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Light and Submerged Macrophyte Communities in Chesapeake Bay: A Scientific Summary

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

by

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SECTION I

INTRODUCTION

The initial focus of submerged aquatic vegetation (SAV) research in the U.S. Environmental Protection Agency (EPA), 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; the dominant species in the lower Bay are Zostera marina and Ruppia maritima. Studies 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 because of 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 limit or control 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. This work is among the first studies in North America to investigate light quality as a major environmental factor affecting the survival of sea grasses.

The overall objectives of this later work were to evaluate more precisely 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 indicate 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, den Hartog and Polderman 1975, Williams 1977, Wetzel et al. 1982).

BACKGROUND

A major goal of CBP-SAV research was to investigate the response of Bay grasses to various environmental variables. Studies centered on the four dominant submerged aquatics 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 attaining 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 grasses, as well as the entire 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 address environmental regulation and control of SAV communities focused on nutrient regulation [primarily nitrogen as ammonium (NH_4) and nitrate

(NO₃), light and photosynthesis, and other biological and physical-chemical factors influencing light energy distribution.

The results of studies in the lower Bay communities suggest a net positive response to short-term nutrient additions and support the observation by others that these communities are nutrient limited (Orth 1977). The most consistent positive response is associated with Ruppia dominated communities, and the most variable is associated with the deeper Zostera community (Wetzel et al. 1979). In contrast, Kemp et al. (1981b) 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, suggest that light and the environmental factors controlling available light are key factors governing plant community growth and productivity. Light-temperature-turbidity regimes and their interaction may explain, in large part, observed variability in distribution and abundance. Changes in these parameters, governed by either natural or man-induced events and, perhaps, determined over longer time scales, influence variation in distribution and abundance in Chesapeake Bay ecosystem as a whole.

Throughout 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 suggest different physiological responses to and control by local environmental conditions, principally light.

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. The experiments were ¹⁴C uptake studies in which 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 percent of ambient light to determine the effect of light quantity on photosynthesis. Experimental designs comparable with these were also conducted for upper-Bay species. Results are discussed later in this paper in Section 3.

In conjunction with these studies, measures of leaf area index (LAI) were also conducted. Physiologically, the photosynthesis-light relationship determines the light levels at which SAV can grow and reproduce, that is, succeed. A greater leaf area exposed to light results 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 per sediment surface area) estimates maximum leaf density and thus potential area available to intercept 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 to evaluate potential morphological adaptation of the plants to various light environments. To complement these specific ¹⁴C studies and LAI measures, field studies were completed to determine the effect of in situ light reduction through artificial shading. Light reductions of 70 to 20 percent of ambient were used. The results of these studies support the

hypothesis that total community metabolism is governed by, and is 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. 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 that determined those environmental variables controlling 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: the epiphytic community as a primary producer and food source, and as a competitor with the vascular plant community for available light. Experiments completed suggest that the epiphyte community at times dominates metabolism of the community and limits light available for vascular plant photosynthesis. What remained to be determined was what environmental conditions favor colonization, and at what point does the resulting colonization stress the vascular plant.

These various research activities provide a data and information base that serve management needs and identify specific research areas where additional information is required for integration and synthesis. The work proposed in the later 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 is directed to our current state of understanding of light energy properties and distribution in Chesapeake Bay and to the relation of this information to past and current knowledge about SAV community growth and survival.

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 macrophyte primary production. Plants absorb light energy for the process of photosynthesis, converting water and carbon dioxide into organic compounds. White light (visible sunlight) is composed of a spectrum of colors that are used selectively by green leaves based on the plant's specific pigment complexes. Chlorophyll requires mainly red and blue light for photosynthesis; these wavelengths are absorbed, and the green and yellow bands are reflected. The accessory pigments also absorb in the blue region.

As light penetrates the water column, the 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 the scattering of light. Selective absorption and scattering by these factors result in attenuation of specific light wavelengths causing a "color shift" (Kalle 1966, Jerlov 1976). Scattering, the change in direction of light propagation, 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 other primary producers for the same wavelengths of light--the red and blue bands.

The temporal and spatial distribution of particulate materials and dissolved substances are largely determined by climatic variables and biological processes. 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 relationships and correlations among the above data and other available information. The measurement and collection of light, water quality 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). There are even fewer studies reporting data for estuarine waters, Chesapeake Bay being no exception. Burt (1953, 1955a, b), using a shipboard spectrophotometer, analyzed filtered seawater samples from 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) report an observed "orange-shift" for measurements made 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 in and around SAV habitats.

Broad band (PAR) transmittance was determined with a Montedoro-Whitney in situ combination beam transmissometer and nephelometer. The transmittance data were used to calculate the attenuation coefficient "defined as the absorption coefficient plus the total scattering

coefficient" (Jerlov 1976, Kiefer and Austin 1974). van Tine (1981) found significant correlations between absence of submerged aquatic vegetation and low transmittance values in an estuary in the Gulf of Mexico.

Total particulate matter (TPM), particulate organic matter (POM), particulate-ATP, particulate chlorophyll a, particulate inorganic matter (PIM) were monitored in light spectral studies. These various measures were used to estimate phytoplankton, zooplankton, detritus, and inorganic fractions of the TPM.

Wind velocity and direction, water current velocity, tidal stage and depth were determined concurrently with the other measures. Kiley (1980) suggests a close relationship between wind and current for the York River. In an effort to explain turbidity values, Williams (1980) calculated significant positive correlations between wind and turbidity for upper-Bay subestuaries. Ginsburg and Lowenstam (1957) and Scoffin (1970) showed a baffling effect of SAV on currents that caused particulate matter to settle out, generally improving the local light environment. Collection and analyses of these data formed the basis for characterization of the natural light environment and of the factors that are principal controls.

Various lines of evidence, as discussed earlier, suggest light in general 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. In the later phases of CBP-SAV research, both field and laboratory studies were designed and carried out in a more quantitative sense on photosynthesis-light relations in Chesapeake Bay SAV communities.

For the field approaches, the entire SAV community and its interactions were included in 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 possible situations where water quality deteriorates to the point where light penetration is reduced. The purpose of these studies is to estimate at what point, relative to light quantity, the SAV communities would die out. 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). With this design, 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, or more specifically light-energy distribution, as a major environmental variable controlling SAV distribution, growth, and survival was postulated. The intent of the remaining sections of this report is to provide the general characteristics of light in natural aquatic systems with emphasis on Chesapeake Bay; to summarize the research results throughout the Bay relative to light and Bay grasses; and to discuss the potential for light or light-related casualty of Bay grass declines.

SECTION 2

LIGHT IN CHESAPEAKE BAY

GENERAL CHARACTERISTICS OF ESTUARINE OPTICAL PROPERTIES

The study of the interaction of solar energy with estuarine waters necessitates not only an understanding of the properties of light and water, but also of 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 packs or quanta (Q) of energy called photons. The energy content (\mathcal{E}) of each quantum is directly proportional to the frequency (ν),

$$\mathcal{E} = h\nu$$

and indirectly proportional to the wavelength (λ),

$$\mathcal{E} = \frac{hc}{\lambda}$$

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 complete spectrum of downward irradiance for incoming solar radiation at the top of the atmosphere, at sea level, and at several water depths is illustrated in Figure 1a. Most of the energy reaching the earth's surface is contained within the shorter wavelengths (0.4 to 1 μ or 400 to 1,000 nm¹). Not surprisingly, this region includes the wavelengths of greatest biological importance, that is, 400 to 700 nm, the photosynthetically active region of the spectrum termed PAR or PHAR. There is almost no energy outside the PAR region at a depth of 1 m. Most of the "missing" energy has been converted to heat by absorption. Only four to 11 percent of incident irradiance between 300-700 nm is reflected from the surface or backscattered out of the water column (called albedo) (Clark and Ewing 1974).

The properties and concepts in optical oceanography are usually divided into two mutually exclusive classes, inherent and 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.

As light passes through the water column, its energy content and spectral quality are changed by absorption and scattering due to 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), measured with the beam transmissometer, generally shows high attenuation at both ends of the PAR. Since α is an aggregated coefficient, it is informative to consider the component parameters that cause the observed attenuation.

¹ 1 nm = 10⁻³ μ m = 10⁻⁹ m

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. Absorption is a thermodynamically irreversible process wherein photons are converted to thermal, kinetic, or chemical energy; photosynthesis is an example. Much of the attenuation in 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 Figure 1). The effect of sea salts on attenuation is insignificant. Pure water or pure seawater show a constant light attenuation. 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 attenuation due to dissolved substances. By subtracting this from the total attenuation coefficient of non-filtered seawater, he was able to calculate the light attenuation due to particulate matter. The energy of blue and red wavelengths is selectively absorbed by particles, as shown in the example given by Prieur and Sathyendranath (1981) (Figure 1b). The shorter wavelengths are also attenuated by yellow substance or Gelbstoff (see Figure 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, that is, the measurement of in situ radiant flux. Irradiance (E) (the flux of light per unit area) is usually collected with a flat circular opal glass (or plastic) diffuser (2π collector). The diffuser is designed so that light received from all angles is transmitted to the sensor according to Lambert's cosine law. In other words, 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_0) is generally in the range of 0.75 to 0.85 downwelling. 2π 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 (spectral irradiance). A family of downwelling spectral irradiance curves, in quanta, is shown in Figure 2 for a Zostera marina bed on the eastern shore of Chesapeake Bay. This figure shows that both total light energy and that of specific wavelengths are lost with depth. At 0.1 meter, for example, a lot of surface insolation, particularly in the photosynthetically important 400-500 range, has been lost.

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 (chlorophyllous pigments). Figure 1b illustrates how combinations of water column

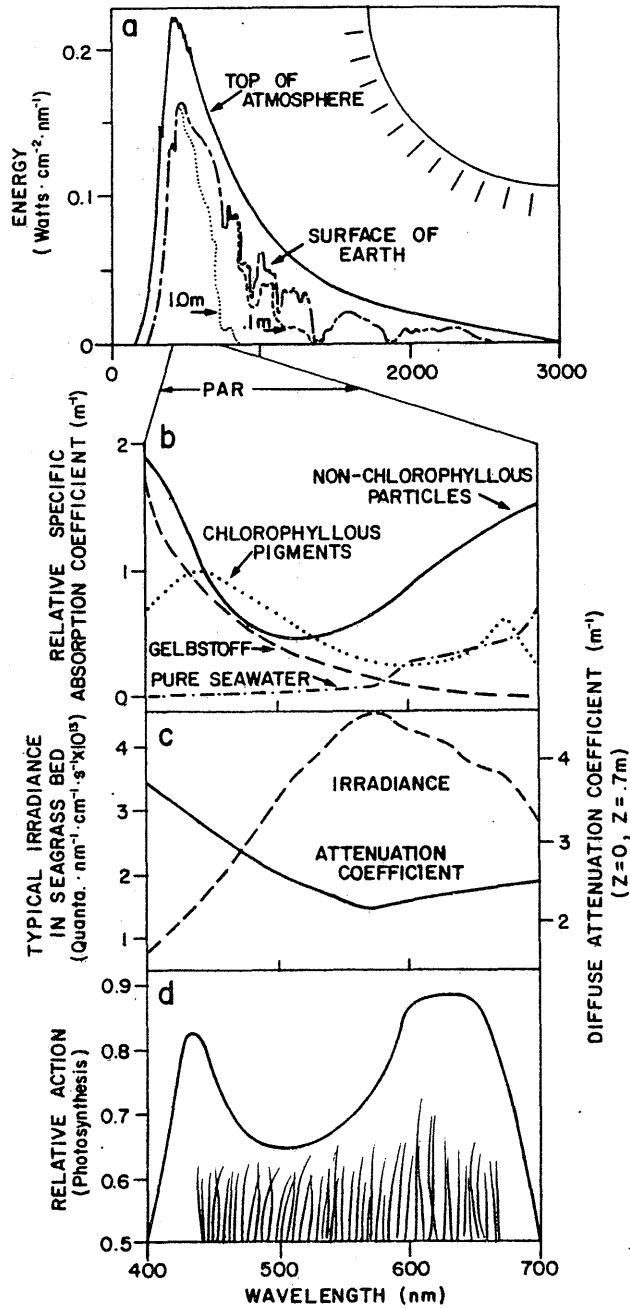


Figure 1. Theoretical path of light from top of atmosphere to benthic estuarine macrophytes. (a) Spectral energy distribution of light at top of atmosphere, at the surface of the earth, and at two depths in the ocean on a clear day (redrawn from Jerlov 1976 and Gates 1971). (b) Relative spectral absorption of various constituents of estuarine waters (redrawn from Prieur and Sathyendranath 1981). (c) Typical spectral irradiance and attenuation in a Chesapeake Bay seagrass bed (Wetzel et al. 1981). (d) Mean quantum action spectrum for higher plants. 1.0 represents the highest photosynthetic response observed by Inada in an individual species (redrawn from Inada 1976).

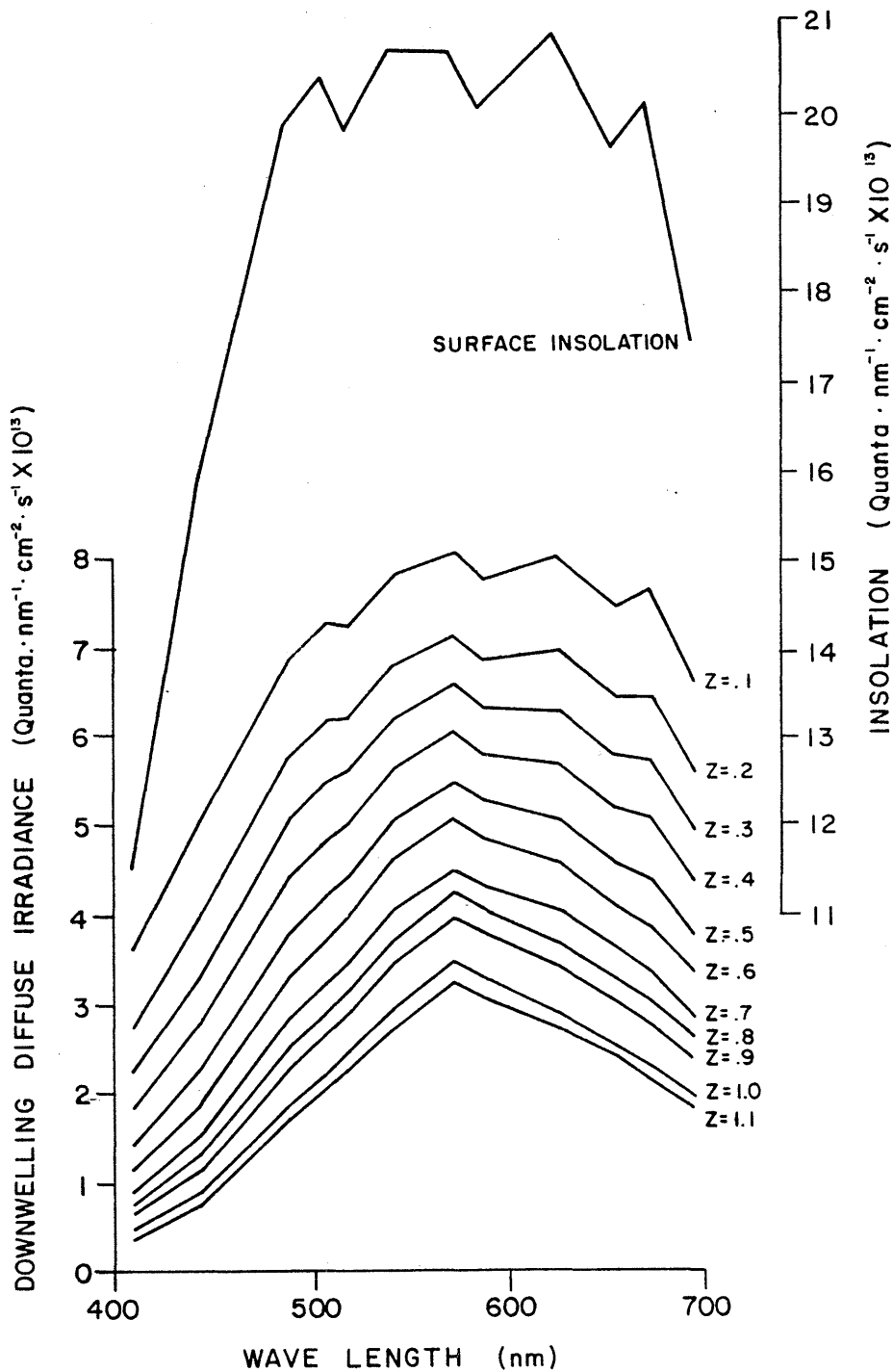


Figure 2. Downwelling spectral quanta irradiance at the surface and at several depths (Z) above the canopy of a *Zostera marina* bed on the eastern shore of lower Chesapeake Bay (Vaucluse Shores) at 1230 E.S.T. on a cloudy April day. The scale for the insolation is on the right (Wetzel et al. 1982).

constituents 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 coefficient² (K_d) expresses the decay of irradiance as an exponential function,

$$k_d = \frac{-\ln \frac{E_2}{E_1}}{(z_2 - z_1)}$$

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 measurement depths in meters. The units of K_d are m^{-1} .

