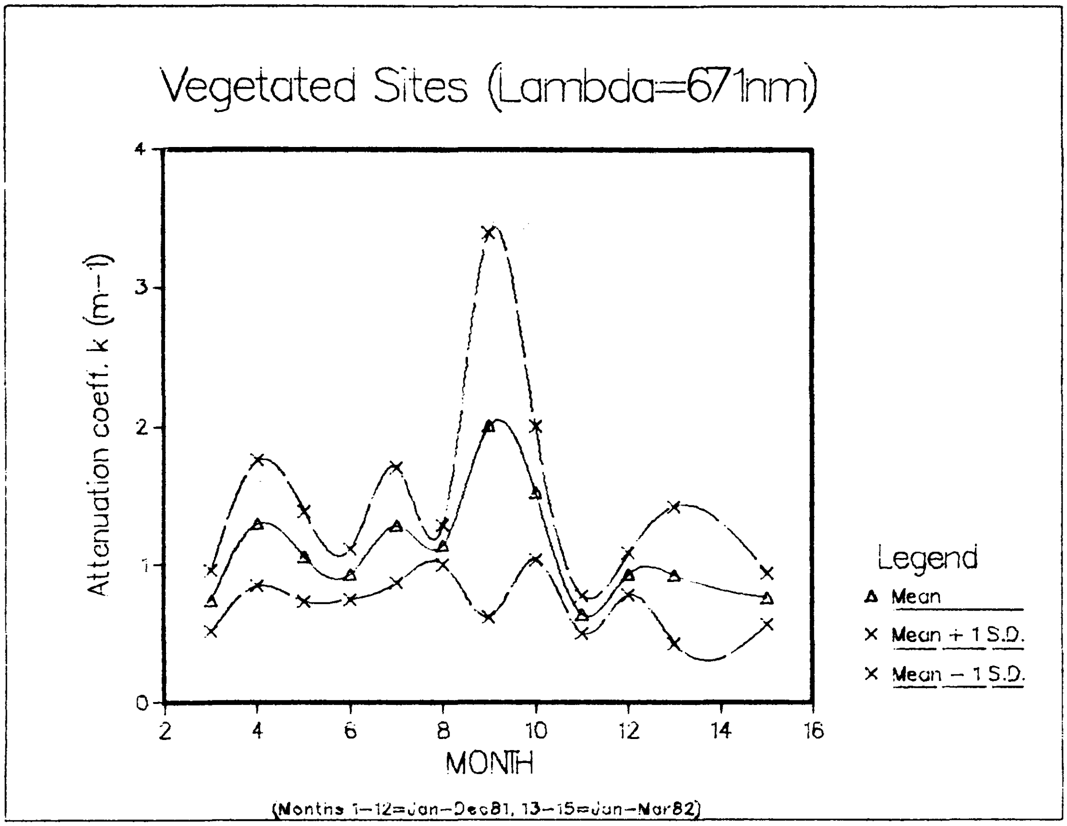

Figure 19. Mean monthly variability of attenuation of light of 671 nm at vegetated sites.

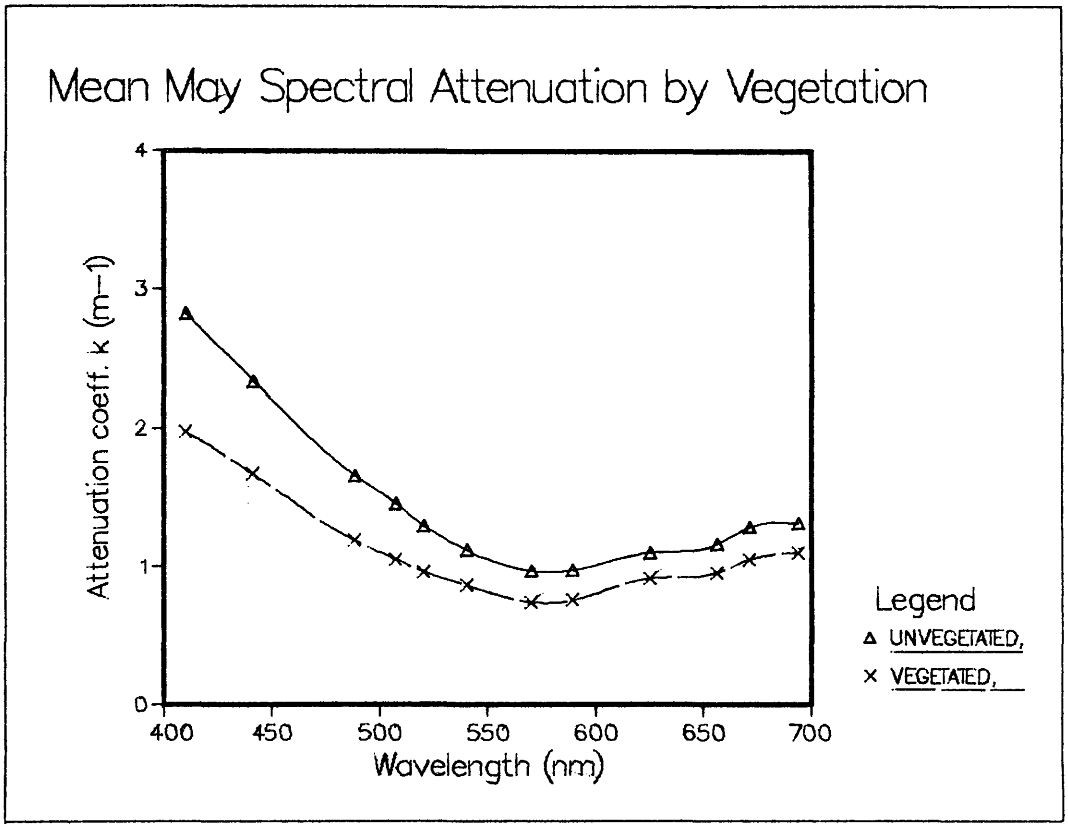

Figure 20. Mean May 1981 spectral attenuation at unvegetated and vegetated sites.

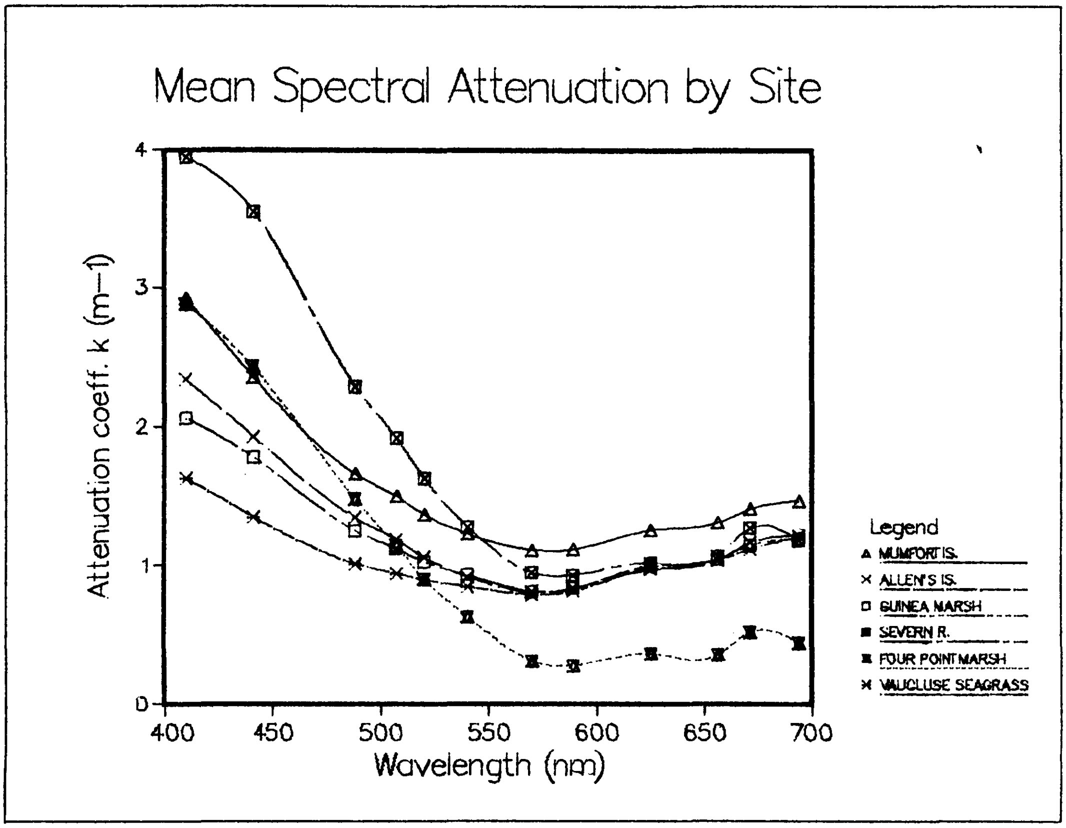

Figure 21. Mean May 1981 spectral attenuation at individual sites.

All mean May coefficients at the vegetated sites - Guinea Marsh, Four Point Marsh and Vaucluse - were below about 2 m^{-1} except those for violet light at Four Point Marsh. However, the attenuation of yellow, orange and red light at the Four Point Marsh site was extremely low - less than 0.5 m^{-1}. This is a reduction of only about 40% per meter. This site and the unvegetated Severn R. site are located very close to each other, both in Mobjack Bay and have a very similar pattern of spectral attenuation but at different magnitudes. Note how the k curves track each other. The mean $k(\lambda)$ for the unvegetated Severn R. site is consistently about 1 m^{-1} higher than that for the vegetated Four Point Marsh site during May. Violet attenuation at the Guinea Marsh and Vaucluse Shore vegetated sites was between about 1.5 and 2 m^{-1}. Attenuation of the rest of their spectra being between 1 and 1.5 m^{-1}. The Vaucluse site had the lowest violet-blue mean attenuation during May while the Four Point Marsh site had the lowest yellow to red attenuation; lower than even the mean winter values at all other sites! Notice that with the exception of the violet light at Four Point Marsh the mean May attenuation for all vegetated sites at all wavelengths was less than about 2 m^{-1}. Thus, the extremely low May attenuation of the longer wavelengths at Four Point Marsh may compensate for the high attenuation of the short wavelengths in terms of total light energy available for photosynthesis.

The spectral attenuation at the Allen's Is. site is intermediate to that of the vegetated and unvegetated sites. That is interesting because this site is intermediate with respect to its vegetation. It was vegetated in the past, but lost its bay grasses with the rest of the lower Bay. However, it has been successfully transplanted by R. J. Orth and associates and has some natural plants coming back (personal communication K. Moore, VIMS). Since this site appears in transition the irradiance measurements taken there have not been included in either the "vegetated" or "unvegetated" means reported herein, but has been treated separately.

A comparison of the mean seasonal $k(\lambda)$ at individual sites (Figs. 22 thru 28) reveals both differences between vegetated (Vaucluse, Guinea, Four Point) and unvegetated (Mumfort, Severn) sites and reveals individual site idiosyncracies. The seasonal means plotted on these graphs were calculated from 1981 and 1982 measurements combined. Therefore "winter" (defined as Jan.-Mar.) at some sites represents values from both years. Since, as explained earlier, the high turbidity season started in March during 1982 and in May during 1981, the resulting combined winter mean includes both high and low values at those sites which were monitored both years.

