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

by

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CONTENTS

List of Figures iii
List of Tables v

I. Introduction 1
 Background 2
 The Research Program on Light and SAV: An Overview . . . 5

II. Light in the Chesapeake Bay 8
 General Characteristics of Estuarine Optical Properties . 8
 Light Attenuation in the Chesapeake Bay 13
 Comparison of Light Attenuation in Vegetated and
 Unvegetated Sites in the Bay 14
 Historical Data Bases and Optical Properties of the
 Chesapeake Bay 20

III. Light and Photosynthesis in Chesapeake Bay SAV Communities . 28
 General Review of Photosynthesis 28
 Photosynthesis of Submerged Vascular Plants in Relation
 to Light and Temperature 29
 Photosynthesis-Light Studies in Chesapeake Bay 32
 P-I Relationship of Major Species 32
 Microcosm Studies 37
 In Situ Studies of Community Response to Light 37

IV. Summary 49

Literature Cited 52

LIST OF FIGURES

<u>Number</u>		<u>Page</u>
1	Path of light from the atmosphere to benthic estuarine macrophytes.	9
2	Downwelling spectral quanta irradiance in a <u>Zostera</u> bed	11
3	Diffuse downwelling spectral attenuation coefficients for Chesapeake Bay	15
4	Lower Chesapeake Bay light study stations	16
5	Diffuse downwelling spectral attenuation coefficients for vegetated and unvegetated sites.	17
6	Downwelling PAR attenuation coefficients for vegetated and unvegetated sites.	19
7	Historical Chesapeake Bay Secchi disk values.	21
8	Summary of the historical chlorophyll <u>a</u> data for the upper and lower Chesapeake Bay	23
9	Historical chlorophyll <u>a</u> data for three regions of Chesapeake Bay	24
10	Enriched areas of the Chesapeake Bay.	26
11	Diagrammatic photosynthesis-light curves	30
12	Photosynthesis-light curves for two upper Chesapeake Bay species	33
13	Photosynthesis-light curves for two lower Chesapeake Bay species	35
14	Vertical distribution of leaf area index for <u>Ruppia</u> and <u>Zostera</u>	38
15	Total chlorophyll in <u>Ruppia</u> and <u>Zostera</u> leaves.	39
16	Suspended solids, light availability and <u>Potamogeton</u> photosynthesis	40

LIST OF FIGURES (continued)

<u>Number</u>		<u>Page</u>
17	The effect of light flux on upper Chesapeake Bay SAV photosynthesis	42
18	Diagrammatic representation of light flux and calculated photosynthetic parameters for an upper Chesapeake Bay site . .	43
19	Apparent productivity and light flux at a <u>Ruppia</u> site	44
20	Apparent productivity and light flux at a <u>Zostera</u> site.	45
21	Apparent productivity vs light flux for three sites in the lower Chesapeake Bay	46

LIST OF TABLES

<u>Number</u>		<u>Page</u>
I	Comparison of PAR Attenuation Coefficients inside and outside a SAV bed	18
II	Secchi Disc Data, upper Chesapeake Bay	22
III	Chlorophyll <u>a</u> Concentrations in the lower Potomac River	20
IV	Freshwater Flows and Hurricanes in Chesapeake Bay	25
V	Suspended Sediment Transport in the Susquehanna River	27
VI	Photosynthetic Parameters for <u>Ruppia</u> and <u>Zostera</u>	34
VII	Literature Review of Photosynthesis-Light Experiments	36
VIII	In situ O ₂ Productivity and Light Experiments	47

SECTION I

INTRODUCTION

The initial focus of submerged aquatic vascular plant (SAV) research in 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 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 and Penhale, 1979).

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 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 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 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 Zostera 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 available light 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 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 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.

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 ^{14}C 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% of ambient light to determine the effect of light quantity on photosynthesis. 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. Physiologically, the photosynthesis-light relationship determines the light levels at which SAV can grow and reproduce, i.e., 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/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 evaluate potential morphological adaptation of the plants to various light environments. To complement these specific ^{14}C 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% 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 light available for vascular plant photosynthesis. What remained was determining what environmental conditions favor colonization and at what point does it stress the vascular plant.

These various research activities provided a data and information base that serve management needs and identified 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 is directed to our current state of understanding on light energy properties and distribution in Chesapeake Bay and 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 photosynthesis in particular wavelength bands controlled by their specific pigment complexes. 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 scattering of light. Selective absorption and scattering by these factors results 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, i.e. 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; Kranch, 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 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 Dunston, 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, the Chesapeake Bay being no exception. Burt (1953, 1955) 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) 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 "which is defined as the absorption coefficient plus the total scattering coefficient" (Jerlov, 1976; Kiefe and Austin, 1974). van Tine (1981) found correlations between absence of submerged aquatic vegetation and low transmittance values in an estuary in the Gulf of Mexico.