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 measures the effects of inherent properties of the layer of water on the propagation of light through that distance. Because 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 or λ) is a particularly useful parameter for comparing underwater irradiance between water bodies, seasons, and wavelengths. Because K_d varies with depth 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 grass-bed. The distribution is a result of the additive effects of the attenuations and scattering of seawater, dissolved substances, non-chlorophyllous particles, and phytoplankton (see Figure 1b). Pierce et al. (1981) determined, by step-wise multiple linear regression, that chlorophylls 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 (α) derived from the beam transmissometer measure two different properties with no simple relation. Calculation of α is based on a spectrally-defined and emission-controlled collimated light source that 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 35.0 meters.

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

² Often incorrectly termed extinction coefficient.

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 by measuring its photosynthetic response. The action spectrum in this figure is normalized to the highest observed photosynthetic rates for red light. 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 because of 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 plankton 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 land runoff, currents, and waves. In shallow areas, this action increases resuspension. 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, average submarine light conditions may be partly 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). 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 between three to six percent at angles greater than 30° from the horizon. Below 30°, the reflectance increases dramatically up to 40 percent at 5°. Reflection below 30° is wavelength dependent. The longer waves are reflected more because 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 differences in depth. These are, of course, highly idiosyncratic for specific systems (Burt 1955b, Scott 1978).

LIGHT ATTENUATION IN CHESAPEAKE BAY

A comparison of diffuse downwelling spectral attenuation coefficients reported for Chesapeake Bay and its tributaries is presented in Figure 3 along with Jerlov's (1976) most turbid coastal water classification curve (Type 9). For Chesapeake Bay, the earliest measurements of $k_d(\lambda)$ were made by Hurlburt (1945) (Figure 3a). His values fall in the lower range of more recent in situ measurements. The shaded areas in Figure 3a represent the range of values measured by Wetzel et al. (1982) from March through

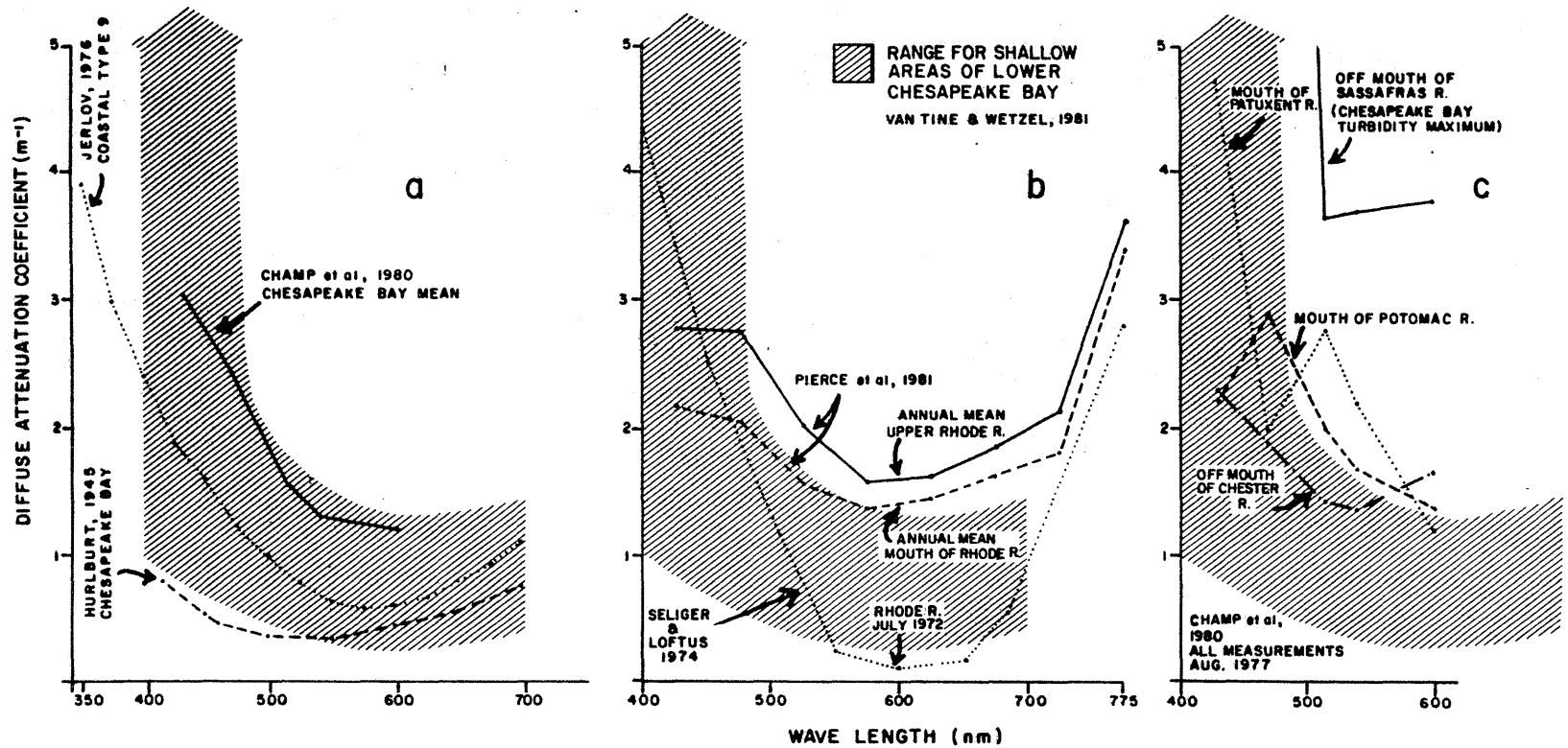


Figure 3. Comparison of diffuse downwelling spectral attenuation coefficients for Chesapeake Bay with Jerlov's most turbid coastal classification. (a) Plotted from tables in Jerlov 1976; Hurlburt 1945; Champ et al. 1980 (b) Plotted from table in Pierce et al., 1981 and calculated from 4π irradiance curves in Seliger and Loftus, 1974 (c) Plotted from tables in Champ et al., 1980.

July, 1981, in shallow regions of the lower Bay ($\ll 3$ m). Jerlov's curve falls in these observed ranges, showing that the data fall within the range of the most turbid coastal waters. Champ et al. (1980) conducted a light characterization survey of Chesapeake Bay during August, 1977. Their mean values are shown in Figure 3a along with their specific site measurements in and near the mouths of the Sassafrass, Patuxent, Potomac and Chester Rivers in Figure 3c. Their mean values fall within the upper ranges measured in the lower Bay (Wetzel et al. 1982).

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 are plotted in Figure 3b. The upriver station was found to be consistently more turbid, presumably because of its proximity to autochthonous 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 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). Seliger and Loftus (1974) derived curves from $4\uparrow$ irradiance measurements in the Rhode River that generally agree with the measurements of Pierce et al. (1981), except in region 500 to 700 nm. Their measures fall within the observations made for the lower Bay (Wetzel et al. 1982). The differences noted in the 500 to 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 to 600 nm. Wetzel et al. (1982) observed similar, very high attenuations in the blue region (400 to 500 nm) at lower-Bay sites during a spring runoff event following a major rain storm. The attenuation of green wavelengths (~ 500 to 550 nm) in the summer 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). Figure 4 illustrates the lower Bay sampling stations.

A summary of the recent Chesapeake Bay data on diffuse downwelling $2\uparrow$ irradiance attenuation coefficients indicates a severe attenuation of light energy in the photosynthetically important (400 to 500 nm blue, and 700 to 775 nm 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 lower-Bay sites during spring runoffs (Figure 5). 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.

Comparison of Light Attenuation in Vegetated and Unvegetated Sites of the Bay

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 (Wetzel et al. 1982). The specific question, what are the light quality differences between vegetated

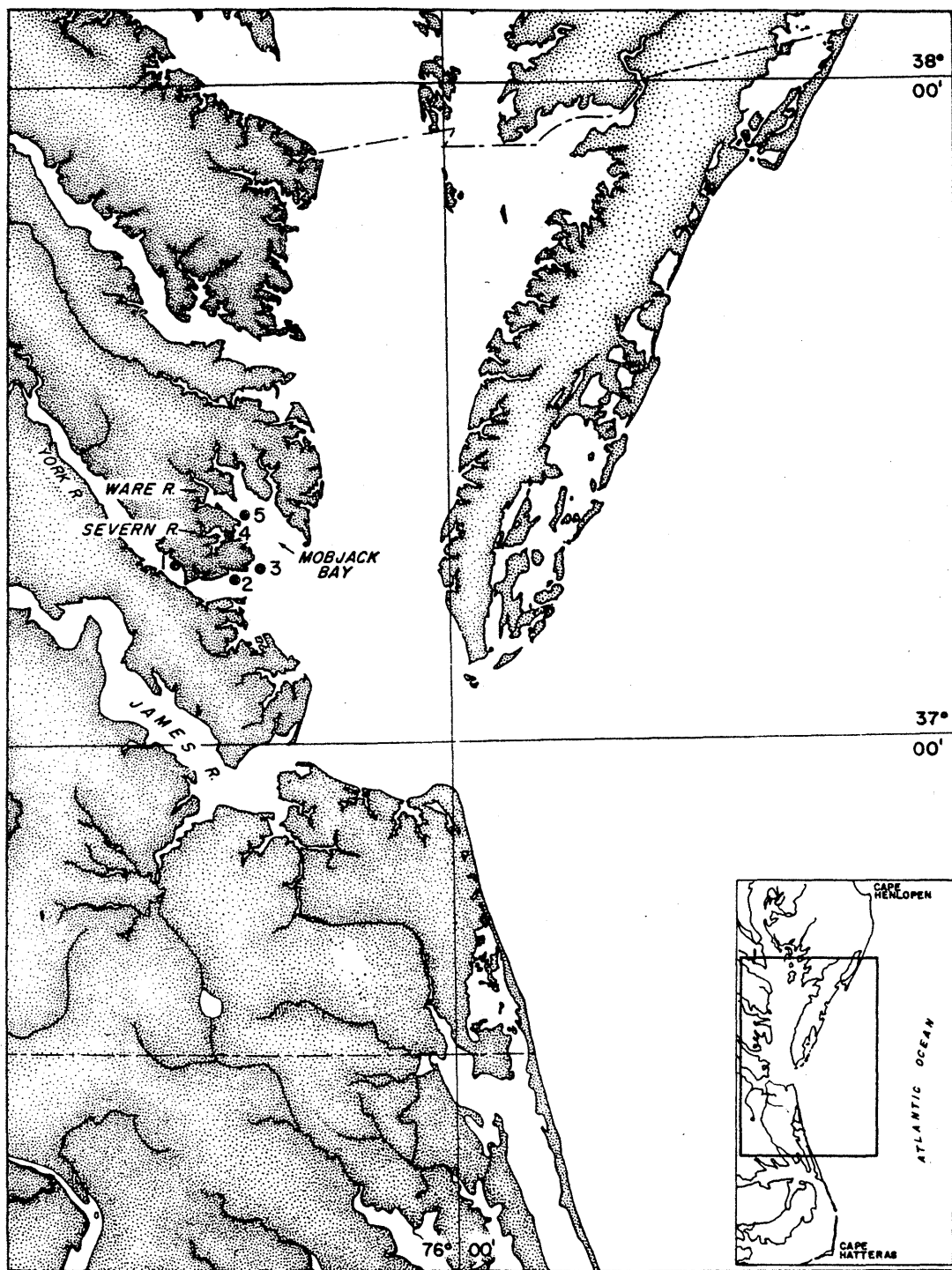


Figure 4. Locations of lower Bay stations (Wetzel et al. 1982).
 (1) Mumfort Is., York R. (2) Allen's Is., York R.
 (3) Guinea Marshes (4) Mouth of Severn R., Mobjack Bay
 (5) Four Point Marsh, Ware R. Mobjack Bay.