Mean seasonal spectral attenuation values were at or below 2 m^{-1} for all seasons except summer at the western shore vegetated sites (Figs. 24, 26). As noted previously, attenuation at the red end of the spectrum was particularly low at Four Point Marsh (Fig. 26). Note how similar autumn, winter and spring appear at this site. Winter and spring mean values were also less than 2.0 m^{-1} at the eastern shore vegetated site (Vaucluse Shores, Fig. 27), but autumn was the most turbid season for this site as it also was for the deep site on the Eastern Shore (Bay, Fig. 28). None of the western shore sites showed this pattern. The light environment, not surprisingly, appears to be quite different in the different masses of water on opposite sides of the Bay. With the exception of fall the mean seasonal attenuation at the deep site (Fig. 28)

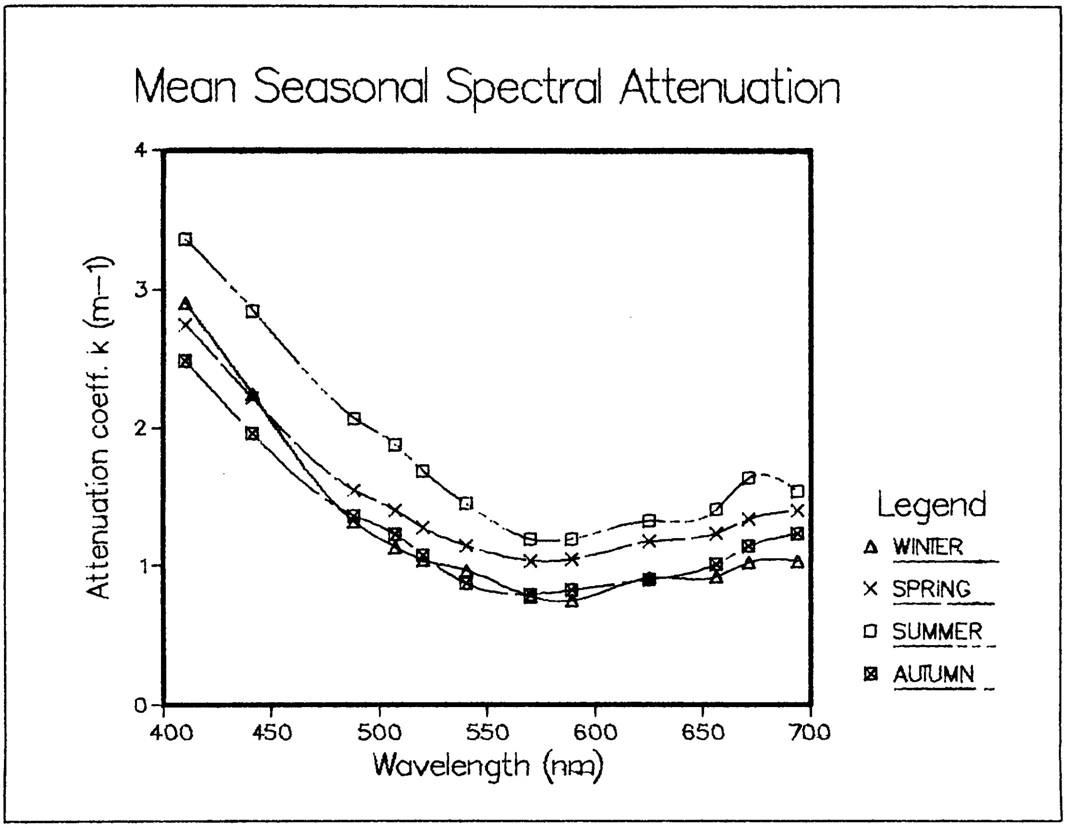

Figure 22. Mean seasonal spectral attenuation at Mumfort Is. (York R.).

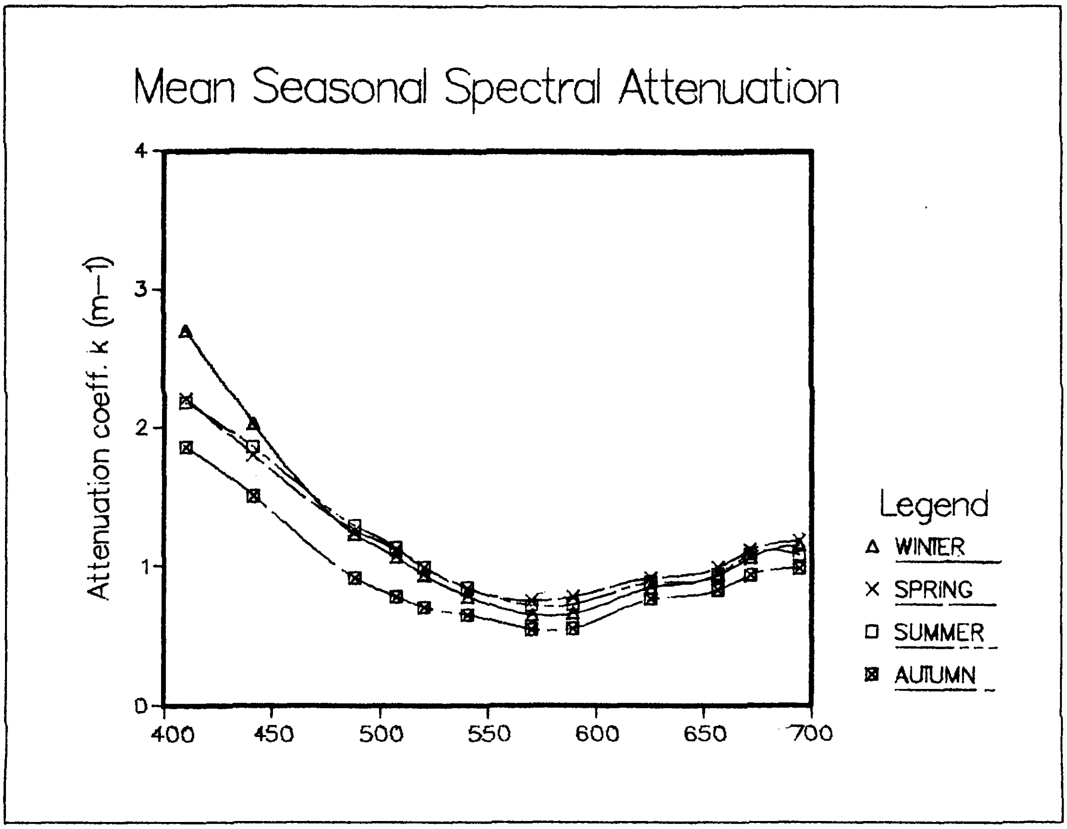

Figure 23. Mean seasonal spectral attenuation at Allen's Is. (York R.).

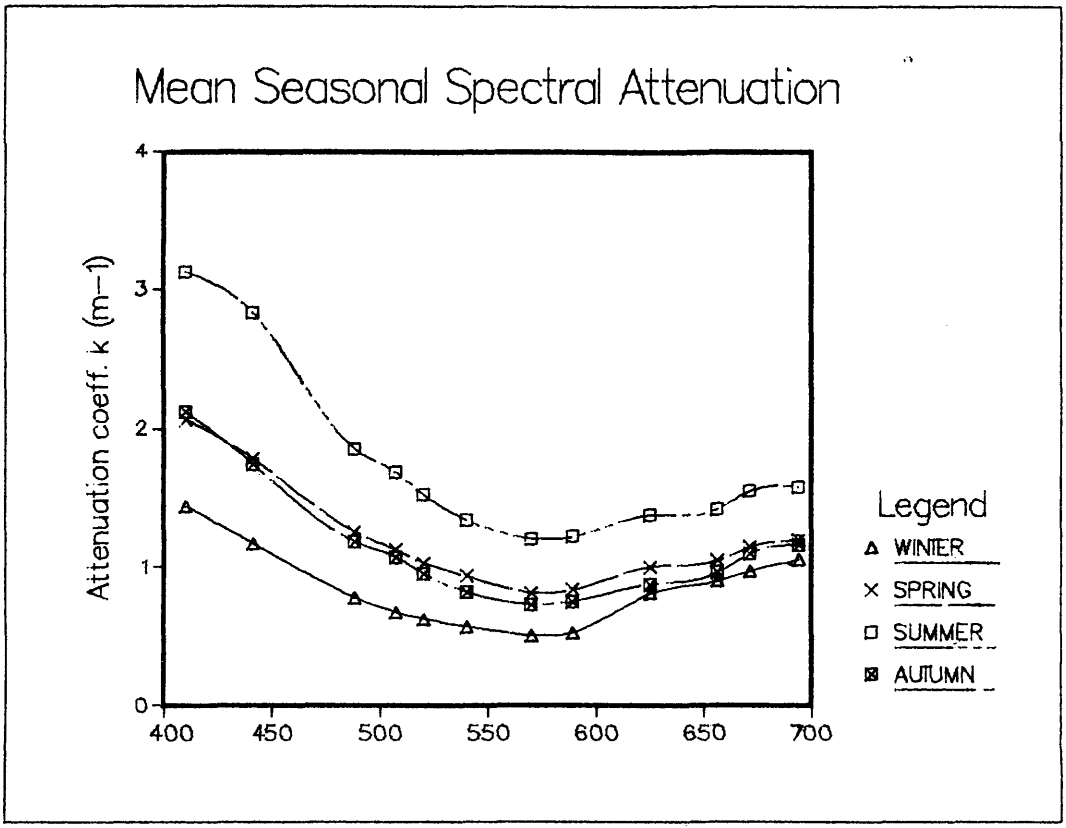

Figure 24. Mean seasonal spectral attenuation at Guinea Marsh.

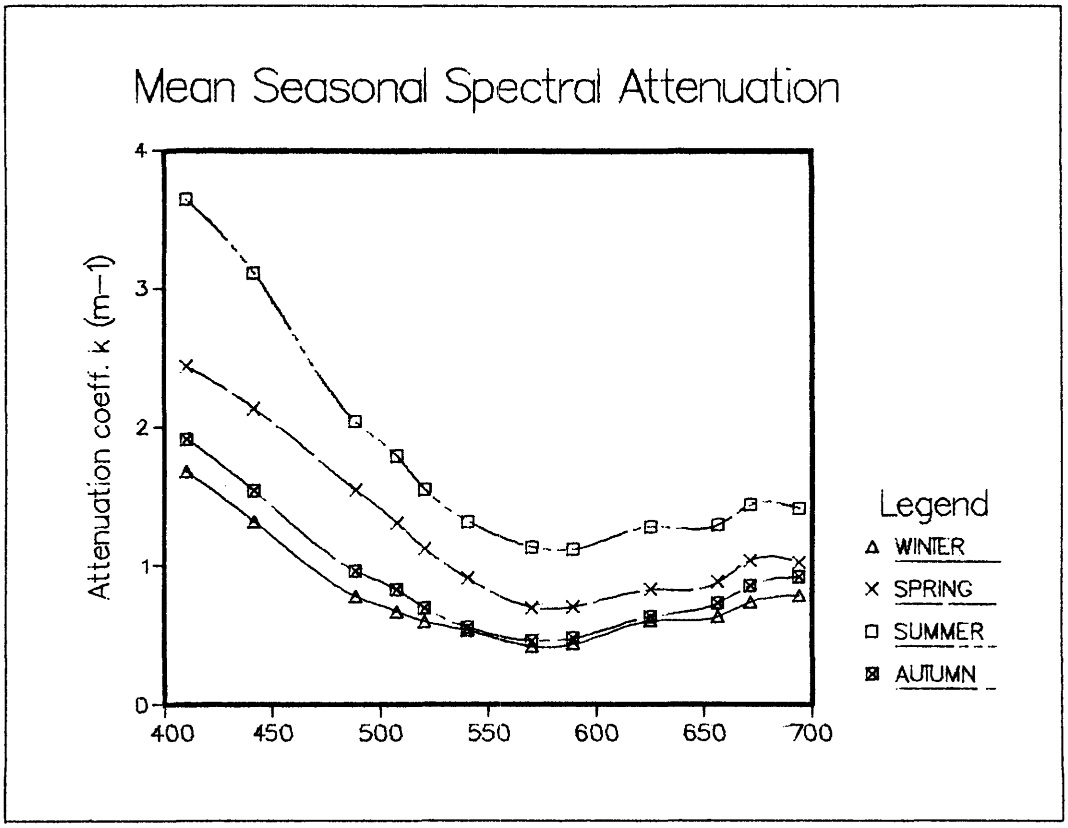

Figure 25. Mean seasonal spectral attenuation at the mouth of the Severn R. (Mobjack Bay).