Total particulate mater (TPM), particulate organic matter (POM) particulate-ATP, particulate chlorophyll a, particulate inorganic matter (PIM), and dissolved nutrients were monotored 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) suggested a close relationship between wind and current for the York River and, 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) have shown a baffling effect on SAV on currents causing particulate matter to settle out thus generally improving the local light environment. Collection and analyses of these data formed the basis for characterization of the natural light environment and factors which are principal controls.

Various lines of evidence as discussed earlier, suggested 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. Both field and laboratory studies were designed and carried out in later phases of CBP-SAV research 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 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 possible situations where water quality deteriorates to the point where light penetration is reduced. The purpose being 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). Using 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 are to: (1) provide in an overview fashion, the general characteristics 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.

SECTION II

LIGHT IN THE 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 H₂O 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 packs or quanta (Q) of energy termed photons. The energy content (ϵ) of each quantum is directly proportional to the frequency (ν),

$$\epsilon = h\nu$$

and indirectly proportional to the wavelength (λ),

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

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 Fig. 1a. Most of the energy reaching the earth's surface is contained within the shorter wavelengths (.4-1 μ or 400-1000 nanometers¹(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. It is seen that 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 via absorption. Only 4-11% of incident irradiance between 300-700 nm is reflected from the surface or backscattered out of the water column (termed albedo) (Clark and Ewing, 1974).

The properties and concepts in 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.

¹ 1nm = 10⁻³ μ m = 10⁻⁹ m

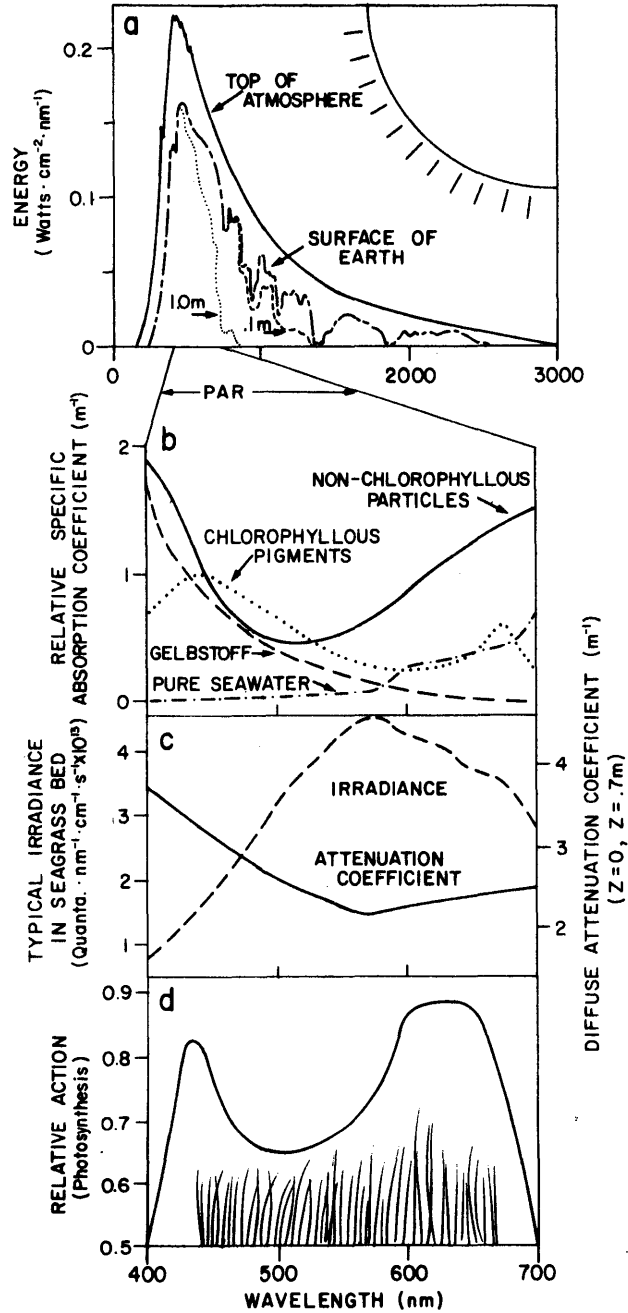


Figure 1. Theoretical path of light from top of atmosphere to benthic estuarine macrophytes. (a) Spectral energy distribution of light at top of atmosphere, at the surface of earth, and at two depths in the ocean on a clear day (Redrawn from: Jerlov, 1976 and Gates, 1971). (b) Relative spectral absorption of various constituents of 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 (Redrawn from Inada, 1976).