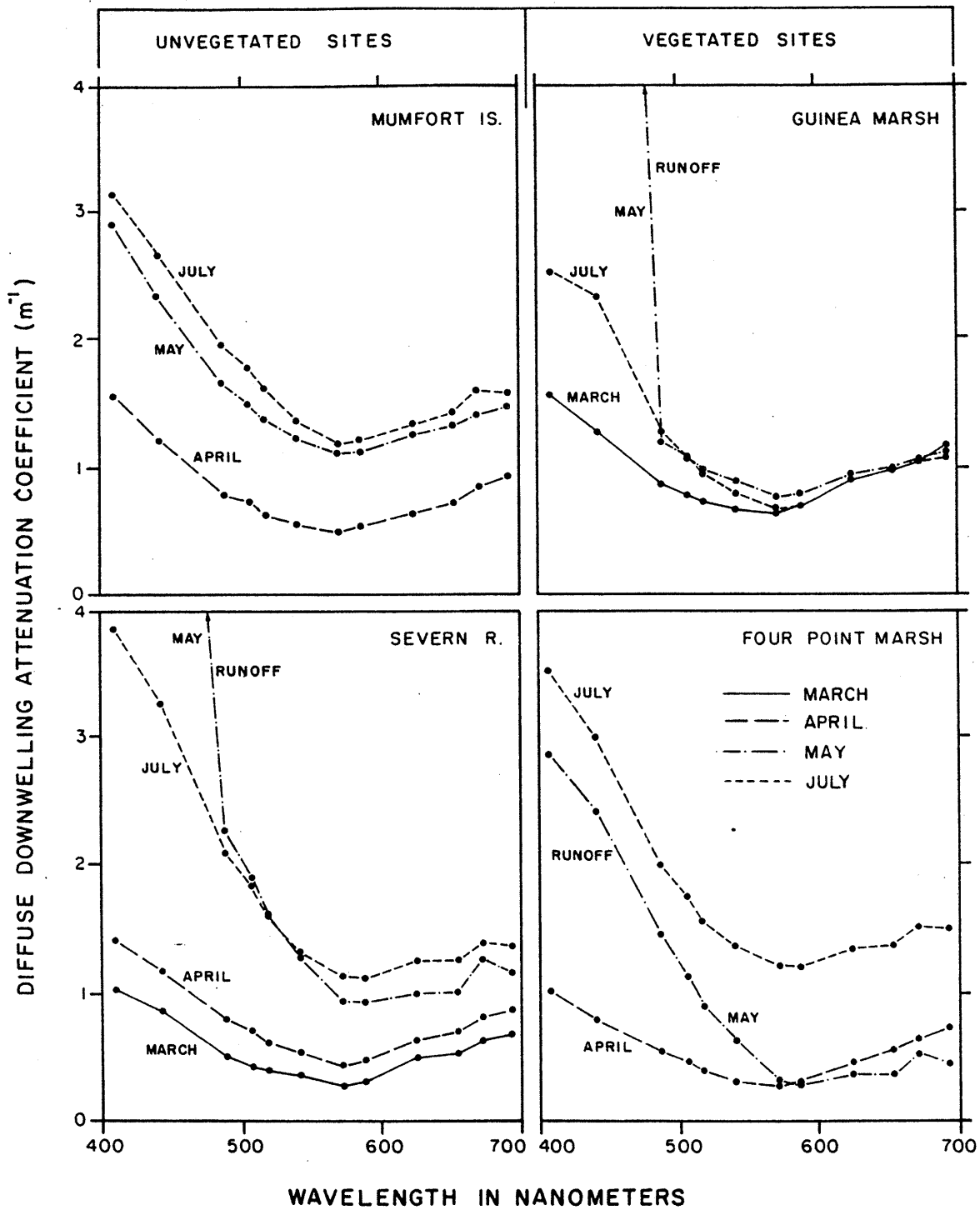


Figure 5. Mean monthly diffuse downwelling spectral attenuation coefficients for vegetated and unvegetated sites in the lower Chesapeake Bay. All coefficients calculated for the depth interval 0.1 to 0.5 m. Mumfort Island (York River) and Severn River sites: unvegetated. Guinea Marsh and Four Point Marsh (Ware River) sites: vegetated (from Wetzel et al. 1982).

and unvegetated sites, was addressed. The sites (Figure 4) were chosen because of their varied vegetational histories (Orth et al. 1981). The Mumfort Island (York River: Station 1) and Severn River (Station 4) sites are presently unvegetated. The Guinea Marsh (Station 3) and Four Point Marsh (Ware River: Station 5) sites have seagrass beds. Both the Severn River and Four Point Marsh sites are affected by agricultural runoff (C. Hershner, personal communication). The Allen's Island site, Station 2, is presently unvegetated, but has recently been replanted by Orth and associates. Twelve wavelengths (410, 441, 488, 507, 520, 540, 570, 589, 625, 656, 671, 694 nm \pm 5 nm) and total PAR were analyzed at depths of 0.1 and 0.5 m. Downwelling irradiance (E_d) was measured as Quanta $\text{nm}^{-1} \text{cm}^{-2} \text{sec}^{-1}$, each reading representing the mean of 250 scans. Diffuse downwelling spectral 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} (Figure 6). A clear seasonal pattern of extreme attenuation of 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 (Figure 6). This was due to a lower attenuation in the 500 to 700 nm region of the spectrum at vegetated sites (Figure 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) was grouped with the unvegetated sites having higher attenuation (Figure 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 analyses were the reduced attenuation in the 500 to 700 nm region at vegetated sites during May.³

Kaumeyer et al. (1981) measured a significant difference in PAR attenuation coefficient inside and outside SAV beds at Todds Cove, Md. during July, August, and September, 1980. The vegetated areas were from 0.4 m^{-1} to approximately 2.0 m^{-1} lower. Significant differences were not found in attenuation inside and outside grassbeds at the Parson Island study site. Table 1 summarizes the results of their studies.

Historical Data Bases and Optical Properties of Chesapeake Bay Waters

Most of the historical light data for 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 (Figure 7). Transparency has decreased since the 1930's,

³ Subsequent measurements and analyses extend and corroborate this conclusion. Not only is the mean violet and blue attenuation lower in vegetated sites but the variation is also less (see Wetzel et al 1982).

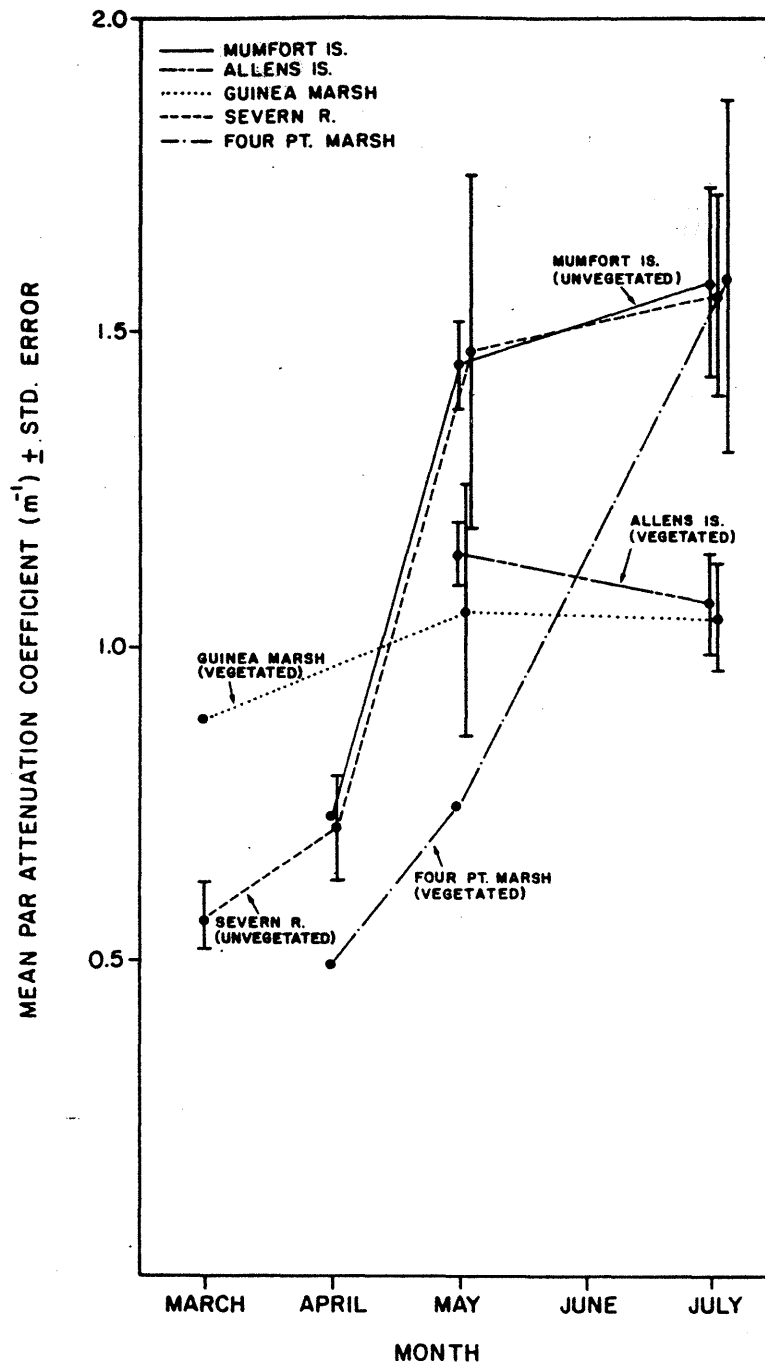


Figure 6. Mean monthly downwelling PAR attenuation coefficient ± 1 standard error of the mean for vegetated and unvegetated sites in the lower Chesapeake Bay (from Wetzel et al. 1982).

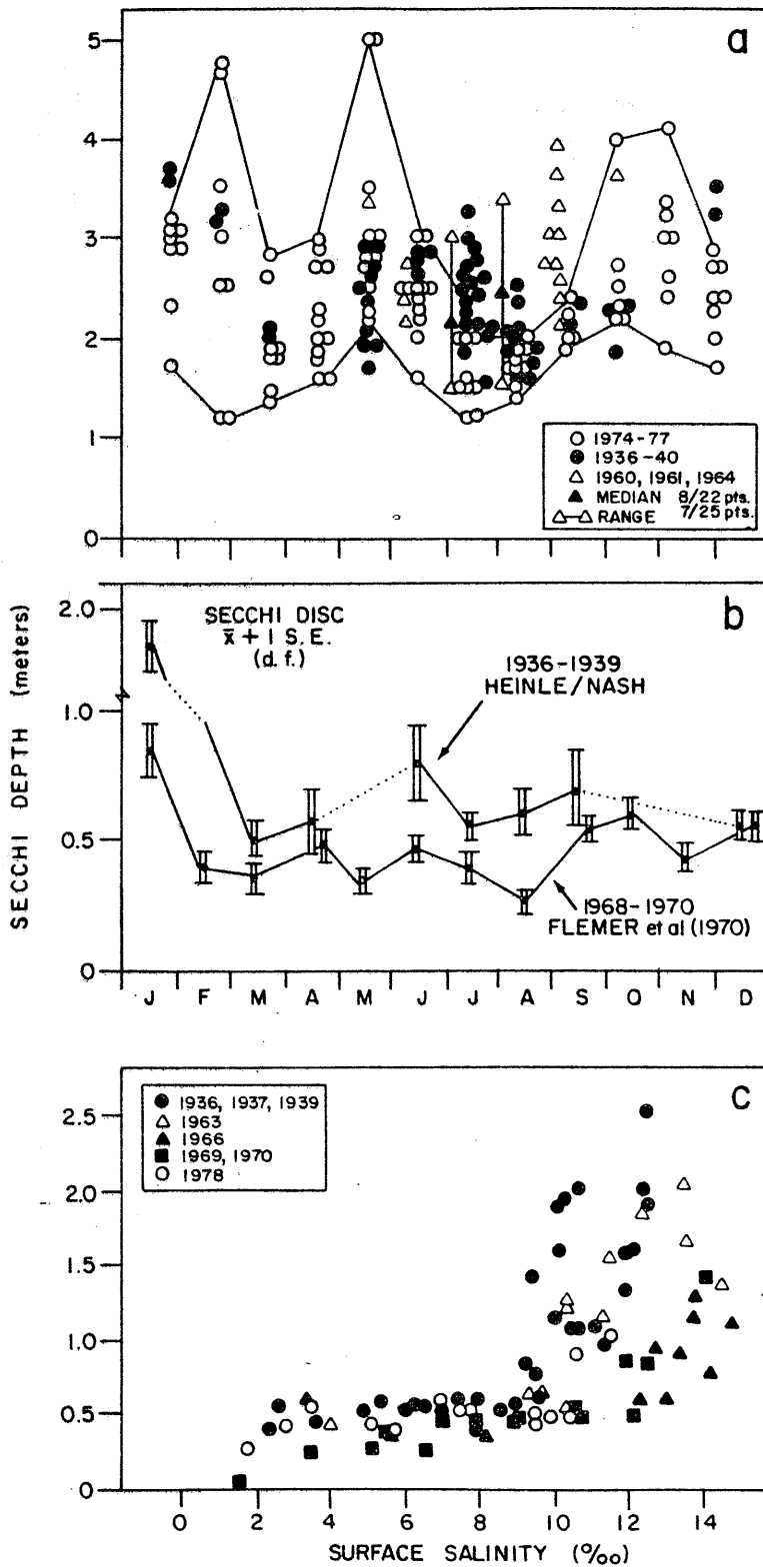


Figure 7. Historical Chesapeake Bay Secchi disc values (from Heinle et al. 1980, and references therein). (a) monthly mid-Bay means. (b) monthly means Patuxent River estuary (from Mihursky and Boynton 1978). (c) Patuxent River Secchi depth versus salinity, July.

Table 1. COMPARISON OF MEAN PAR ATTENUATION COEFFICIENTS INSIDE AND OUTSIDE OF VEGETATED AREAS AT TODDS COVE, MD., 1980 (KAUMEYER ET AL. 1981)

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

especially during the winter in the mid-Bay region (Figure 7a). An increase in turbidity, as estimated by Secchi disc measures, has been quite dramatic in the Patuxent (Figures 7b, 7c). Mid-1970's Secchi disc data for rivers in the upper Chesapeake Bay are reported in Table 2 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 (Figures 7b, 7c).