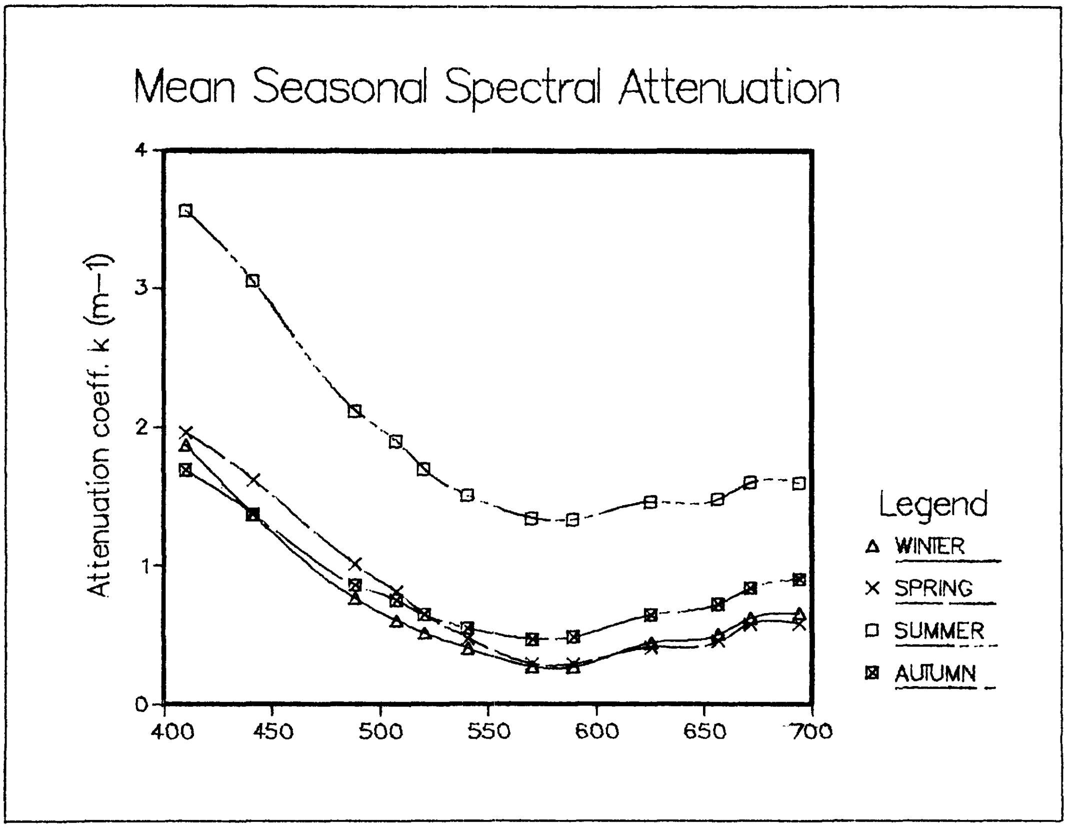

Figure 26. Mean seasonal spectral attenuation at Four Point Marsh (mouth of Ware R., Mobjack Bay).

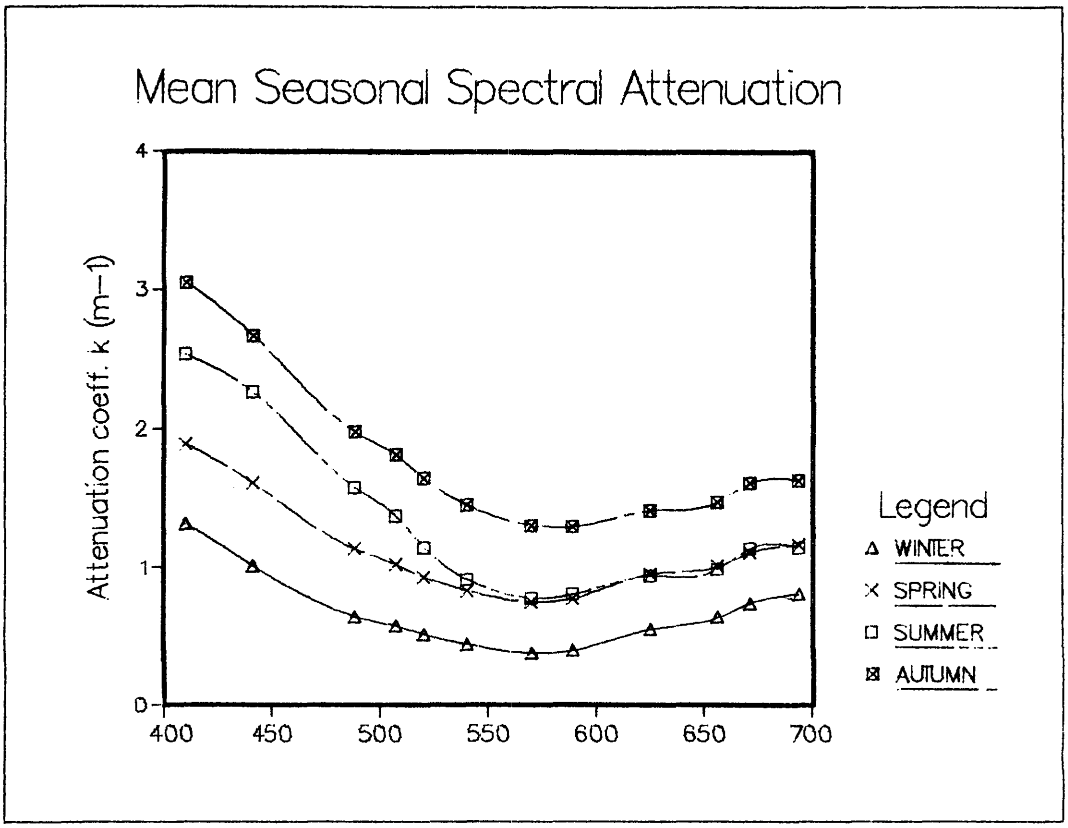

Figure 27. Mean seasonal spectral attenuation at Vaucluse Shores Zostera bed (Eastern Shore).

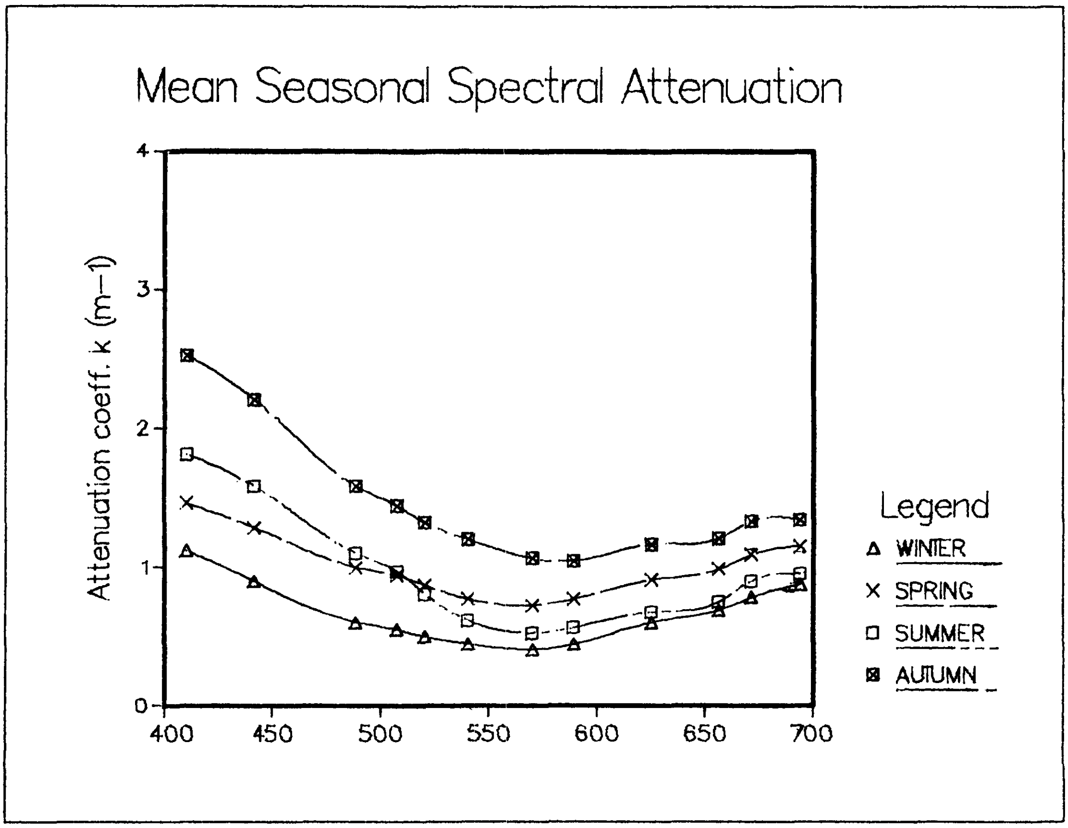

Figure 28. Mean seasonal spectral attenuation at the Deep Station (Bay) at Vaucluse Shores (Eastern Shore).

was consistently lower than the corresponding values at any other site. Note the relative color shift from blue to red between spring to summer at this site (the intersection of the 2 seasonal curves). This shift also occurs in modified form at the eastern shore seagrass site (Vaucluse, Fig. 27). Here the penetration of blue light is reduced significantly but the penetration of red light is not increased.

The western shore unvegetated sites (Mumfort, Severn, Figs. 22, 25) both had mean spring violet attenuation values between 2 and 3 m^{-1}, definitely higher than the corresponding values at any vegetated site. Each of the seasonal mean curves for Mumfort Is. (Fig. 22) are high compared to the other sites. The autumn and winter mean $k(\lambda)$ for the Severn R. site are, however, similar to the corresponding curves for vegetated sites.

The Allen's Is. site (Fig. 23) is once again difficult to classify. Its mean spring $k(\lambda)$ is intermediate, summer low, winter high and fall is about average.

The mean monthly water column attenuation for selected wavelengths at individual sites is presented in Figs. 29 through 35. The wavelengths presented in these figures (410, 441, 488, 570, 671, 694 nm) were selected not only for their biological relevance with respect to photosynthetic action spectra and *in vivo* pigment absorption peaks, but to outline the extremes and means of the full set of 12 wavelengths measured with more clarity and less confusion than is possible by showing the entire set measured. A spline interpolation was used to connect the discrete measurements.

A seasonal pattern of turbidity at all sites is most obvious. As mentioned previously the high turbidity at the unvegetated sites (Figs. 29, 32) clearly starts in May and continues through October, during 1981. This is especially obvious for the shorter wavelengths. The onset of high turbidity appears earlier in 1982, during March, with violet attenuation approaching or exceeding 3.0 m^{-1} at the unvegetated sites. At Guinea Marsh (vegetated, Fig. 31) the violet attenuation increased gradually from a low of about 1.5 m^{-1} in March of 1981 to a peak of between 3.5 and 4.1 m^{-1} during September, declining dramatically to winter levels in November. As of March 1982, no increase was evident. The attenuation of longer wavelengths at Guinea Marsh peaked sharply in September and declined during October to reach otherwise constantly low values during November. A similar pattern of attenuation for the longer wavelengths of light was found at the other western shore vegetated site, Four Point Marsh (Fig. 33). However, May 1981 values were extraordinarily low (0.5 m^{-1}) for the red end of the PAR at this site. Simultaneously, the violet-blue attenuation during May was higher than the other vegetated sites. The Allen's Is. site (Fig. 30) shows much less monthly variation than any other western shore site.

The eastern shore vegetated site at Vaucluse (Fig. 34) reached its maximum short wave attenuation during October, but also peaked in April. The minima occurred during March, May and June 1981 and January 1982. The long wave attenuation followed the same pattern but with much less magnitude. March, May and June, 1981 were also the months of maximum net productivity for the benthic *Zostera* community at this site (Murray & Wetzel, 1982). The same

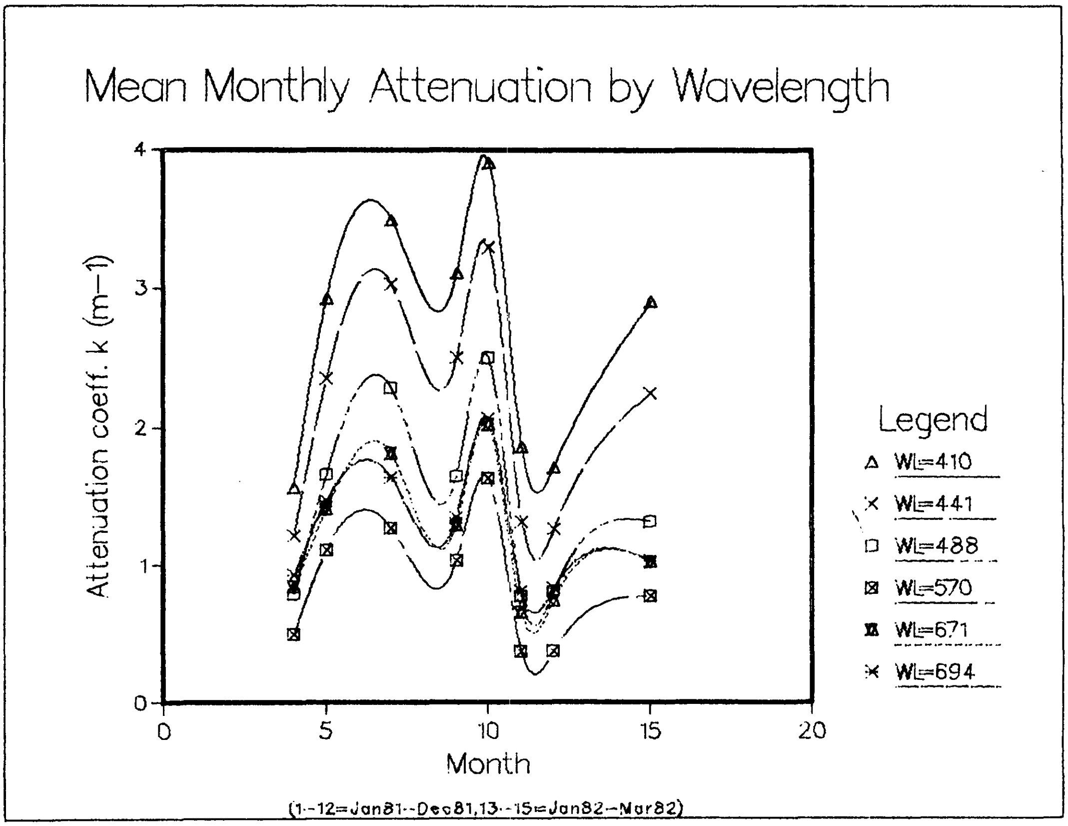

Figure 29. Mean monthly attenuation of selected wavelengths at Mumfort Is. (York R.).