Increases in chlorophyllous pigments, due to phytoplankton blooms caused by increased nutrients, can have a severe effect on light attenuation in the photosynthetically critical blue and red spectral regions (Figures 1b, 1d). Historical chlorophyll data for 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 $\mu g L^{-1}$ were not unusual. In contrast, lower-Bay concentrations have not significantly changed (Figure 8b). Concentrations in the Patuxent River have increased

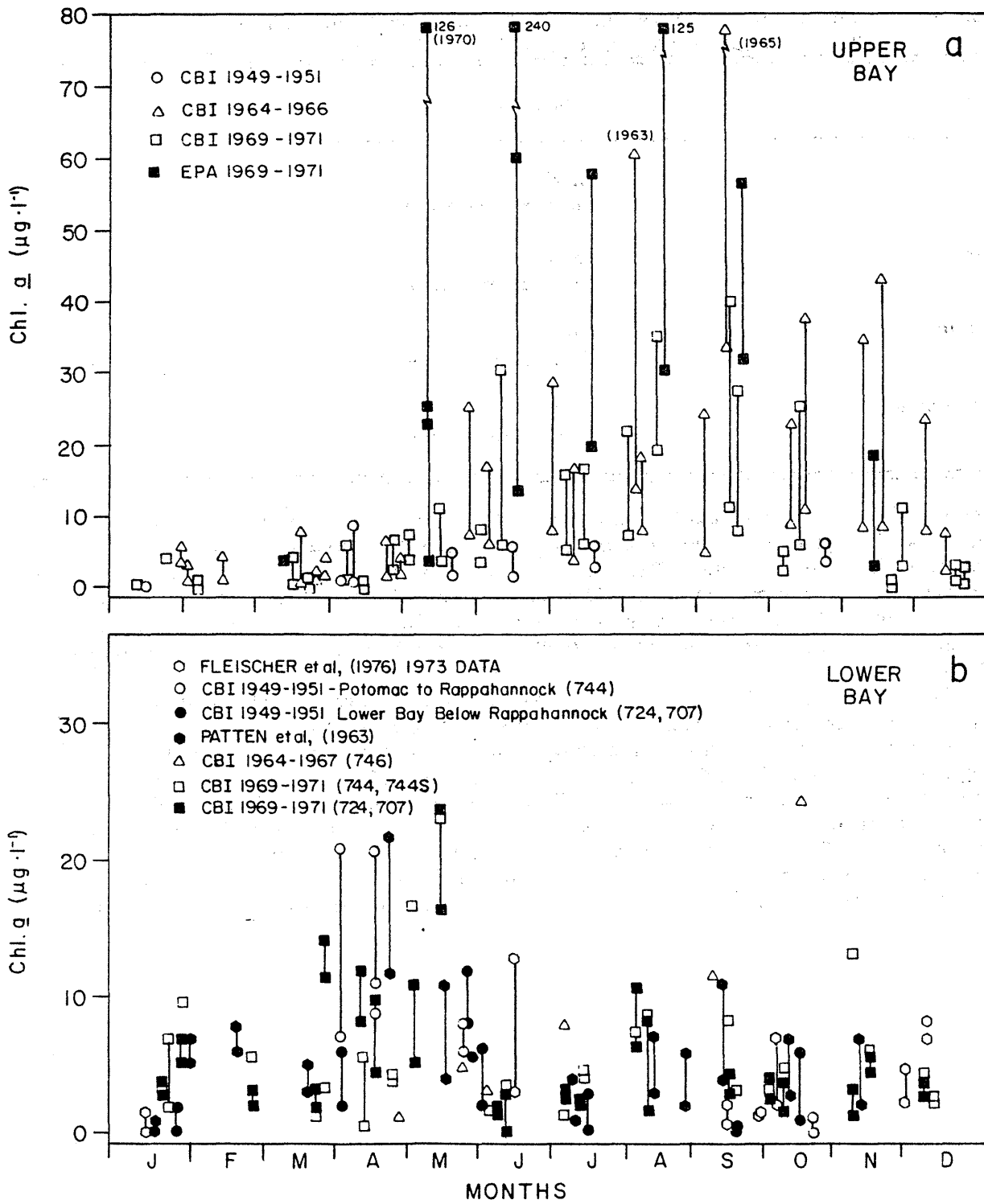


Figure 8. Summary of historical chlorophyll a data for the Chesapeake Bay. (a) upper Bay. (b) lower Bay (Redrawn from Heinle et al. 1980).

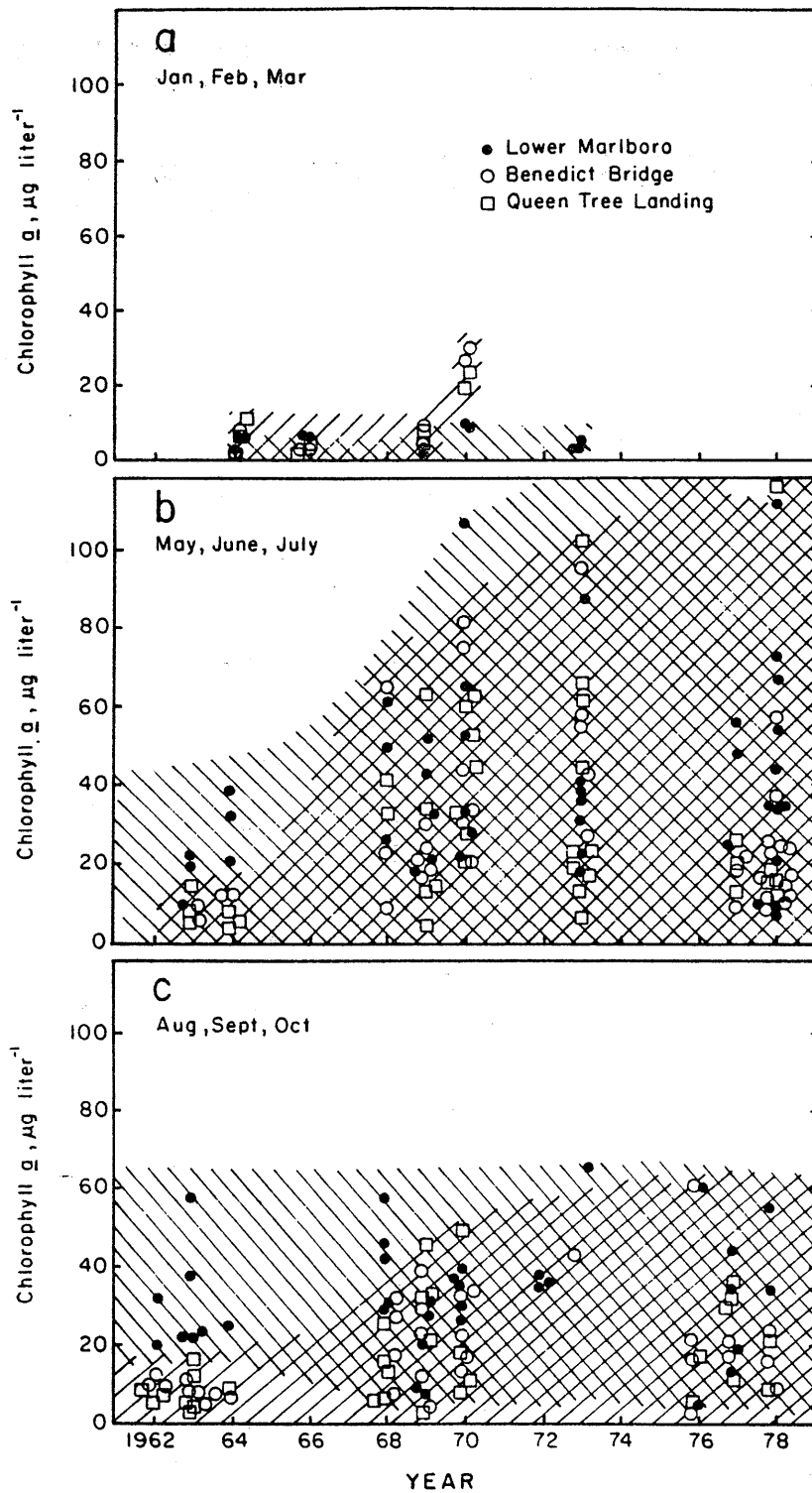


Figure 9. Summary of historical chlorophyll a data for three regions of the surface waters of the Patuxent R., Md. (a) January-March (b) May-July (c) August-October. (Cross hatching is to clarify general trends for each site.) (Redrawn from Heinle et al. 1980).

Table 2. 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 and Bohemia Rivers	33.0	35.1	-	25.7	36.3
Sassafras River	34.3	52.3	-	29.2	51.1
Howell and Swan Points	33.8	75.4	-	61.2	57.7
Eastern Bay	67.3	62.5	76.5	54.6	75.9
Choptank River	60.7	62.5	84.3	61.5	64.3
Little Choptank River	64.5	59.4	66.8	63.8	78.5
James Island and Honga River	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 and Wicomico Rivers	55.4	58.9	65.8	61.0	58.9
Manokin River	94.2	94.7	101.3	107.4	81.0
Patapsco River	73.7	80.0	67.8	-	70.1
Big and Little Annemessex Rivers	109.7	92.7	96.3	88.1	85.1
Gunpowder and Bush River Headwaters	42.9	38.3	46.7	-	53.8
Pocomoke Sound, Maryland	101.6	82.0	-	96.8	85.9
Magothy River	83.8	97.3	73.4	-	74.4
Severn River	97.3	70.4	79.5	-	86.4
Patuxent River	80.3	80.8	61.5	66.8	62.7

Continued

Table 2. AVERAGE SECCHI DISC DATA (cm) BY RIVER SYSTEM, MARYLAND
CHESAPEAKE BAY, 1972-1976a (AS REPORTED IN STEVENSON & CONFER
1978) (CONTINUED)

River System	1972	1973	1974	1975	1976
Back, Middle and Gunpowder Rivers	79.5	75.7	73.2	75.4	61.2
Curtis and Cove Point	45.2	77.0	81.8	58.9	73.7
South, West and Rhode Rivers	74.7	66.0	61.2	48.5	67.1
Chester River	76.2	73.4	100.1	87.9	85.1
Love and Kent Points	89.7	74.7	117.6	72.1	89.9
Smith Island, Maryland	78.5	76.2	89.7	139.4	87.6
Average	70.1	71.1	79.5	76.2	71.4

significantly in both the upper and lower portions (Figure 9), especially during late spring and early summer (Figure 9b). Levels in excess of 100 $\mu\text{g L}^{-1}$ were common in the summer throughout the 1970's -- this is twice the concentration measured during the previous decade.

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

Table 3. RANGES OF CONCENTRATIONS OF CHLOROPHYLL a ($\mu\text{g l}^{-1}$) AT SURFACE AND BOTTOM DEPTHS IN THE LOWER POTOMAC RIVER DURING 1949-1951, AND 1965-1966 (HEINLE ET AL. 1980)

Month	1949-1951		1965-1966	
	Surface	Bottom	Surface	Bottom
January	1-2	1-2	3.2-4.6	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

2.0 times higher presently than earliest data show. There have been upstream increases in the Magothy, Severn (Md.), and South Rivers. Concentrations up to 100 μL^{-1} were measured in the upper Potomac in the mid-1960's. Concentrations in the lower Potomac were generally higher in the 1960's than 1950, except in March and April (Heinle et al. 1980). 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

Table 4. ANNUAL MEAN FRESHWATER FLOWS AND OCCURRENCE OF HURRICANES TO ALL OF CHESAPEAKE BAY (CUBIC FEET PER SECOND) FOR 1951-1979 (HEINLE ET AL. 1980).

Year	Bay Annual Average	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
1966	53,300	
1967	77,200	
1968	60,100	
1969	54,900	
1970	77,200	64,540
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

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 that they defined as deviations in concentrations of chlorophyll a from historic, natural periods of stability or steady state

concentrations. Figure 10 shows the regions of the Bay that are categorized as moderately or heavily enriched. Many of these areas have experienced declines in Bay grasses on a time scale overlapping the enrichment.

Changes in dissolved organic materials, inorganic particulate matter, and allochthonous organic particulate matter in the Bay are mainly determined by inputs (runoff) of freshwater to the tributaries and by additional input due to storm events. Table 4 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 that favor phytoplankton blooms.

Suspended sediment transport and discharge of the Susquehanna River, the major source of freshwater to the Bay, are given in Table 5.

Table 5. SUSPENDED SEDIMENT TRANSPORT AND DISCHARGES OF SUSQUEHANNA RIVER (GROSS ET AL. 1978)

Calendar Year	Annual suspended sediment discharged (millions of metric tons per year)	
	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

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 the lower reaches of the river during years of low flow and no major flooding. During major floods, however, these deposits are eroded and transported into the Bay. Thus, dams effectively increase the amount and variability of sediment discharged under flood conditions.

It is evident that major storms, such as hurricanes, significantly increase freshwater input, but there is also an apparent wet-year, dry-year cycle imposed on the data. The five-year-flow averages (Table 4) 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

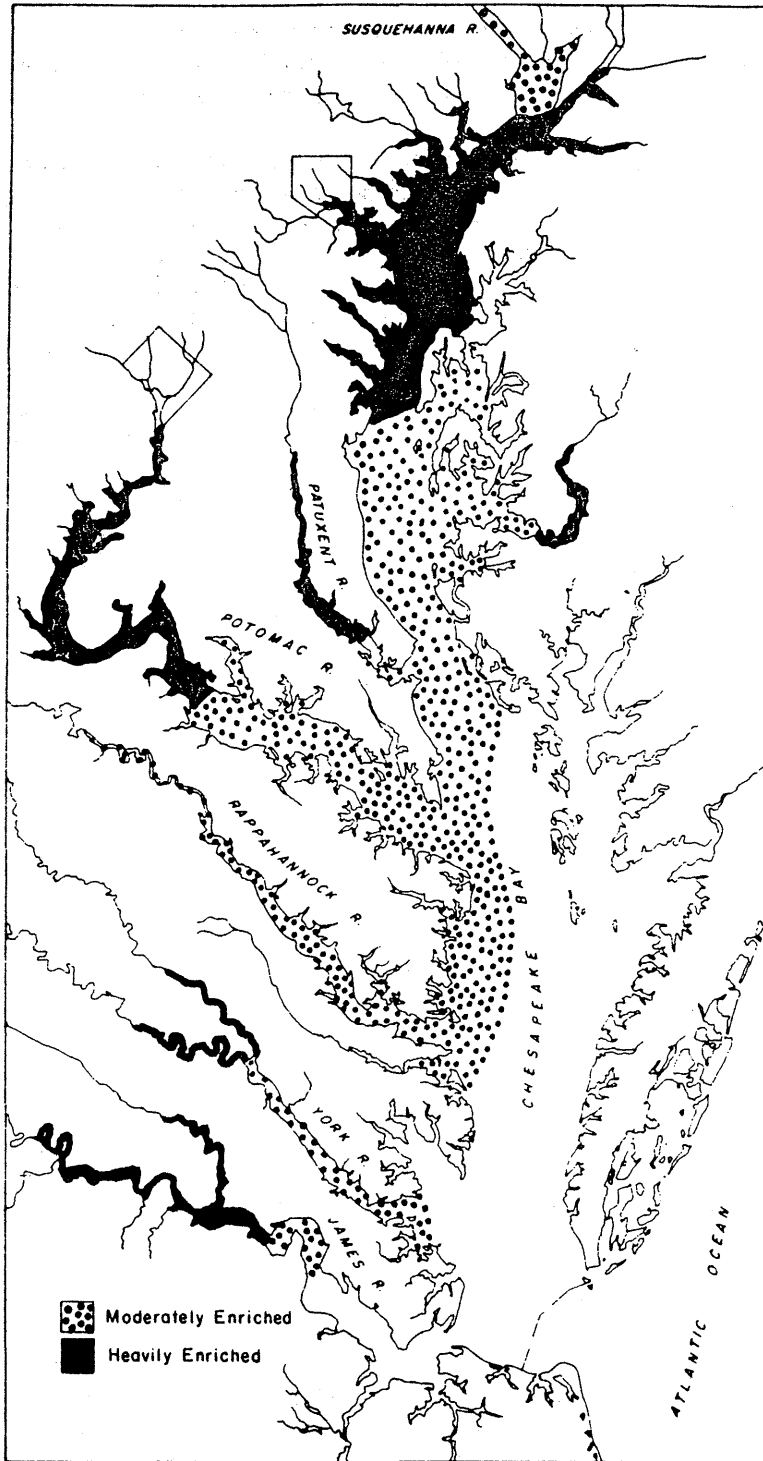


Figure 10. Portions of the Chesapeake Bay considered enriched by Heinle et al. 1980. Enrichment is defined as increase in chlorophyll a levels from historic, natural periods of stability.

major storms) influence water quality and optical properties of Bay waters. However, cause and effect relations are still poorly understood and resultant optical properties of Bay water are determined and controlled by multiple influences: runoff; nutrients; suspended particulates (both living and dead); and, as the principal driving forces, the general climatic regime.

SECTION 3

LIGHT AND PHOTOSYNTHESIS IN CHESAPEAKE BAY SAV COMMUNITIES

GENERAL REVIEW OF PHOTOSYNTHESIS

Photosynthesis is the process in 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 CO₂ using ATP and NADPH and the production of carbohydrates. The first two steps are light-dependent and are collectively referred to as the "light reaction". The third step is light-independent and termed the "dark reaction".

The photosynthetic pigments have characteristic light energy absorption spectra in the photosynthetically active region, 400 to 720 nm. Chlorophyll a absorbs light more effectively at higher wavelengths (>600 nm); accessory pigments such as chlorophyll b, carotenoids, and others are more effective at shorter wavelengths (<600 nm). Chlorophyll a and the accessory pigments absorb and transfer light energy at varying efficiencies to specialized chlorophyll a molecules (P700) where they are used directly for biochemical reactions.

The photochemical reactions are driven by units of light energy called photons (quantum energy). The 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; light energy transfer by chlorophyll a and accessory pigments is less efficient. The quantum yield, the moles of O₂ produced or CO₂ fixed per photon of light absorbed, is used to estimate the transfer efficiency.

The light utilization spectra of a particular species is called the action spectra, a characteristic curve obtained by combining the light absorption spectra and the quantum yield of intact plant cells. The action spectra is an important feature because it reflects the ability of a species to adapt to various light spectral regimes (Figure 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 material, dissolved organic compounds, and other water column constituents (discussed in Section 2).

A general approach to the investigation of photosynthesis is to construct light saturation curves for various species (Figure 11a). An examination of photosynthesis-light curves (P-I curves) shows that photosynthesis (P) increases with increasing light to a point of optimal irradiance (I_{opt}) where, over a range of irradiance, the photosynthetic 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). Alpha (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 Figure 11b. Plants adapted to high and low light environments, termed 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 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.

PHOTOSYNTHESIS OF SUBMERGED VASCULAR PLANTS IN RELATION TO LIGHT AND TEMPERATURE

In situ studies of submerged angiosperms point to the important role of light in seagrass production and distribution (Jacobs 1979, Mukai et al. 1980). In a study of Zostera in Denmark, Sand-Jensen (1977) showed a positive correlation between leaf production and insolation over a nine month period. Biomass and photosynthesis rates of Posidonia declined with depth near Malta (Drew and Jupp 1976); this was probably due to decreased light penetration with depth. In before and after studies of an estuary that was closed to the sea, Neinhuis and DeBree (1977) report that the Zostera population increases in density and extends to a greater depth; they suggest that this is probably due to an increase in water transparency.

In situ light manipulation experiments 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 percent, in situ Zostera densities were only five percent of that of the control (Backman and Barilotti 1976). In similar studies, Congdon and McComb (1979) report that lower than ambient light levels result in lower Ruppia biomass; as shading duration increases, higher light levels are required to sustain a high biomass.

Studies involving the epiphytic community, those organisms directly attached to submerged angiosperm blades, suggest that epiphytes have a detrimental effect because they shade the macrophytes. Both Kiorbe (1980) and Phillips et al. (1978) provide data to indicate that epiphytic development suppresses macrophyte growth. Sand-Jensen (1977) reports that Zostera photosynthesis is reduced by up to 31 percent due to a decreased penetration of light and inorganic carbon through the epiphytic community to the seagrass blades. Johnstone (1979) hypothesizes that the rapid linear growth of Enhalus leaves (up to two cm day⁻¹) is related to a shading effect from epiphytes. In contrast, the data of Penhale and Smith (1977) suggest that an epiphytic community may be beneficial in certain environments. For Zostera exposed at low tide, epiphytes prevent desiccation damage by trapping a film of water, and probably reduce 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). The

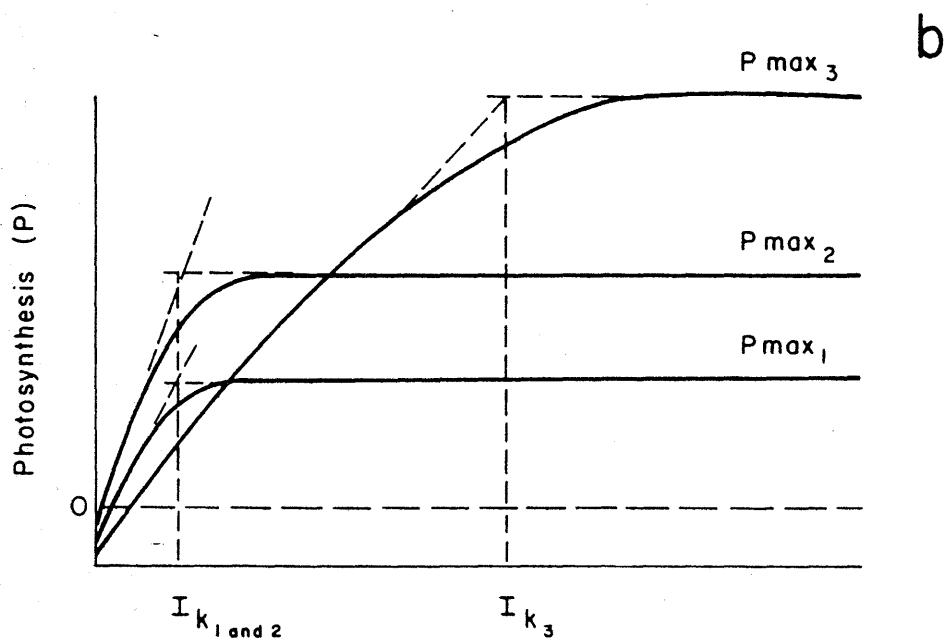
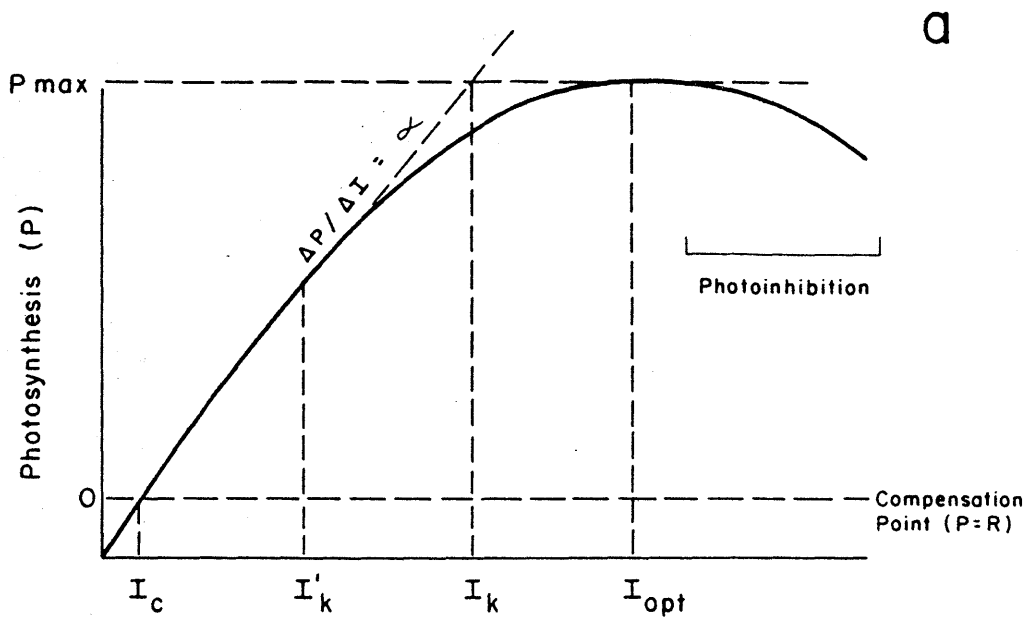


Figure 11. Diagrammatic photosynthesis-light relationships. See text for description of parameters.

biogeography of marine and brackish water plants points to a temperature effect on worldwide distribution; for example, genera such as Zostera, Ruppia, Phyllospadix, and Posidonia occur mainly in temperate zones while genera such as Thalassia, Syringodium, and Halophila occur mainly in subtropical and tropical zones. Drew (1979) reports that the P_{max} of four seagrass species collected near Malta increases in direct proportion to temperature, up to temperatures [30 to 35°C (86 to 95°F)] where tissue damage occurred; decreases are not observed at environmental temperatures. In contrast, Penhale (1977) observed a decline in P_{max} from 22 to 29°C (71.6 to 84.4°F) for Zostera in North Carolina where environmental temperatures reach 34°C (93.2°F). 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 report that a greater temperature tolerance Vallisneria, in conjunction with the temperature dependence of photosynthesis, results in a temporal partitioning of production. Vallisneria apparently favored in midsummer conditions; Myriophyllum spring and fall conditions.

Sun and shade species have been described for submerged macrophytes (Spence and Crystal 1970a, 1970b; Titus and Adams 1979). Sun species generally exhibit higher P_{max} values than shade species that exhibit 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) report that the total chlorophyll content is 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 decreasing 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. The chlorophyll a to chlorophyll b ratio, however, 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 percent of its foliage within 30 cm (11.7 inches) of the surface, and the latter had 62 percent of its foliage within 30 cm of the bottom. Myriophyllum, an introduced species, has often displaced the native Vallisneria; a contributing factor 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) concludes that changing leaf area is 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 Chesapeake Bay system: Myriophyllum spicatum and Potamogeton perfoliatus in the upper Bay, and Zostera marina and Ruppia maritima in the lower Bay. These experiments used whole plants or leaves subjected to various light intensities (created through the use of neutral density screens) and various temperatures.

The second approach used microcosms in which the effects of various concentrations of phytoplankton and suspended solids on light penetration and on Potamogeton photosynthesis were determined.

The third experimental design involved 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. The experimental design and methods for each of these studies are detailed in Kemp et al. (1981b) and Wetzel et al. (1982).

P-I Relationship of Major Species

P-I curves were constructed for whole plants of M. spicatum and P. perfoliatus at 21°C (69.8°F) (Kemp et al. 1981b) (Figure 12). Both species exhibited the characteristic photosynthetic response to light with light saturation occurring between 600 and 800 $\mu\text{E m}^{-2} \text{sec}^{-1}$. Myriophyllum exhibited a greater P_{max} and a greater I_k than Potamogeton; however, the two species exhibited similar α . Although these species occur in the same general locale, they do not form dense, mixed bed stands where they would be in direct competition for light.

The photosynthetic response to light and temperature was determined for isolated Z. marina and R. maritima leaves (Wetzel et al. 1982). Since these species co-exist in the lower Chesapeake Bay, an evaluation of 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 about 300 $\mu\text{E m}^{-2} \text{sec}^{-1}$ while that of Ruppia occurs about 700 $\mu\text{E m}^{-2} \text{sec}^{-1}$. 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; the situation is reversed at colder temperatures (Figure 13). A summary of the data shows that Ruppia exhibits the greater P_{max} at temperatures greater than 8°C (46.4°F) (Table 6). 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.

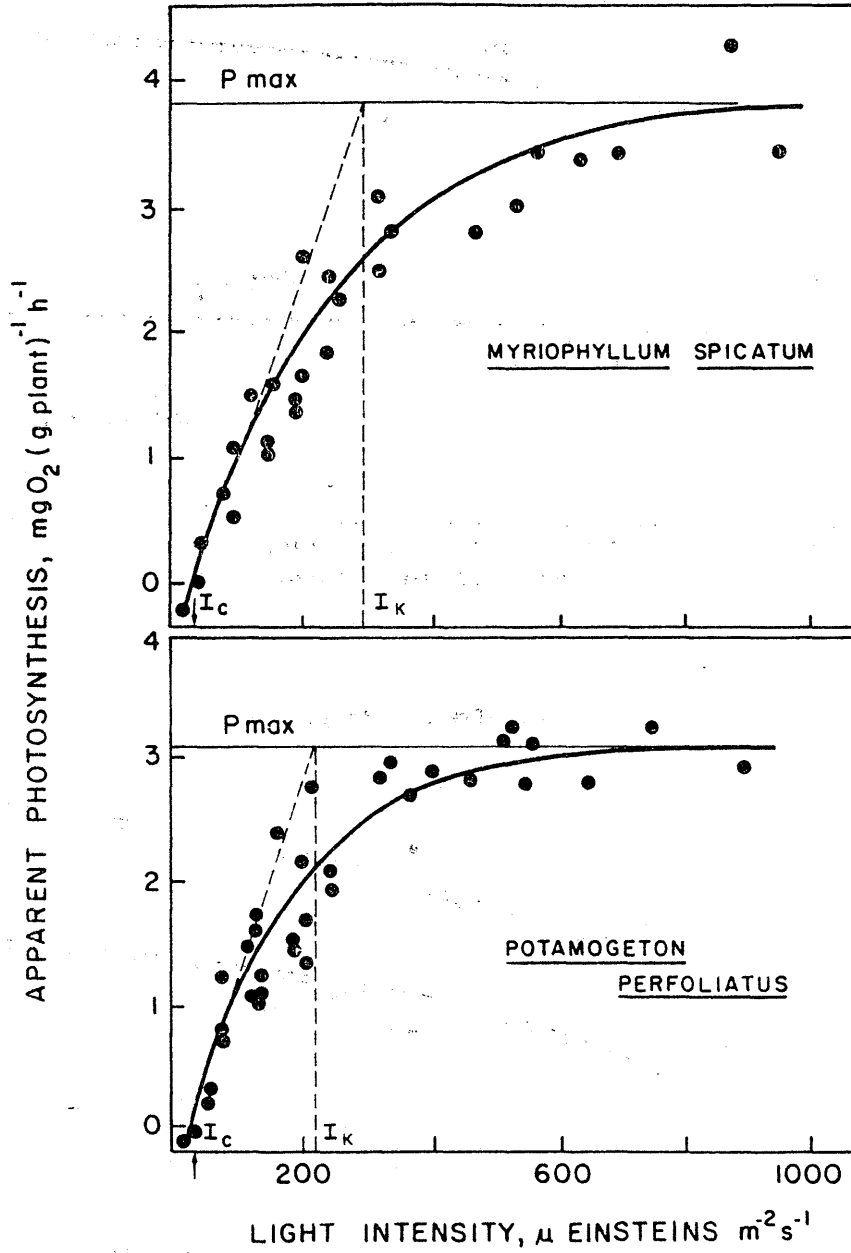


Figure 12. Photosynthesis-light curves for two species of upper Chesapeake Bay submerged vascular plants (from Kemp et al. 1981c).