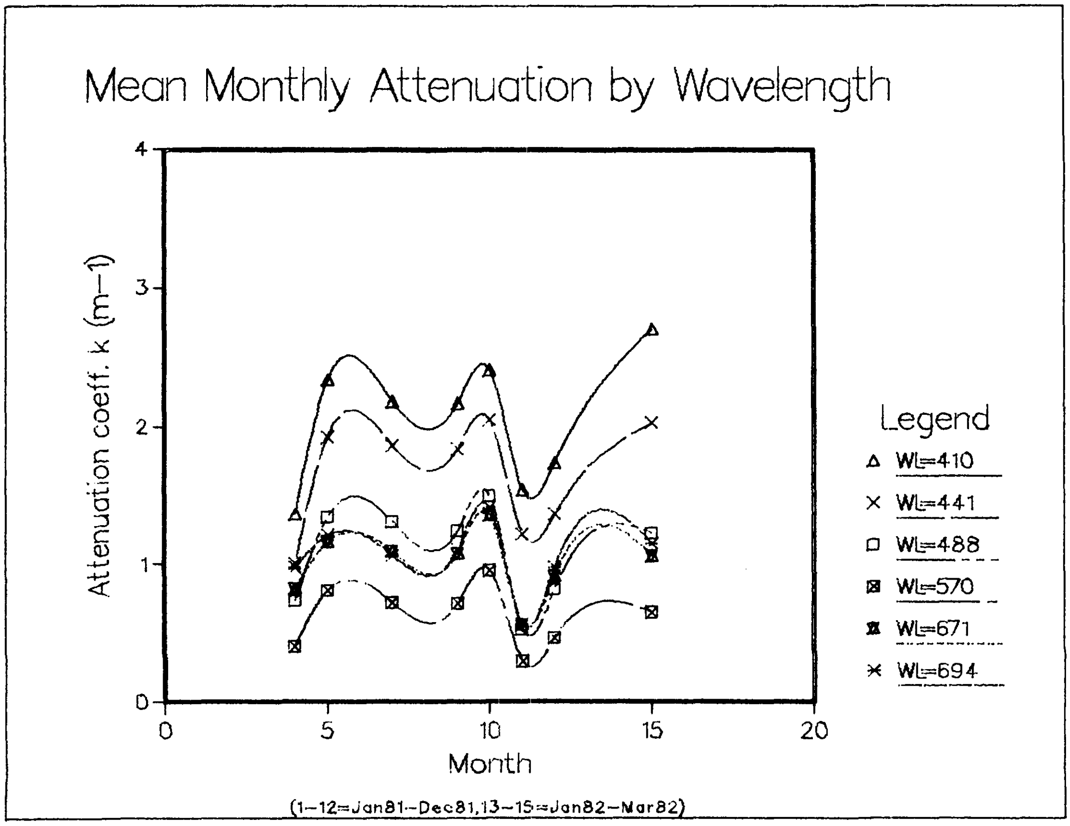

Figure 30. Mean monthly attenuation of selected wavelengths at Allen's Is. (York R.).

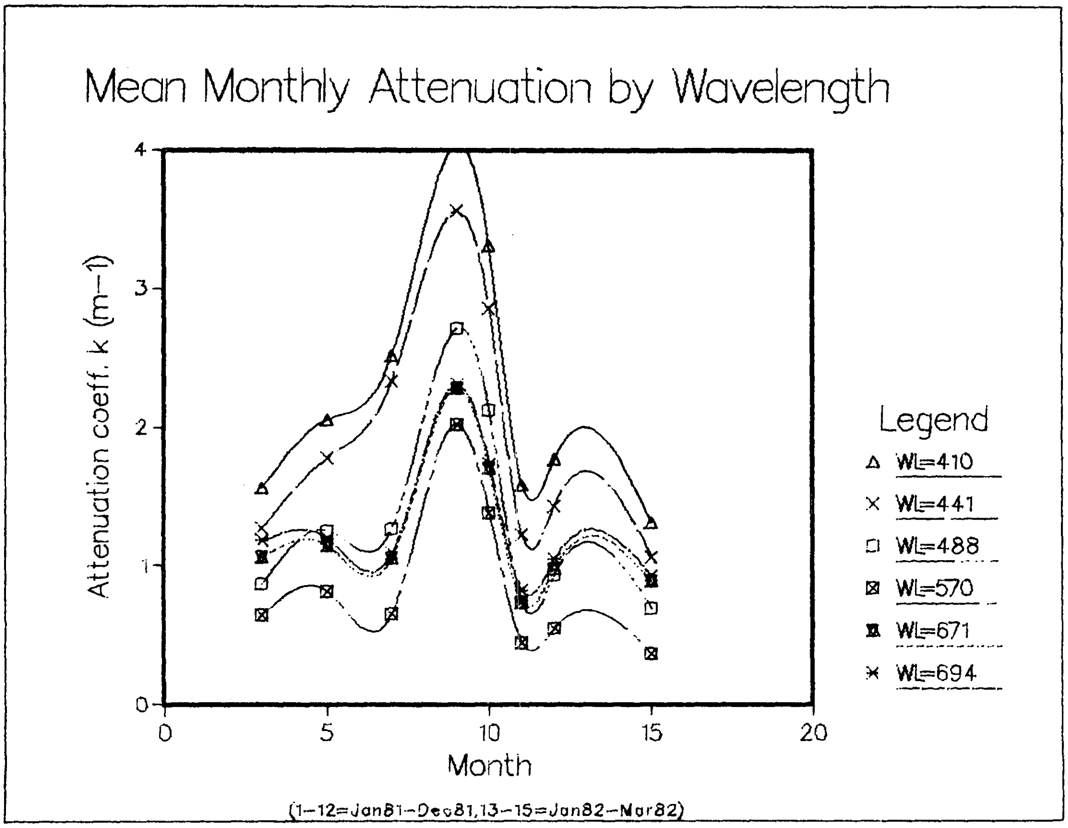

Figure 31. Mean monthly attenuation of selected wavelengths at Guinea Marsh.

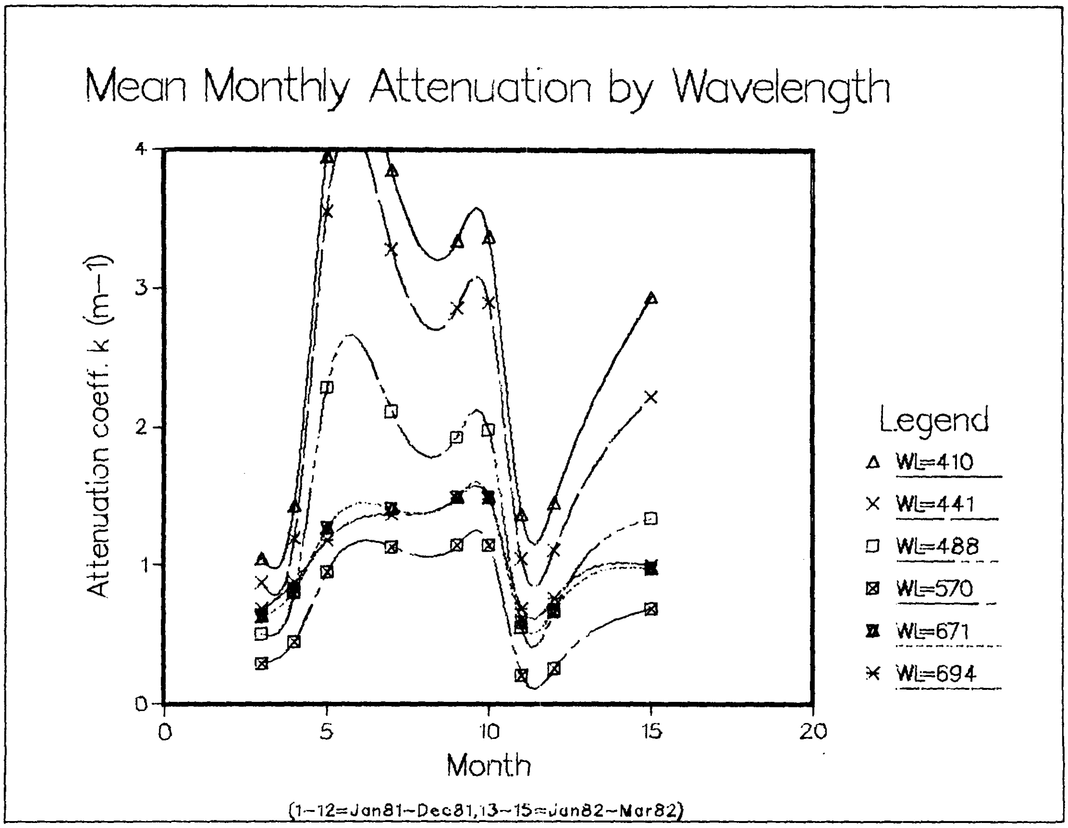

Figure 32. Mean monthly attenuation of selected wavelengths at the mouth of the Severn R. (Mobjack Bay).

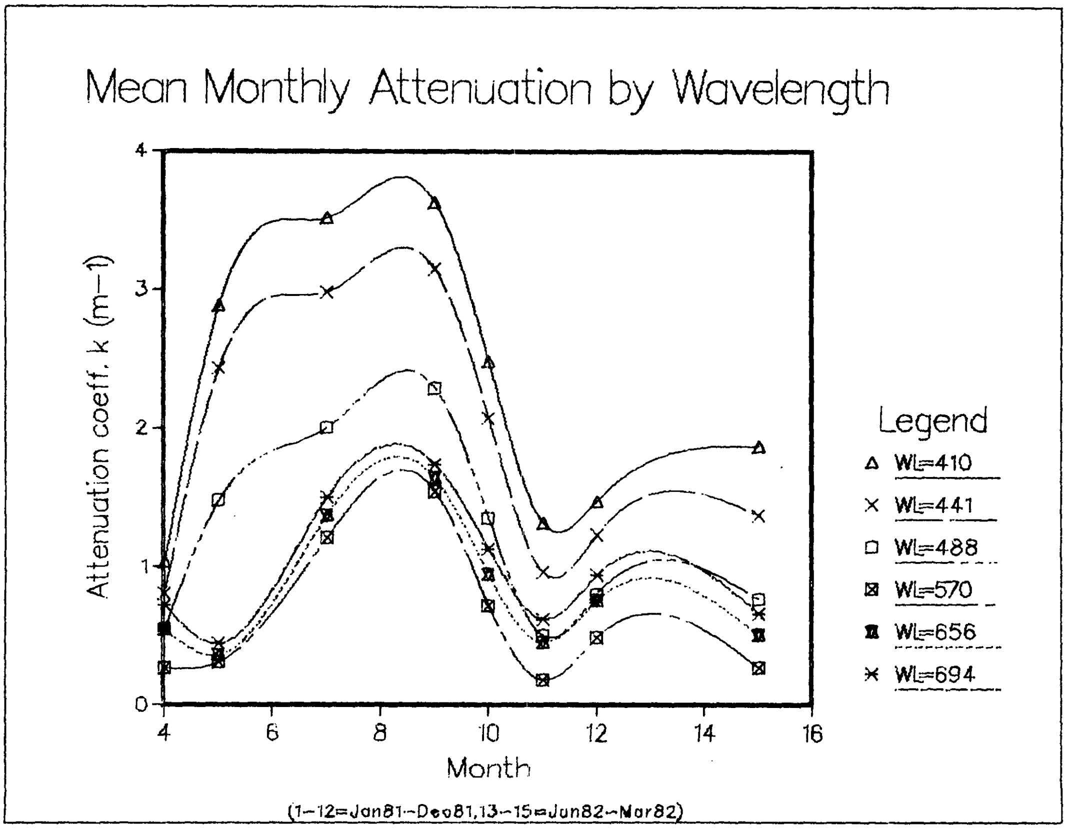

Figure 33. Mean monthly attenuation of selected wavelengths at Four Point Marsh (mouth of Ware R., Mobjack Bay). Note: Horizontal axis differs from other figures in this series.