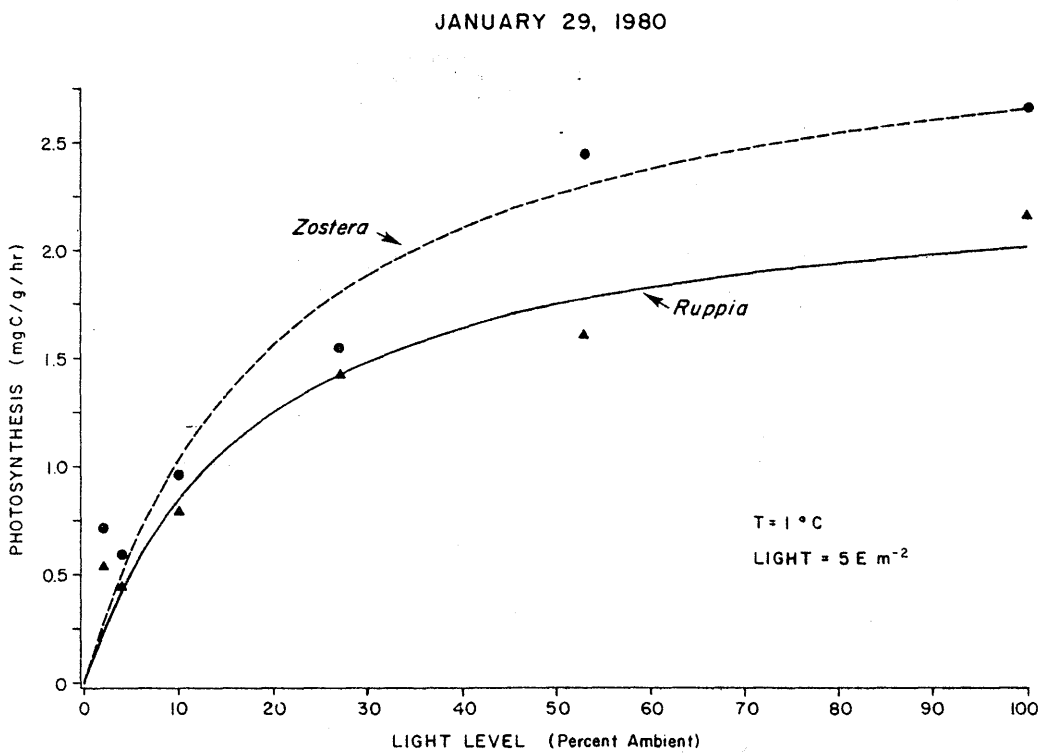
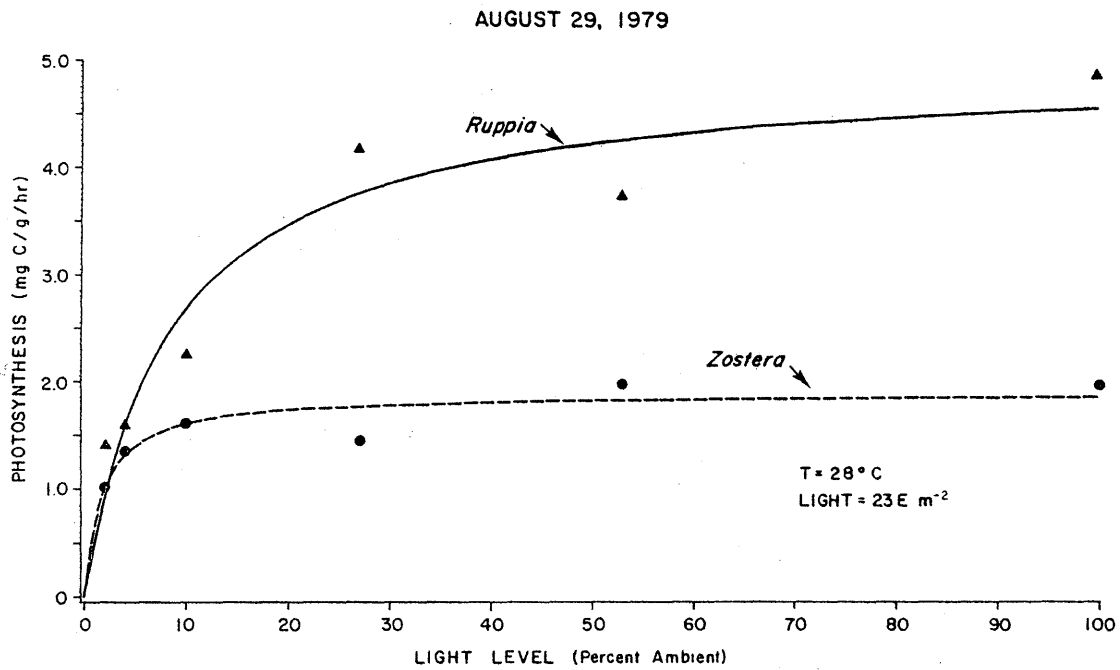


Figure 13. Photosynthesis-light curves for *Ruppia* and *Zostera* from a mixed bed site on the Eastern Shore, Virginia. Light is total light flux during 4 h ¹⁴C incubations (from Wetzel et al. 1982).

Table 6. PHOTOSYNTHETIC PARAMETERS FOR RUPPIA MARITIMA AND ZOSTERA MARINA LEAVES AT VARIOUS TEMPERATURES. THE LIGHT IS THE TOTAL LIGHT FLUX DURING THE 4h ¹⁴C INCUBATIONS (FROM WETZEL ET AL. 1982)

TEMP °C	LIGHT E m ⁻²	P (mg C g ⁻¹ h ⁻¹)		INITIAL SLOPE	
		<u>Ruppia</u> max	<u>Zostera</u>	<u>Ruppia</u>	<u>Zostera</u>
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

The data from these experiments relate to how plants capture light and process it, and suggest mechanisms for the species distribution of Ruppia and Zostera in the lower Chesapeake Bay. The results also show that temperature largely influences the distribution of these plants. 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 shaded by the longer leaved Zostera. During 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. (1981c) compared values of photosynthetic parameters taken from the literature on submerged angiosperms (Table 7). 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 $\mu E m^{-2} sec^{-1}$ and I_k from 70 to 350 $\mu E m^{-2} sec^{-1}$.

Table 7. SUMMARY OF PHOTOSYNTHESIS-LIGHT EXPERIMENTS FOR SELECTED SUBMERGED AQUATIC ANGIOSPERMS^a (FROM KEMP ET AL. 1981c)

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

- 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 O₂ 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 (uE m⁻² sec⁻¹) assuming 1 mW cm⁻² = 2360 Lux = 0.86 cal cm⁻² h⁻¹ = 46 uE m⁻² sec⁻¹.
- d Values for I_C are not available for experiments using the ¹⁴C method which cannot measure negative net photosynthesis.

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 (Figure 14). The wider the bar, the more concentrated the leaf material. 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. Ruppia exhibits much greater leaf area than Zostera at the lower canopy (0 to 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 (Figure 15). The highest concentrations of chlorophyll are at mid-canopy for Zostera and at 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 are adaptations that contribute to Ruppia's success in mixed bed areas. These estimates give us information on how changes in light quantity (from water quality changes) will affect the success of mixed SAV beds.

Microcosm Studies

The microcosm studies of Kemp et al. (1981b) show a negative effect of suspended sediments on Potamogeton photosynthesis (Figure 16). Two concentrations of fine sediment particles (<64 μ m in diameter, representative of particle size in nature), kept in suspension with recirculating pumps, reduced light availability in the two treatments and resulted in significantly lower photosynthesis of Potamogeton compared with 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, however, the effect of suspended sediments on photosynthesis would be 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 similar in design to the ¹⁴C studies on individual species were used to decrease available light.

A summary of the upper Bay Potamogeton community response to light is presented in Figure 17, which includes estimates from both early (May) and

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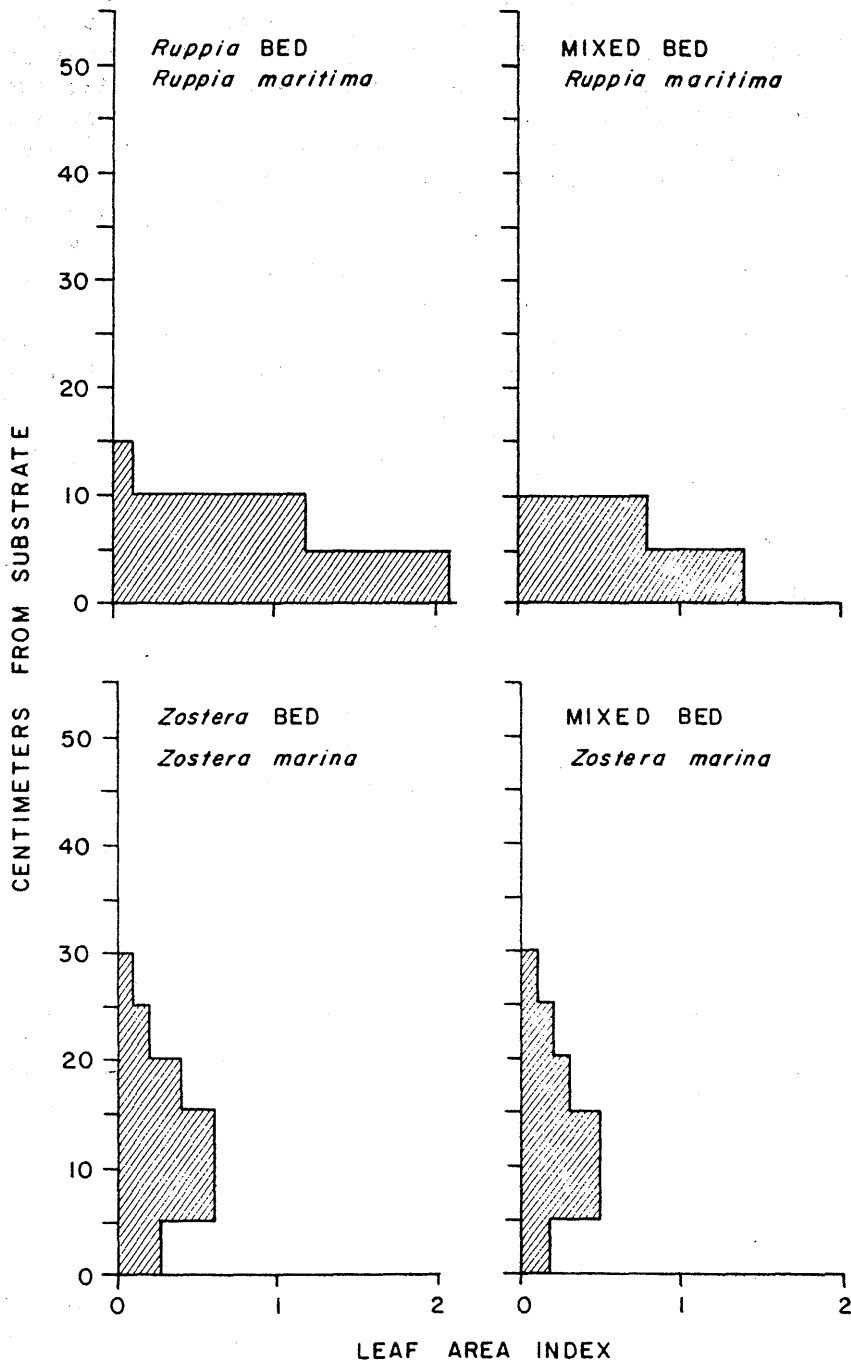


Figure 14. Vertical distribution of one-sided leaf area index (m^2 plant m^{-2} substrate) for *Ruppia* and *Zostera* at three vegetated sites on the Eastern Shore, Virginia (from Wetzel et al. 1982).

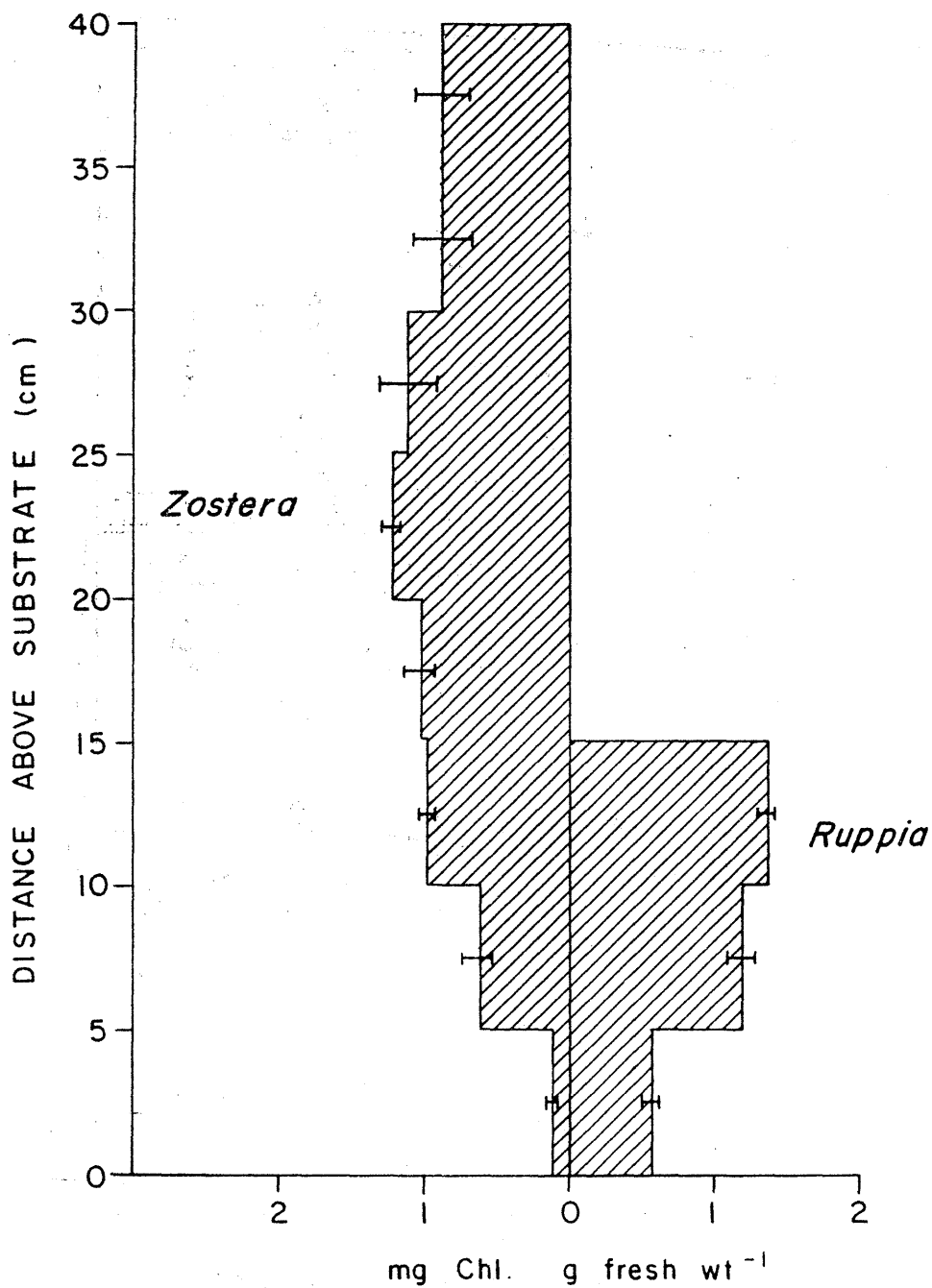


Figure 15. Vertical distribution of total chlorophyll for *Ruppia* and *Zostera* from a mixed bed area on the Eastern Shore, Virginia. Values \pm standard error, $n = 3$ (from Wetzel et al. 1982).

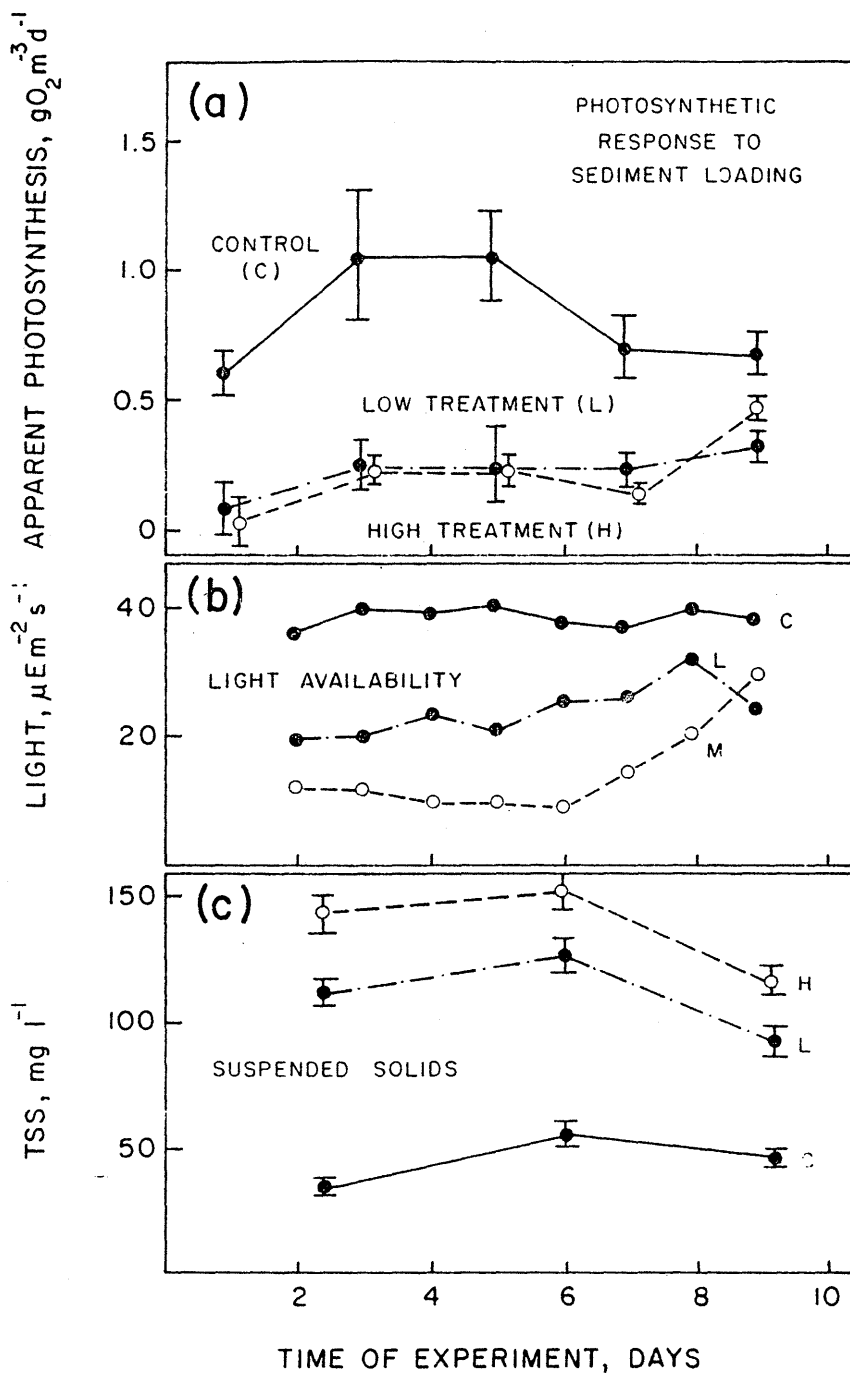


Figure 16. Effect of (c) total suspended solids (TSS) on (b) light availability and (a) rate of photosynthesis of Potamogeton perfoliatus (from Kemp et al. 1981).

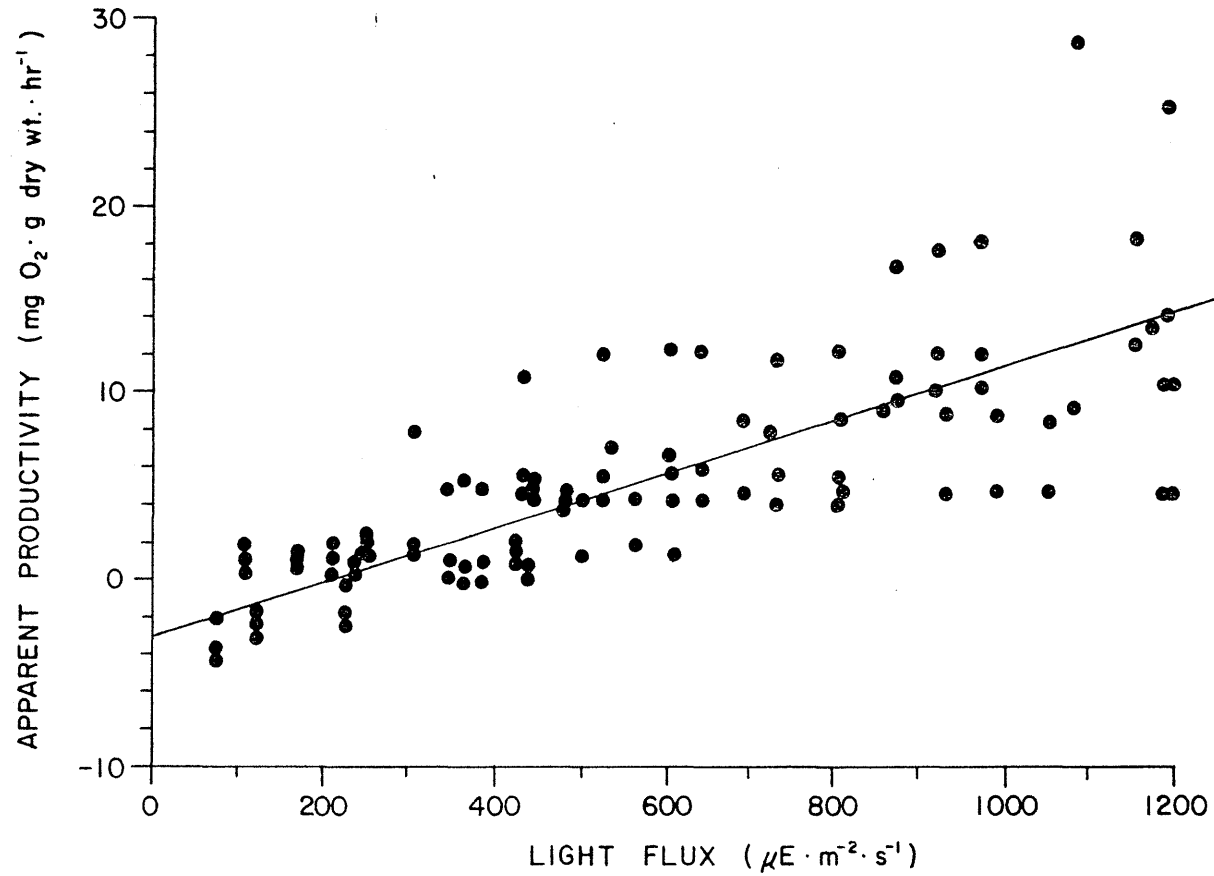


Figure 17. Response of upper Chesapeake Bay submerged vascular plants to light flux (from Boynton, unpublished data).

late (August) periods in the growing season (Boynton, unpublished data). The I_c of the plant community occurs at about $200 \text{ uE m}^{-2} \text{ sec}^{-1}$, and data suggest that the community is not light-saturated in the ranges of measured in situ light flux. If the community were light-saturated, the rate of change would approach zero (P_{\max}) with the line in Figure 17 leveling off. An analysis of the seasonal trends suggests no differences in the regression of light and community metabolism between seasons.

Based on these and other studies, Kemp et al. (1981b) conclude 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 (Figures 18a, 18b). Photosynthetic parameters, I_c , I'_k , and P_{\max} were calculated from a P-I curve (Figure 18c). These parameters are identified for each light penetration curve and suggest that for much of the daylight period, the plant community is light-limited or undersaturated, as it is not operating at P_{\max} . At early morning and dusk periods of the day, the community is apparently heterotrophic (i.e., no net production).

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 regimes and under artificial shading conditions. The shallow Ruppia areas exhibited higher light and temperature regimes than the deeper Zostera areas; the mixed bed was intermediate between the two.

Short-term shading experiments resulted in a general decrease 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 (Figure 19). Based on P-I curves, Ruppia was light-saturated during much of the day and was not photoinhibited. The unexplained afternoon depression that occurred while light was increasing may be due to increased community respiration rates under these high summer temperatures. A similar pattern was observed for the Zostera site where shading also resulted in decreased apparent productivity (Figure 20). In contrast, the afternoon depression in productivity rates of the Zostera bed was not so dramatic as in the Ruppia bed. This trend in Zostera seemed to follow the decreasing light availability unlike the response in Ruppia. These results are similar to those found throughout the study and support previous conclusions that the two communities are physiologically (i.e., temperature and light response) quite different.

Plots of apparent productivity versus light flux at the top of the canopy were used to compare all three habitats (Figure 21). Differences among the three sites were characteristically 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 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. As evidenced by its high apparent productivity rates, Zostera appears adapted to lower light levels. The erratic pattern of data points and the greater number of negative rates for Ruppia strongly suggest different community behavior. At the community

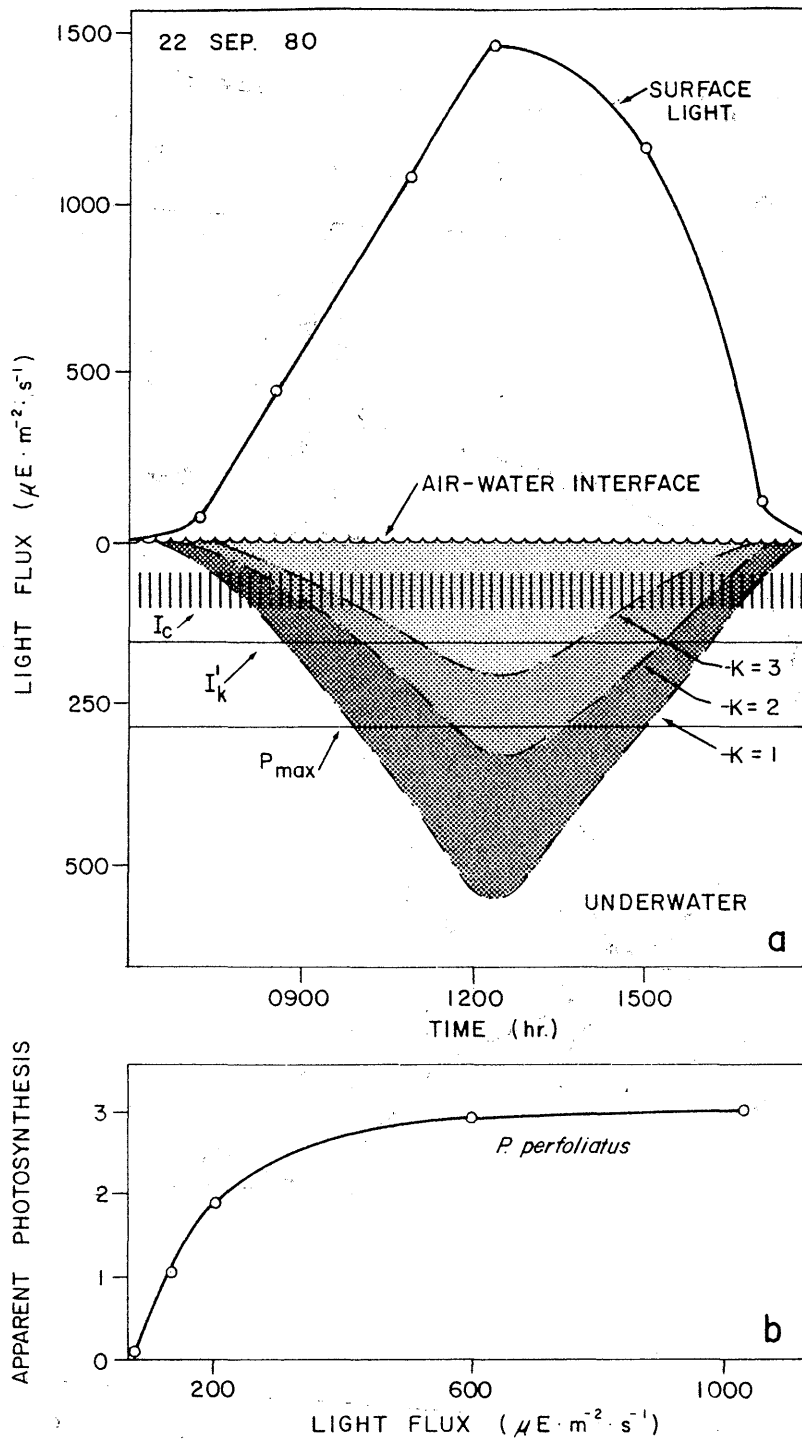


Figure 18. Diagrammatic representation of (a) surface and underwater light flux at Todds Cove, upper Chesapeake Bay calculated for three light extinction (K) coefficients. (b) I_c , I'_k and P_{max} calculated from P-I curve of *Potamogeton perfoliatus* (from Kemp et al. 1981c).