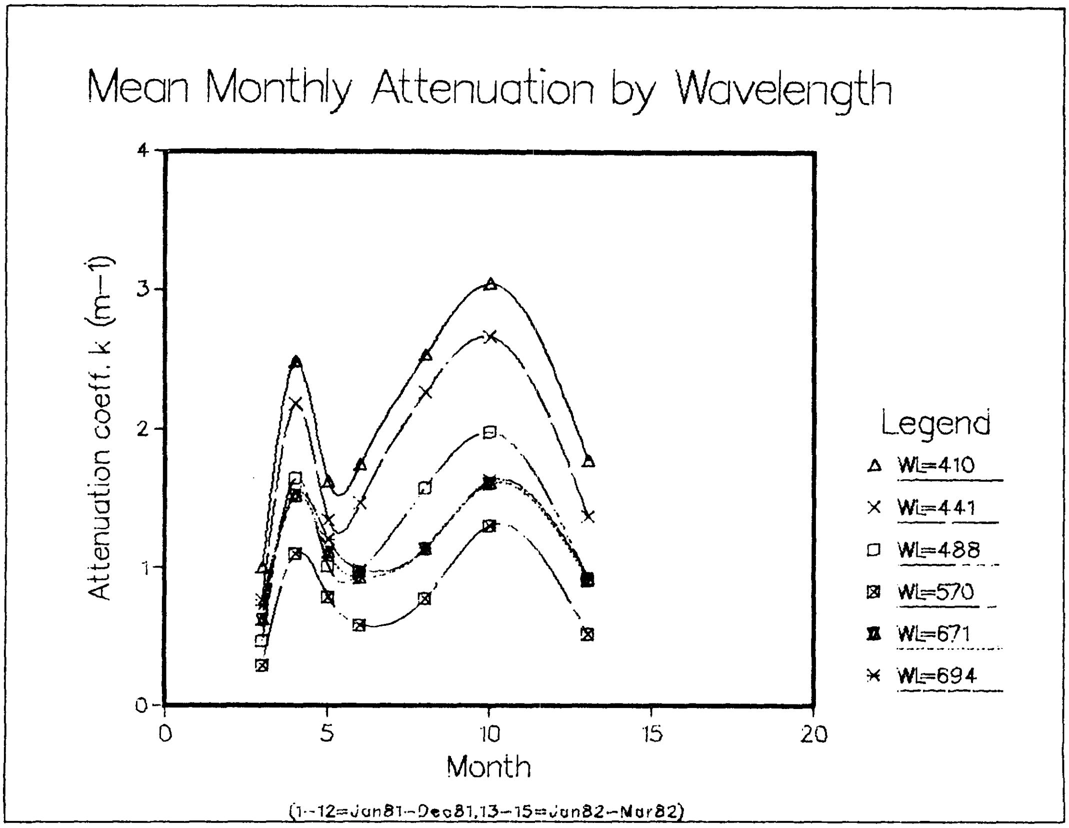

Figure 34. Mean monthly attenuation of selected wavelengths in the Zostera bed at Vaucluse Shores.

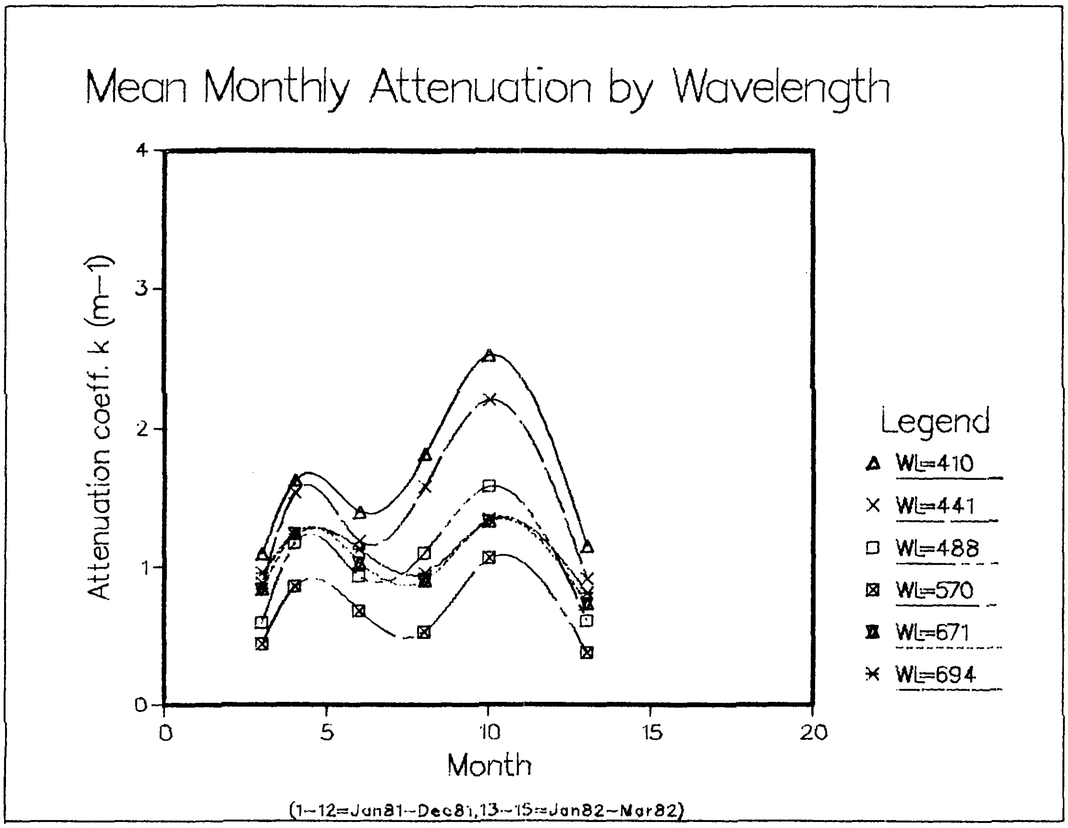

Figure 35. Mean monthly attenuation of selected wavelengths at Deep Station (Bay) at Vaucluse Shores.

pattern of attenuation, but with less extreme oscillation is apparent at the deep water station (Fig. 35) adjacent to the Vaucluse site.

In summary, attenuation across the entire spectrum at unvegetated sites appears to begin earlier in the year and increase at a more rapid rate than at vegetated sites.

Relative Potential Benthic Photosynthesis

Potential benthic production is determined both by the light available for photosynthesis at the bottom of the water column and by the inherent photosynthetic response of the plants present. Limiting our discussion to green plants and using published photosynthetic action spectra, mean seasonal attenuation coefficients and incident irradiance measurements we can calculate the relative potential photosynthetically storable radiation, PSR (Morel, 1978; Smith, 1979). The results of these calculations for spring are presented in Figure 36. Spring was chosen for this example not only because it is the season with the greatest difference in attenuation between vegetated and unvegetated sites, but because it is the season of highest net seagrass community productivity (Murray and Wetzel, 1982; Wetzel et al., 1982).

Curve "a" (Fig. 36) represents the mean incident spectral irradiance during clear spring days at noon. Notice how the quantum distribution decreases rapidly below 500 nm. The estimated total attenuation coefficients for both vegetated and unvegetated sites are shown as curves "b". These represent the spring spectral attenuation from just above the water's surface to a depth of 1.0 m for calm, clear days around noon. The attenuation at the unvegetated sites is higher at all wavelengths than that at the vegetated sites during spring: especially for wavelengths less than 500 nm. This difference increases from .23 m^{-1} at 507 nm to .51 m^{-1} at 410 nm. There is a difference between site types of about .1 m^{-1} from 570 to 700 nm.

The resulting estimated benthic irradiance for both vegetated and unvegetated sites is shown as curves "c". (Note that the verticle axis is less than one-fifth that of the verticle axis for curve "a"). Compare these with curves "a" to ascertain the dramatic decreases in irradiance through just 1.0 m of water. The benthic irradiance at the average spring unvegetated site ranges from 0.21 $cm^{-2} \cdot s^{-1}$ at 410 nm to 2.13 $cm^{-2} \cdot s^{-1}$ at 570 nm. The corresponding irradiance for vegetated sites is .349 and 2.37 respectively.

The relative photosynthetic action spectrum for Ulva taeniata, a typical shallow water estuarine green algal specie is plotted as curve "d" after Haxo and Blinks (1950) and Halldall (1974). The photosynthetic pigment complex of green algae is very similar to that of seagrasses. The useable light energies of highest photosynthetic efficiency fall between 400-500 nm and between 650 and 680 nm.

The potential PSR for the average spring vegetated and unvegetated site is presented as curve "e". This is simply the normalized (0-100) product of curves "c" and "d". The resulting potential PSR curve is a function therefore of incident radiation, total attenuation and the inherent spectral efficiency of "green marine plant" photosynthesis. This PSR spectral distribution

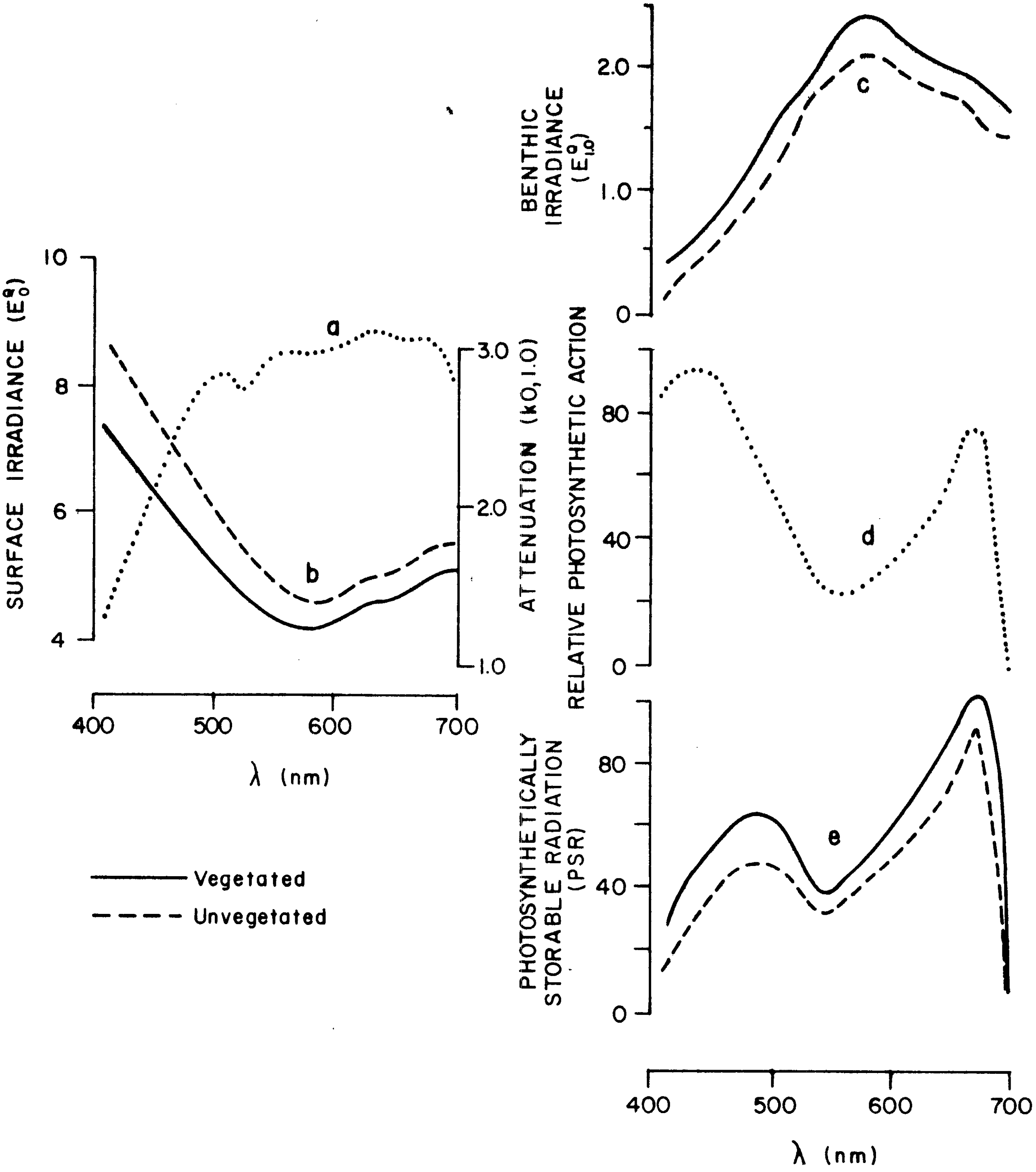

Figure 36. Relative potential spring PSR for vegetated and unvegetated sites. Solid lines represent vegetated areas, dashed lines represent unvegetated. (a) Mean spring surface irradiance at noon on a clear day, (b) total attenuation, (c) benthic irradiance at 1.0 m, (d) relative photosynthetic action spectrum, (e) relative potential photosynthetically storable radiation (PSR).

includes two peaks; one broadly centered about 490 nm in the blue end and the other extending from about 590 to about 690 nm. The blue peak has been shifted from about 440 nm in the action spectrum to about 490 nm in the PSR due to the combined effects of the high attenuation of violet and the low original violet insolation. Much of the difference between the mean vegetated and mean unvegetated PSR curves lies within the blue peak. The unvegetated blue peak is quite insubstantial (below 50) whereas the vegetated peak is from 12 to 16 relative units higher. In a marginal light environment this difference in potential storable radiant energy may be quite important. In the red peak region the difference between the two curves is much lower - from 5 to 8 units between 590 and 670 nm.

DISCUSSION

In the lower Chesapeake Bay the light available to benthic plants may not include great quantities of energy at the wavelengths which can be most efficiently used by those plants. The greatest loss of potential energy appears to be in regions of the spectrum most significant for photosynthesis. Whether the difference in light quality between vegetated and unvegetated sites is causal, and the direction of that causality cannot be determined by the work reported here. But, there does appear to be a negative correlation between light quality and the presence of seagrasses. A consideration of the direction of the causality may be irrelevant and analagous to asking the question, which came first, the chicken or the egg? That is, does the baffling effect of seagrasses cause settling of the fine suspended material thus reducing the scattering and absorption (lowering attenuation) and allowing more light energy to reach the benthos? Or, does a water body with relatively little suspended material provide a light environment suitable for seagrasses to survive, grow and thus baffle the water and maintain water clarity so light can continue to reach the benthos -- etc.?

Yes--to both. Ecosystems are comprised of dynamically interconnected biological and physical components which interact materially and energetically. The morphogenesis of an ecosystem from simple pioneer beginnings to a mature dynamically stable climax stage involves a continual reciprocal induction process between its physical and biological parts. This is achieved through sensitive feedback mechanisms. A mature ecosystem is a homeostatic entity capable of internal adjustment to a range of external conditions - within limits.

Let's define the benthic seagrass community and its overlaying water column an ecosystem. The water clarity is affected by the baffling effect of the plants (Ginsburg and Lowenstam, 1958; Scoffin, 1970; Wanless, 1981; Boynton and Heck, 1982) and the plants are certainly affected by the water clarity. A minimal water clarity is necessary for a seedling of seagrass to successfully colonize a suitable barren substrate and to grow vegetatively to some minimal size necessary to provide the baffling necessary to induce settling (Boynton and Heck's (1982) "critical bed size") and trapping of enough of the fine particles to clear the water column to maintain a tolerable light environment for continued growth. If during the early seedling stage the water clarity is insufficient than the ecosystem will not succeed to the self regulatory, homeostatic stage and a seagrass community will not be established.

A model of a seagrass ecosystem including the water column is shown in Figure 37 as an aid to the conceptualization of the sensitive feedback relationship between the seagrass community and water clarity. Of particular interest is the relationship between critical bed size and sedimentary baffling and attenuation.

Due to the dynamic nature of the littoral zone and coastline, normal variations in physical parameters may often exceed an established seagrass community's ability to adjust and survive on a local scale. Rapid recolonizing - both vegetatively and sexually (via seeds) would be expected *if water clarity permits*, but, if--due to nutrient enrichment and subsequent plankton blooms or particle runoff, or both--the light environment becomes unsuitable for the re-establishment of a new seagrass community, than the net seagrass ecosystem size may dimish despite survival of the established beds not affected by normal local disturbances. That is, since there appears to be thresholds below which the critical feedback between biological and physical parameters of the system cannot be established (critical bed size and a minimal light environment) -- replacement of seagrass communities lost due to normal processes may be impossible during periods of reduced water quality.

The historical pattern of increasing nutrient enrichment of the Chesapeake Bay from agricultural runoff and municipal sources and its presumed contribution to excess planktonic productivity (Heinle et al, 1980) coupled with the particulate load associated with runoff may have altered the water clarity enough to account for the decline in submerged aquatic vegetation via the mechanism discussed above. Our measurements of spectral irradiance and attenuation in the littoral zone of the lower Chesapeake would certainly lead us to believe that there isn't much light to spare--especially at the frequencies most efficiently used by green plants for photosynthesis.

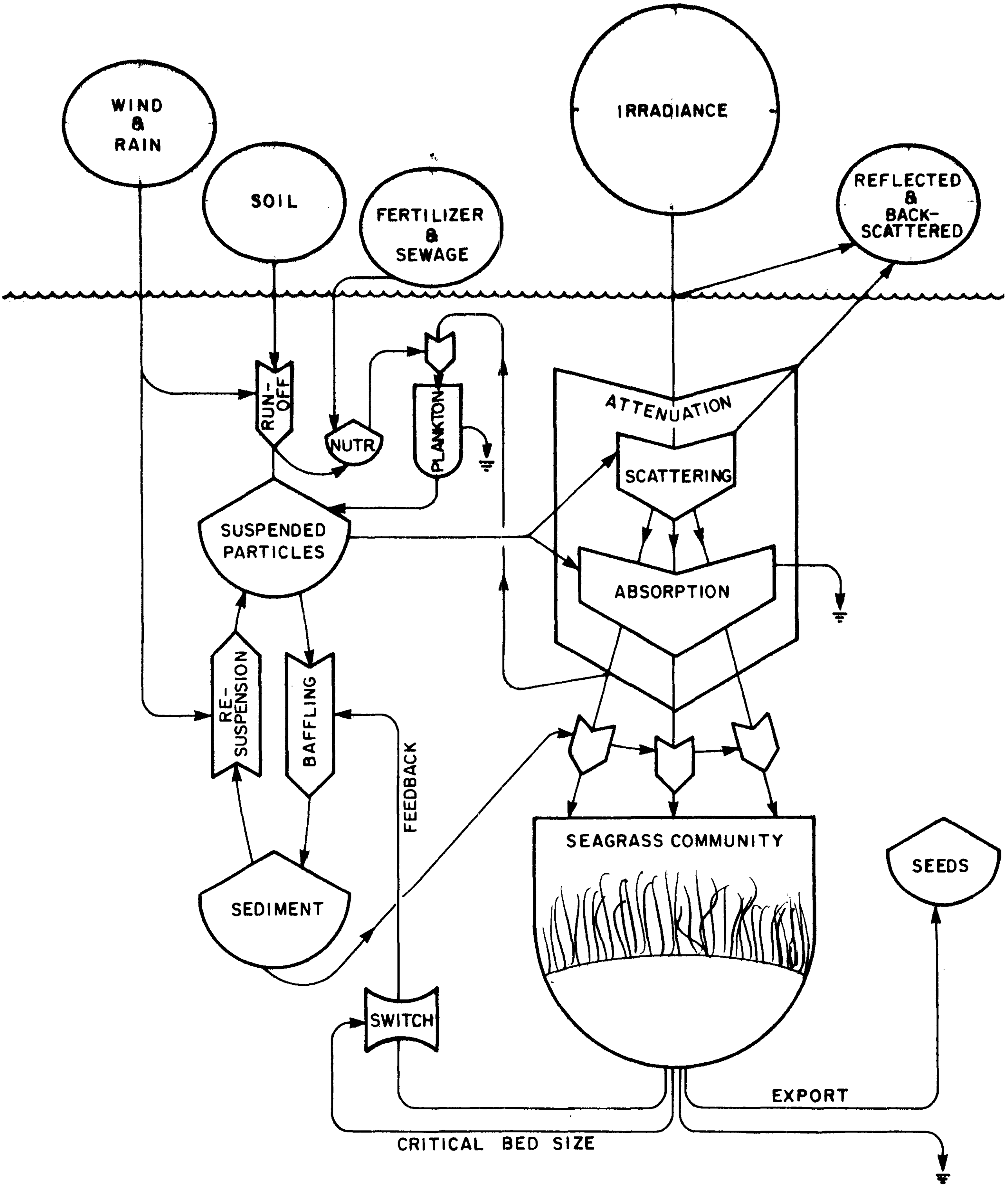

Figure 37. Conceptual model of critical feedback between biological and physical components of the seagrass ecosystem. (Symbols after Odum, 1983).

CONCLUSIONS

1. A seasonal pattern of spectral attenuation occurs in the shallow waters of the Lower Chesapeake Bay. Summer has the highest, spring and fall are intermediate and winter has the lowest.

2. The onset of high attenuation differs from year to year.

3. The seasonal pattern of attenuation differs between vegetated and unvegetated sites. The transition from low winter attenuation to high summer attenuation is more abrupt at unvegetated sites. There is a shorter high attenuation season at vegetated sites.

4. There is a significantly greater attenuation of violet light in unvegetated sites during spring, especially during May 1981 and March 1982. During May, 1981, 63% less violet light was able to pass through a meter of water at the average unvegetated site than at the average vegetated site; 88% less through 2.0 meters. (A difference of 1.0 m^{-1} at 441 nm).

5. The variability of violet attenuation was greater at unvegetated sites during the high turbidity seasons.

6. The pattern and magnitude of spectral attenuation differed on opposite sides of the Bay.

7. There is a reduction of potential photosynthetically storable radiation (PSR) at unvegetated sites. Less light is available at those wavelengths most efficiently used by green marine plants for photosynthesis.

8. A critical feedback between the biological and physical components of the seagrass/water column ecosystem must be established if the system is to maintain homeostasis.

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Chapter 4

SPECTRAL DISTRIBUTION AND ATTENUATION OF UNDERWATER LIGHT IN A TROPICAL MANGROVE CREEK AND SEAGRASS BED, LAGUNA DE TERMINOS, CAMPECHE, MEXICO: A PRELIMINARY ANALYSIS.[1,2]

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[1] This research was supported in part by the U.S. Environmental Protection Agency, Chesapeake Bay Program Grants R805975 and X003245-01 the College of William and Mary, Virginia Institute of Marine Science, Department of Wetlands Ecology.

[2] Contribution no.   , the Virginia Institute of Marine Science, Gloucester Point, VA 23062.

ACKNOWLEDGEMENTS

We want to extend thanks to all our Mexican colleagues who accepted and worked closely with our contingent of fourteen scientists, especially Ramiro Roman, Director of the Centro de Ciencias del Mar y Limnologia (UNAM), who provided us lodging, space, logistical support and a friendly atmosphere and Drs. Alejandro Yanez and Vivianne Solis of the Universidad National Autonoma de Mexico (UNAM) for their many contributions.

Thanks also to our fearless leader, Dr. J. W. Day, Jr. for organizing the expedition, and to Chris Madden and Linda Deegan for their help in the field.

We also thank Ms. Carole Knox and Nancy White for their expert secretarial services and Ms. Melissa van Tine for her editorial assistance.

INTRODUCTION

There has been a paucity of systematic experimental studies of spectral irradiance in marine environments (Jerlov 1976) and even fewer studies have been reported for estuarine waters (Wetzel et al. 1981; Champ et al. 1980; Pierce et al. 1981). None, to our knowledge, exist for Laguna de Terminos except a qualitative description of turbidity patterns (Day and Yanez-Arancibia 1980), depicting an east to west gradient corresponding with the predominate wind-driven circulation of lagoon water (Gierloff-Emden 1977).

The present work to describe the light environment, was designed as part of a Winter 1981 multi-disciplinary, U.S.-Mexican ecosystem study of the lagoonal seagrass beds. Wetzel et al. (1982) provide a description of the study site, Estero Pargo (see Fig. 1). Estero Pargo Creek drains an extensive mangrove swamp dominated by *Rhizophora mangle*, and the mouth opens on an extensive seagrass bed dominated by *Thalassia testudinum*.