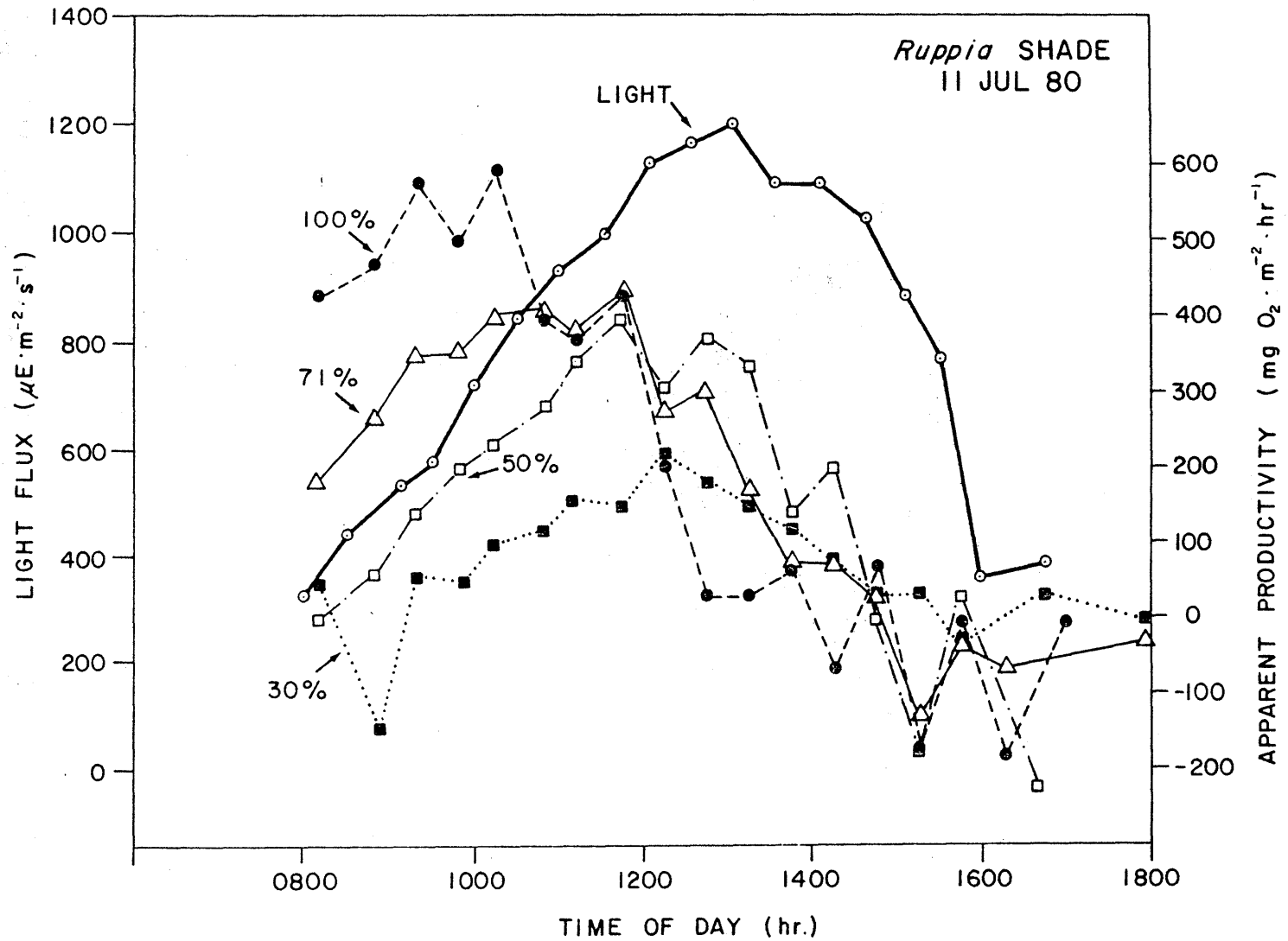


Figure 19. Apparent productivity and light flux at the canopy top vs. time of day from *Ruppia* experiments at 100, 71, 50, and 30% of ambient light at the canopy top (from Wetzel et al. 1982).

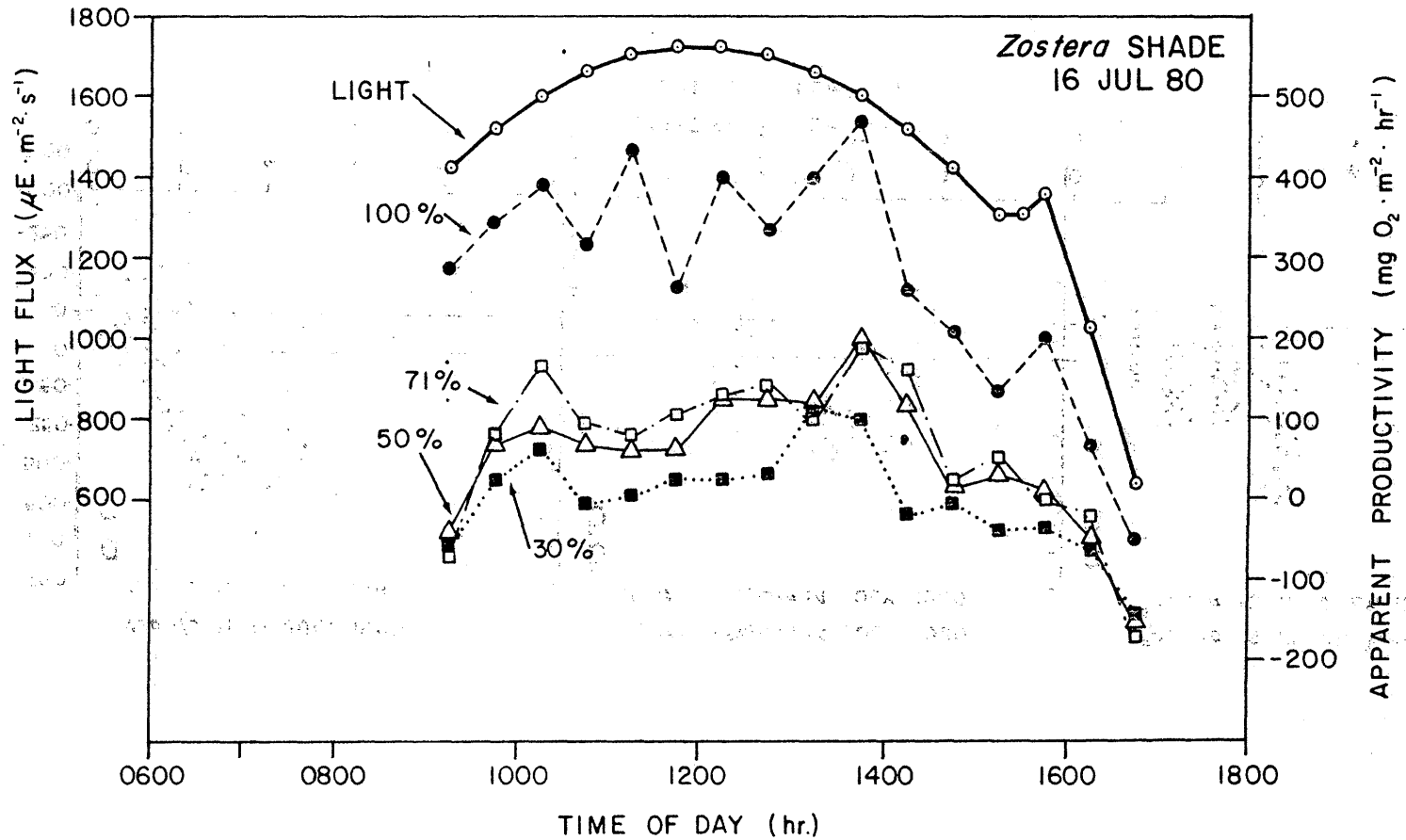


Figure 20. Apparent productivity and light flux at the canopy top vs. time of day for *Zostera* experiments at 100, 71, 50, and 30% of ambient light at the canopy top (from Wetzel et al. 1982).

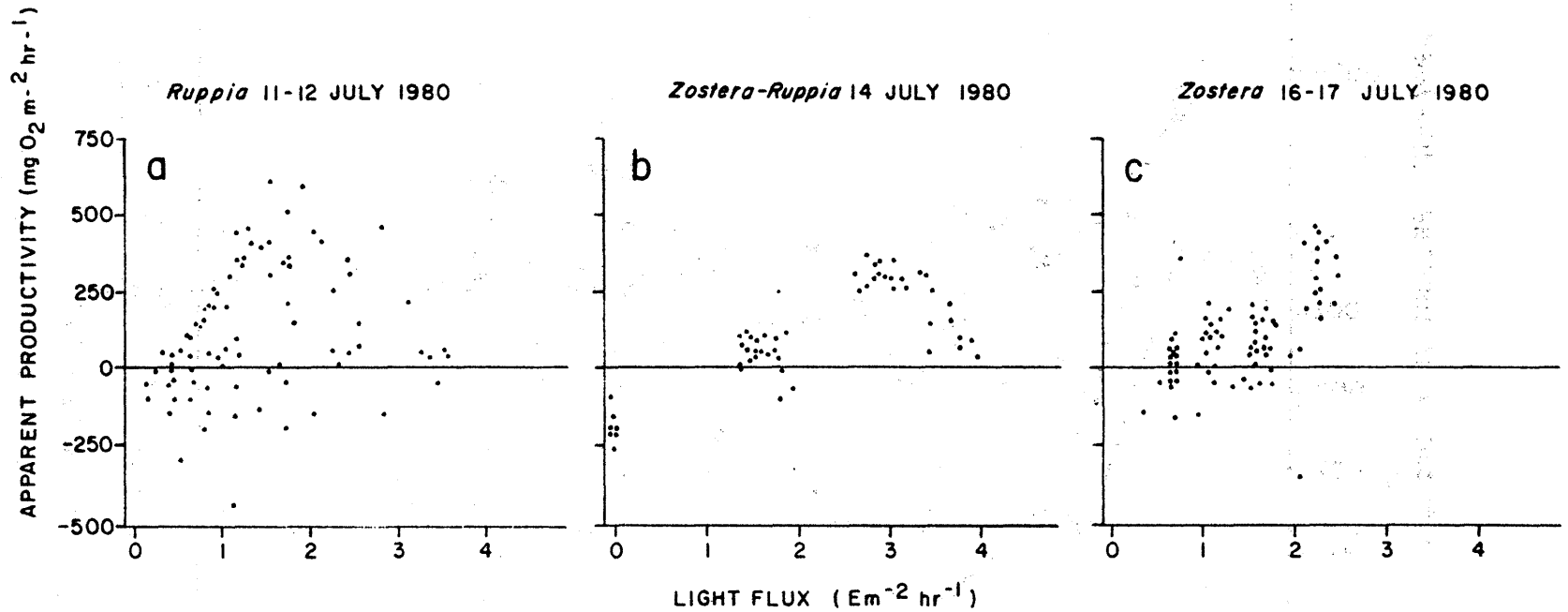


Figure 21. Apparent productivity versus light flux for (a) Ruppia, (b) mixed Ruppia-Zostera, and (c) Zostera areas, Eastern Shore, Virginia (from Wetzel et al. 1982).

level, the differences 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. Under the influence of changes in water quality, these data show that mixed beds would probably survive better than a bed containing a single species.

A summary of linear regression analyses of apparent productivity versus light flux at the top of the canopy for the three areas is presented in Table 8. 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 of O_2 productivity asymptotically approaches P_{max} . Therefore the linear relationship does not adequately describe the

Table 8. APPARENT O_2 PRODUCTIVITY AND LIGHT: LINEAR REGRESSION ANALYSIS FOR LOWER BAY STUDIES (FROM WETZEL ET AL. 1982)

[mg O_2 m^{-2} h^{-1} vs. μE m^{-2} h^{-1} (AT CANOPY TOP)]							
DATE	AREA	N	m	b	r	μE m^{-2} h^{-1}	I_c μE $m^{-2} sec^{-1}$
14 Feb 80	<u>Zostera</u>	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	<u>Ruppia</u>	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

Table 8. (CONTINUED)

[mg O₂ m⁻² h⁻¹ vs. uE m⁻² h⁻¹ (AT CANOPY TOP)]

DATE	AREA	N	m	b	r	uE m ⁻² h ⁻¹	I _c uE m ⁻² sec ⁻¹
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

I

N = number of observations

m = slope

b = y-intercept

r = correlation coefficient

I_c = estimated light compensation point (x-intercept)

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, because of increased respiration, to the point that daily community production is negative. This corresponds to the characteristic midsummer die off of Zostera in these areas (Wetzel et al. 1981). Except for the studies carried out in 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 increases in early afternoon during high light and temperature conditions. These conditions are prevalent at midday 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 in the Vacluse Shores study area.

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

SECTION 4

SUMMARY

The apparent optical properties of estuarine water create, in general, a light-limited environment for the process of photosynthesis. Water in itself, suspended particles, and dissolved compounds all interact to both attenuate total photosynthetically active radiation as well as to spectrally shift (selectively absorb) wavelengths most important for autotrophic production. Plant pigment systems, in general, 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.

However, data on spectral characteristics and specific waveband attenuation in estuarine and coastal environments are lacking. Our summary of available data, Section 2, indicates that few studies have been completed that characterize these optical properties of estuarine waters and even fewer that can evaluate the data in terms of potential control on rates of photosynthesis. It is difficult, therefore, if not impossible at the present time, to speculate as to the importance or generality of specific waveband attenuation relative to photosynthesis and to autotrophic production in Chesapeake Bay as well as in other estuaries. It has only been within the past few years that submarine spectral irradiance studies have become technologically feasible, and this is reflected in the general paucity of information.

Studies in Chesapeake Bay indicate reductions in both light quality and quantity at selected study sites and during various periods of the growing season for submerged aquatic plants. Recent measures of diffuse downwelling attenuation coefficients (Section 2) in lower Bay communities indicate a severe attenuation of light energy in the photosynthetically important violet blue (400 to 500 nm) region and in the near infrared (700 to 775 nm) region of the spectrum. Also for the March through July period of study, there appears to be a progressive increase in attenuation in these spectral regions.

Comparison of vegetated and non-vegetated areas in Chesapeake Bay with regard to light quality and quantity suggests some improvement (lower attenuation) in the vegetated areas, although the data are quite variable. In the upper Bay, Kaumeyer et al. (1981) report significant differences for one site and not for another. In the lower Bay, comparison of four sites (two vegetated and two non-vegetated) indicates some differences in light quality. There are at these lower Bay sites, some improvements in attenuation in the 400 to 500 nm region in spring months (see recent report by Wetzel et al. 1982 for an updated analysis of this and additional data). The only definitive light quality differences between the sites was reduced attenuation in the 500 to 700 nm region in vegetated areas during spring, an important period in the growth of Zostera dominated communities. Diffuse downwelling attenuation in some photosynthetically sensitive spectral regions is severe. This, coupled with the general increase in attenuation during the growing season and at higher temperatures, indicates the plant communities are undoubtedly light stressed.

There is a much larger data base on plant response to total available light energy (PAR) for Chesapeake Bay as well as for 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 $\mu\text{E m}^{-2} \text{sec}^{-1}$, but differ in P_{max} and I_k . M. spicatum appears adapted 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; 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 are, in general, operating under sub-optimal light conditions. There was no apparent light saturation reached for upper-Bay communities; that is, net apparent community productivity did not asymptotically approach a maximum value. Studies in lower-Bay communities suggest that Z. marina is light-limited the majority of its growing seasons and only in more shallow R. maritima areas did the community photosynthetic response become light-saturated. 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 as a whole are light-stressed.

Historical data relative to light (turbidity and indirectly, nutrients) and to past distribution and abundance on submerged aquatics indicate progressive Bay-wide changes in systems structure and function. Heinle et al. (1980) and Orth et al. (1971) 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) note and document the generalized increase in nutrients (and loadings) and chlorophyll concentrations in major tributaries of Chesapeake Bay over the past several decades. Orth et al. (1981) conclude, for roughly the same time scale, that the general pattern of disappearance of submerged plant communities follows a "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 total PAR and factors increasing diffuse downwelling attenuation in the 400-500 nm region are principal driving functions controlling plant growth and survival. The specific factors at present that appear to have the greatest impact are suspended particles, both organic and inorganic, which are controlled, in large part, by climatic conditions (runoff and nutrient loading) and indirectly by associated changes in physical-chemical regimes (salinity and temperature).

In summary, it appears that Bay grasses are living in a marginal light environment, and that progressive changes in water quality as discussed by Heinle et al. (1980) will further stress plant communities. To conclude

that light has been singularly responsible for recent declines in the vegetation goes beyond the data available. The data do indicate, however, the extreme sensitivity of vegetation to both qualitative and quantitative reductions of available light, and that over the past several decades water quality throughout the Bay, particularly in the tributaries, has progressively declined. Further changes in these parameters can only affect Bay grasses in an adverse way. Results show that SAV can adapt to changes in the availability of light. Long-term shading experiments (in progress) will address this question further.

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