METHODS

In situ measurements of downwelling 2π spectral irradiance were made as quanta nm^{-1} cm^{-2} s^{-1} at 12 biologically significant wavelengths ± 5 nm (410, 441, 488, 507, 520, 570, 589, 625, 656, 671, 694) using a Biospherical Model MER-1000 submersible spectroradiometer (Booth and Dunstan 1979) that had recently been calibrated using U.S. Bureau of Standards lamps. Each measurement taken was the mean of 250 individual scans made over a several-second interval to eliminate wave-crest refraction distortions, effects of non-random distribution of particles in the water column, and nonuniform sky conditions. Measurements were made at the mouth of Estero Pargo Creek over a *Thalassia testudinum* bed, at a site approximately 1 km up the creek off the U.N.A.M. Centro de Ciencias del Mar y Limnologia dock and at an intermediate midstream site. Measurements at the *Thalassia* site were made periodically throughout the daylight hours during 3 days coinciding with other studies (Wetzel et al. 1982). Measured depths ranged from .75 to 1.1 m. The diffuse vertical attenuation coefficient (k) was assumed to be an exponential function of depth (Jerlov 1976) and calculated for each wavelength as:

$$k_{(o,z)} = \frac{-\ell n\ (E_z/E_o)}{z}$$

where E_z is downwelling irradiance at depth z and E_o is insolation just above the water surface.

RESULTS

The downwelling spectral irradiance for noon and 1:00 p.m., both at the surface (incident irradiance) and at a depth of just less than a meter (benthic irradiance) are presented in Fig. 2 along with their corresponding attenuation coefficients, for a clear sky day at the *Thalassia* site. The noon

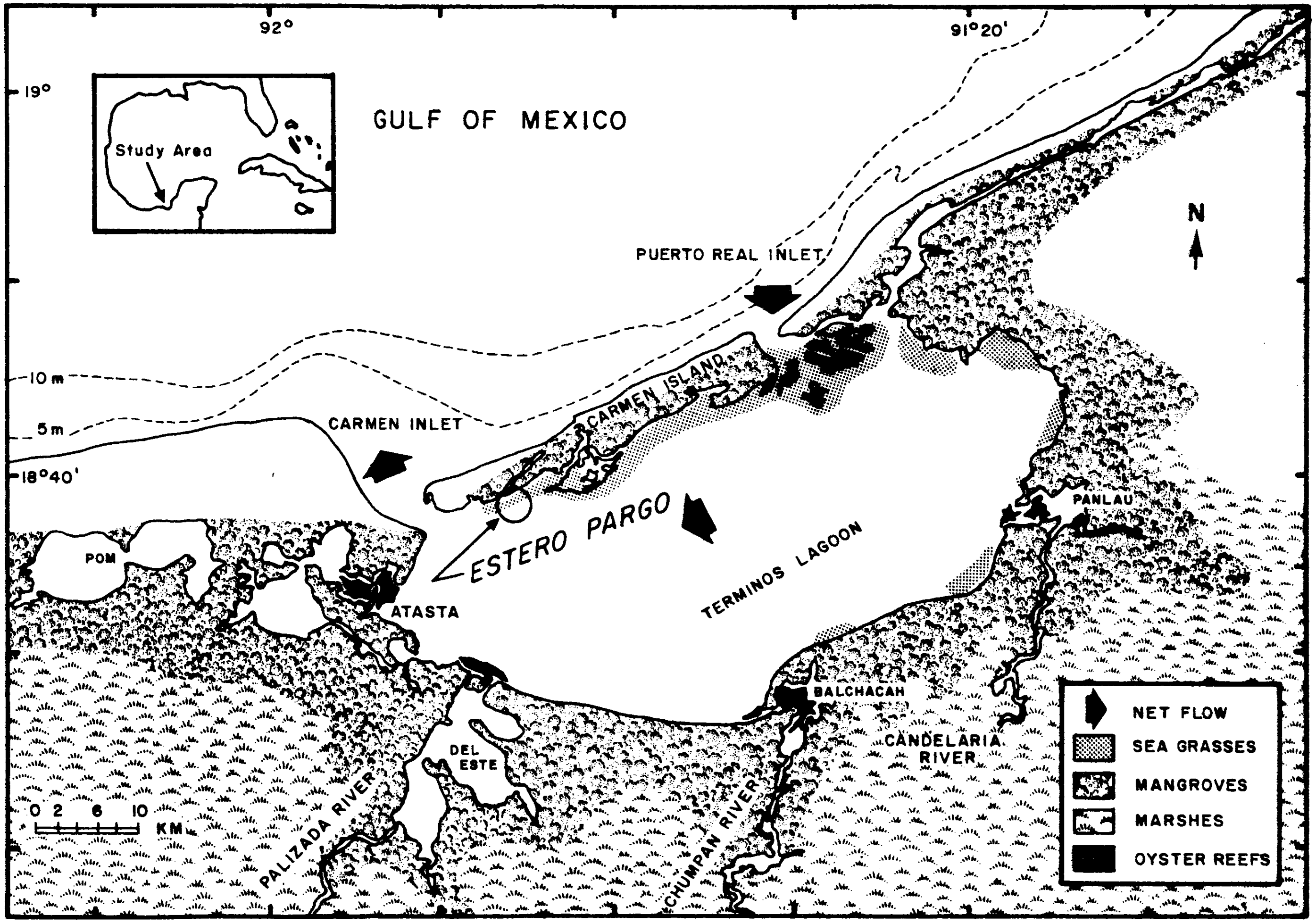

Figure 1. Map of Study Site

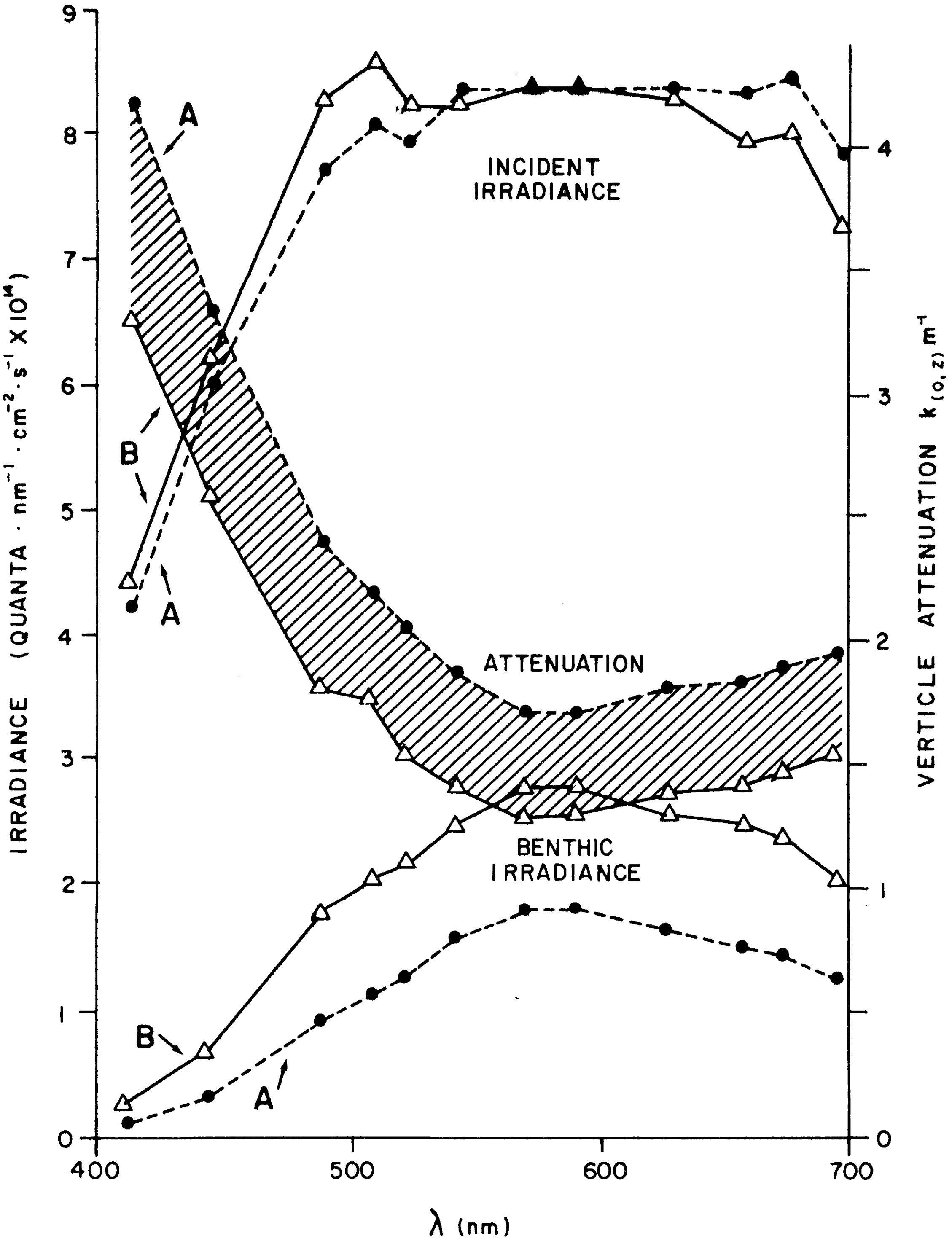

Figure 2. Downwelling spectral irradiance and spectral attenuation coefficients over a Thalassia testudinum bed off the mouth of Estero Pargo Creek on a clear day. (A) 1200 C.S.T., 10-15 knot sw wind, z = .88 m, (B) 1300 C.S.T., Calm, z = .85 m. Shaded area represents difference in attenuation which may be due to wind driven resuspension. (Each point is the mean of 250 scans).

TABLE I

		Daily Mean k			
Color	(nm)	Feb. 6	Feb. 8	Feb. 10	Grand Mean
Violet	410	3.64	3.48	5.27	4.13
	441	3.02	2.77	4.26	3.35
Blue	488	2.22	1.92	2.99	2.38
Green	507	2.05	1.76	2.74	2.18
	520	1.90	1.66	2.55	2.04
	540	1.75	1.54	2.34	1.87
Yellow	570	1.63	1.40	2.10	1.71
	589	1.66	1.40	2.08	1.71
Orange	625	1.86	1.52	2.26	1.88
Red	656	1.94	1.53	2.25	1.91
	671	2.06	1.58	2.34	1.99
	694	2.11	1.65	2.40	2.05
	PAR (400-700)	2.01	1.74	2.54	2.10
	n	2250	1250	500	400
	z(m)	.98-1.1	.85-.91	.76	.76-1.1
	t	1430-1730	1115-1400	1115-1200	1115-1730

measurement (A) was made during a 10-15 knot s.w. wind but an hour later (B) the wind had diminished. There is a sharp attenuation of blue and violet light below about 500 nm, while the lowest attenuation occurs in the yellow region between 550-600 nm. As indicated, although little appreciable difference exists between the two insolation curves, there is a considerable increase in attenuation, across the spectrum, between the windy noon and the calm 1:00 p.m. values (shaded area of Fig. 2). Noontime PAR (Photosynthetically Available Radiation) insolation is about 23 x 10^{16} quanta$\cdot$cm$^{-2}\cdot$s^{-1}, while benthic PAR irradiance is only 3-6 x 10^{16} quanta$\cdot$cm$^{-2}\cdot$s^{-1}.

Mean daily spectral attenuation coefficients are shown in Table I for three of five days at the *Thalassia* site off the mouth of the creek. Attenuation per meter of the shortest wavelengths ranged from a mean daily low of 3.64 to a high of 5.27, representing the highest values observed at the site. The mid-band yellow light (570-590) was least attenuated, ranging from 1.40 m^{-1} to 2.10 m^{-1}. The grand weekly mean attenuation coefficients represent the average of 4,000 scans. Climatic conditions ranged from windy and cloudy to clear and calm and covered the time period, 1115 to 1730 C.S.T. Depths ranged from .76 to 1.1 m. The grand mean (Fig. 3-(1), curve C) should well characterize spectral attenuation at this site during the "El Norte" season, as the 5-day measurement period was an interim between two such storm events.

Comparison of spectral attenuation coefficients along a 1 km upstream transect (Fig. 3-(1)) revealed a dramatic decrease of violet and blue light (400-500 nm). Attenuation was higher at all wavelengths upstream (A) than at the mouth (C), the difference assymptotically increasing to almost 3.0 m^{-1} at the violet end of the spectrum and approaching zero in the red region (650-700 nm). Midstream attenuation (B) was intermediate between the extremes.

DISCUSSION

As light passes through a body of water, its energy content and spectral quality are changed by absorption and scattering due to the water itself, dissolved substances, and suspended particles. The combined effect of these processes is termed attenuation. Backscattering, the change in direction of light propagation caused by diffraction, refraction, and reflection, is wavelength dependent in an irregular and complex manner. Scattering is of less importance in determining attenuation in shallow water since usually no more than 0.5% of the incident irradiance is back-scattered out of the medium (Clark and Ewing 1974). Lateral and forward scattering increase the path of light thereby exposing it to more absorption. The resulting absorption the thermodynamically irreversible process of photon conversion into thermal, kinetic, or chemical energy, e.g. photosynthesis), accounts for most of the apparent attenuation observed in natural bodies of water.

Much of the attenuation of long wavelengths is due to water itself (James and Birge 1938); the effect of sea salts is insignificant (cf., Clarke and James 1939). The energy of blue and red wavelengths is selectively absorbed by particles (Burt 1958; Prieur and Sathyendranath 1981). The shorter wavelengths also are strongly attenuated by dissolved organic material and

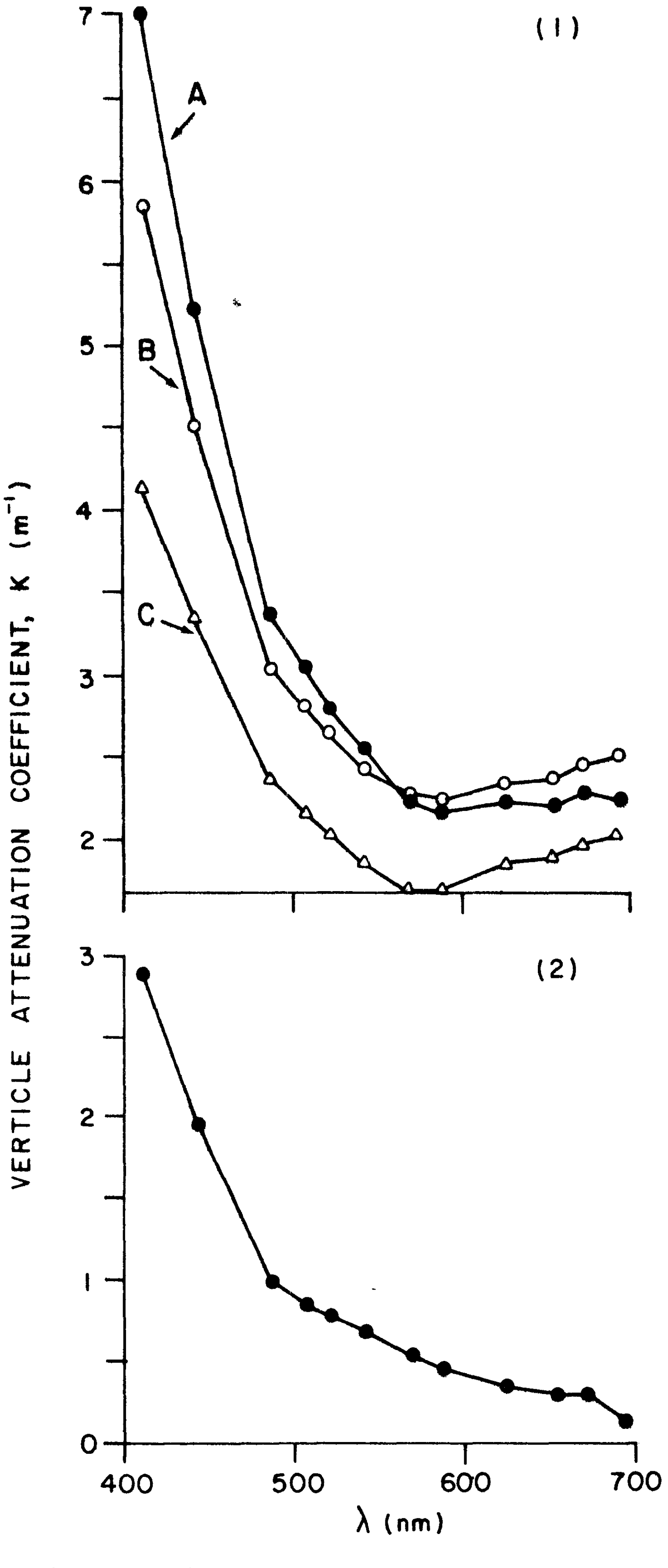

Figure 3. (1) Comparison of diffuse downwelling spectral attenuation coefficients at three sites in Estero Pargo Creek. (A) Upstream off the U.N.A.M. dock (B) midstream, (C) off the mouth in a Thalassia bed. Data for curves A and B represent the mean of 250 scans. Curve C represents the mean of 4000 scans taken during 3 days. (2) The difference in downwelling spectral attenuation coefficient between the upstream site and the mouth of Estero Pargo Creek. The curve represents the arithmetic difference between curves A and C, Fig. 3-(1).

complexes of this material, or Gelbstoff ("yellow substance"), the collective name given these complexes by Kalle (1966). Gelbstoff is formed from carbohydrates produced by the decomposition of organic matter. At Estero Pargo much potential organic material is provided in the wet season by mangrove litter fall, which ranges from about 1 to 4 $gm \cdot m^{-2} \cdot day$ and takes several months to decompose (Day and Yanez-Arancibia 1980). Further, absorption in the blue and red regions of the spectrum by chlorophyll-bearing phytoplankton also contributes to the total spectral attenuation that characterizes a specific body of water.

Figure 4 is a schematic representation of spectral energy flow through a marine environment. The relative proportions of the various constituents discussed above determine the ultimate light quality and light quantity available to power photosynthetic reactions. The diagram uses the typical noon clear sky irradiance distributions measured above and below water at the Estero Pargo seagrass site. Typical curves of spectral absorption due to dissolved organic matter (including Gelbstoff), non-green particulate matter, chlorophyll and pure seawater are shown impinging on the path of light from surface to bottom. Rain and wind ("Nortes") cause runoff with increased dissolved organics and resuspension of particulate matter and benthic chlorophyll-bearing microalgae, thus increasing particle scattering, absorption and consequently attenuation. The specific spectral energy distribution at a depth thus depends on both the physical and biological characteristics of the water column and the forcing functions impringing on the system.

In Estero Pargo Creek the dominating influence seems to be from dissolved organics. If the spectral attenuation coefficients for the mouth of the creek are subtracted from those at the upstream site (curve A - curve B, Figure 3-(1)), the resultant curve (Fig. 3-(2)) may represent the attenuation due solely to the constituents of the water column present upstream but not downstream. If one compares the resultant curve with the specific absorption curves in Figure 4 it can be seen that it matches the shape of the dissolved organic curve very closely. The extreme attenuation of the short wavelengths decreases downstream as the diluting effect of the waters from the lagoon become more apparent. The creek waters no doubt affect the light environment in the grassbed at its mouth, contributing to the high violet-blue attenuation.

An example of the effects of resuspension caused by wind can be seen in Figure 2. The shaded area of the figure represents the decreased attenuation corresponding to a decrease in wind from 10-15 knots to calm during a 1 hour interval. Both sets of measurements were taken during a clear sky. Notice that although the incident irradiances at the mid-spectral region (550-625 nm) are almost identical, the attenuation coefficients and benthic irradiances differ significantly. This is probably due to resuspended particulate matter and benthic micro-algae.

SUMMARY

Laguna de Terminos is a relatively large tropical estuary (2500 km^2) that supports one of the most extensive nearshore fisheries in the Gulf of

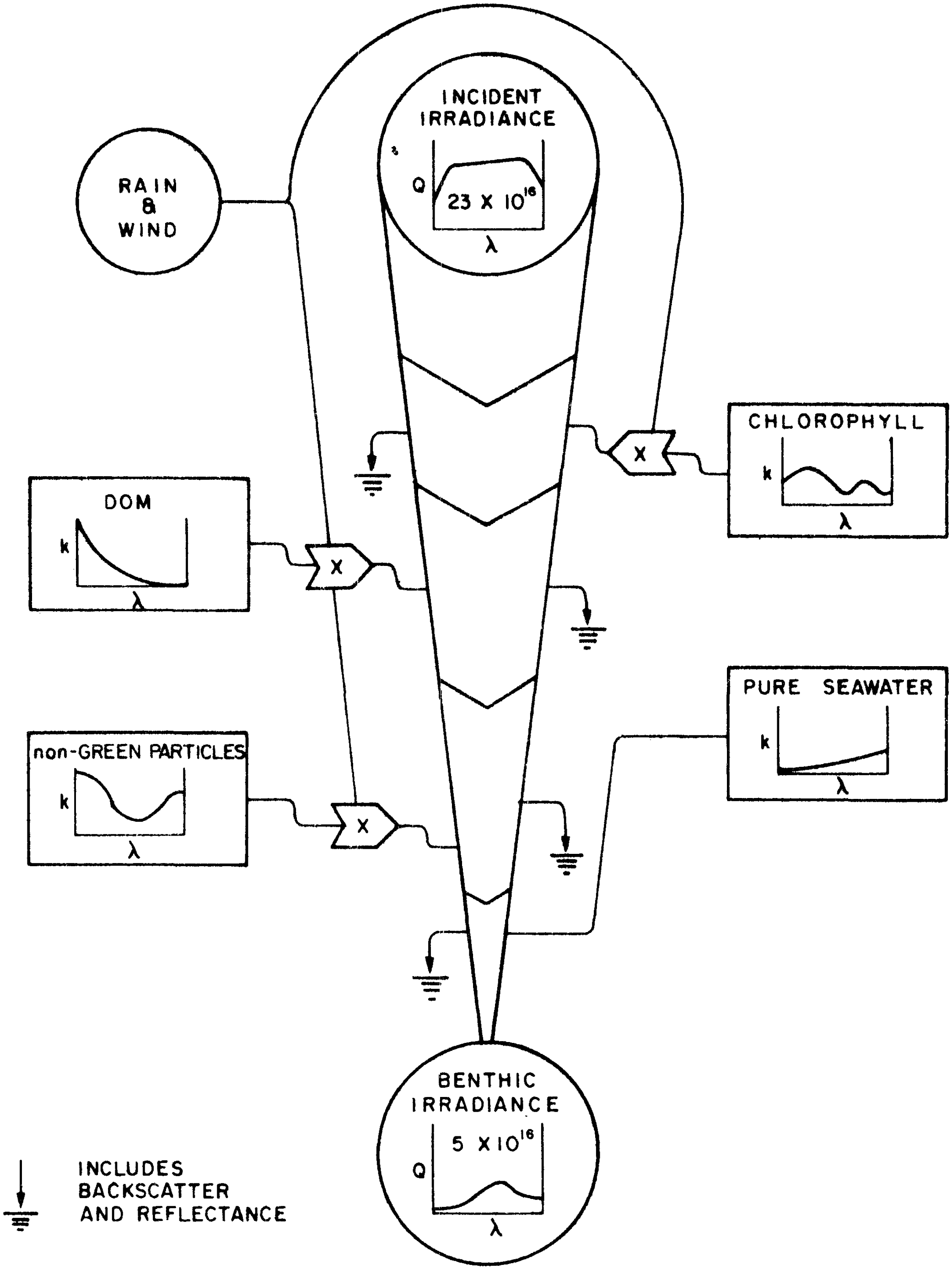

Figure 4. Schematic representation of spectral attenuation through an estuarine water column. (Q = quanta$\cdot$nm$^{-1}\cdot$cm$^{-2}\cdot$s^{-1}; λ = wavelength, 400-700 nm; k = specific absorption coefficients, m^{-1}; numbers for irradiance are PAR integrals, quanta$\cdot$PAR$\cdot$cm$^{-2}\cdot$s^{-1}. Energy circuit language after Odum 1972; specific absorption curves redrawn from Prieur and Sathyendranath, 1981).

Mexico. In part, the support is provided by the extensive seagrass beds (Thalassia testudinum) occupying the shallower lagoon areas. As part of a joint U.S.-Mexico study of these vegetated communities, we present our preliminary analysis of submarine light quality and quantity and several factors possibly controlling light energy distribution in this estuarine environment.

At the Estero Pargo study site, which represents an area of seagrasses that are probably light-stressed (Wetzel et al. 1982), there is a significant attenuation (2 to 4 m^{-1}) of the photosynthetically important short wavelengths, 400-500 nm. Incident noon PAR irradiance was about 23 x 10^{16} quanta cm^{-2} s^{-1} and benthic irradiance (z=1m) was 3 to 6 x 10^{6} quanta cm^{-2}. s^{-1}. In the adjacent mangrove swamp channel (Estero Pargo Creek) there is extreme blue-violet attention which is probably due to dissolved organics originating from mangrove litter fall and decomposition.

At the Thalassia study site, wind events, even relatively mild conditions (10-15 kts), effect both light quality and quantity reaching the plant canopy. Since the greatest attenuations occurred in a spectral region (400-525 nm) which is extremely important for absorption by chlorophylls and accessory pigments in higher plants, the observed benthic irradiance distribution has significant implications for seagrass community productivity.

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