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 which cause the observed attenuation.

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 Fig. 1). The effect of sea salts on attenuation is insignificant. Pure water or pure seawater shows 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 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 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, 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_0) is generally in the range of .75 to .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, i.e., spectral irradiance. A family of downwelling spectral irradiance curves, in quanta, are shown in Figure 2 for a Zostera marina bed on the Eastern Shore of the Chesapeake Bay.

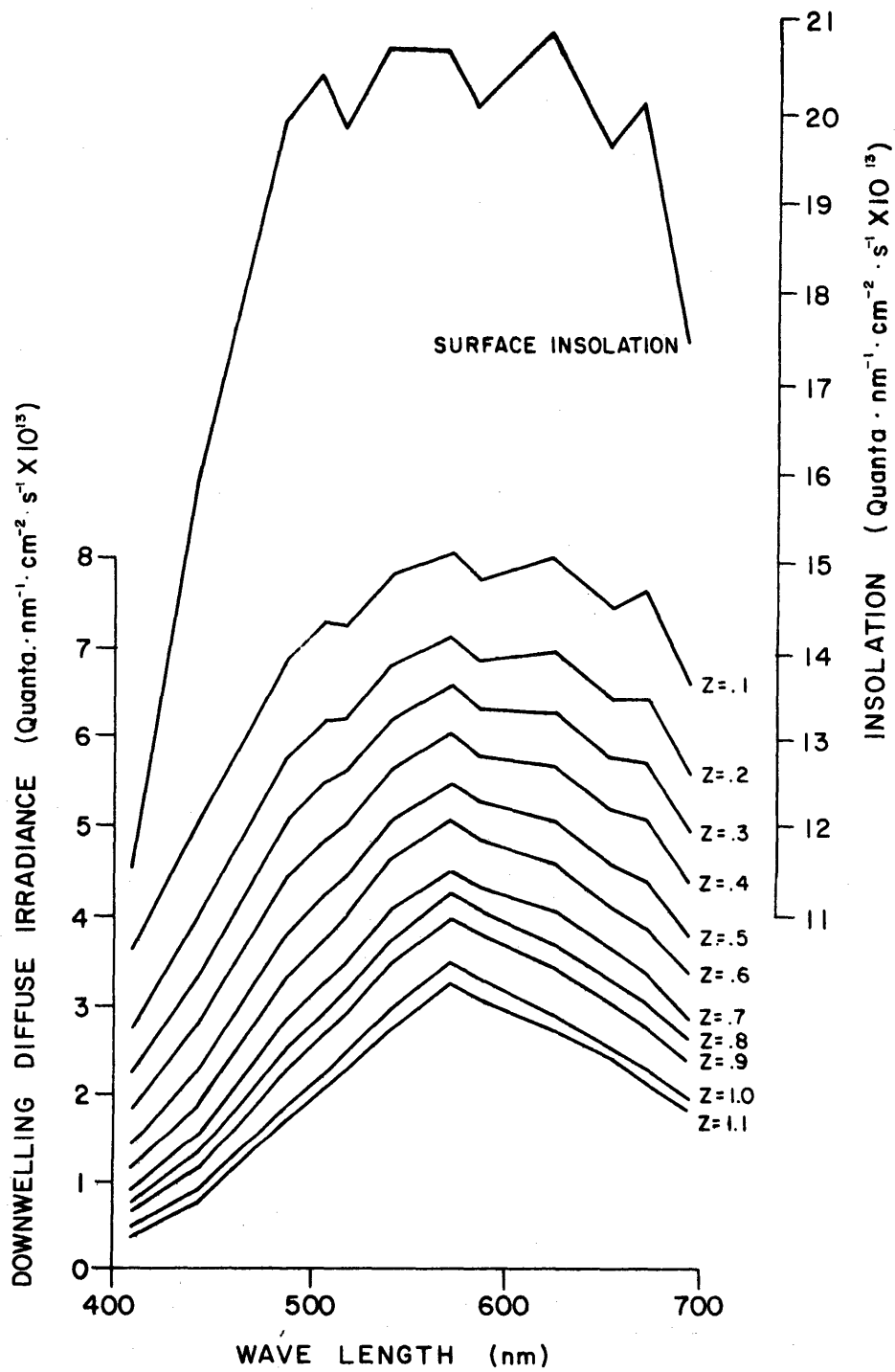


Figure 2. Downwelling spectral quanta irradiance at the surface and at several depths above the canopy of a *Zostera marina* bed on the Eastern Shore of the lower Chesapeake Bay (Vaucluse Shores) at 1230 E.S.T. on a cloudy April day. The scale for the insolation is on the right (Wetzel et al., 1981).

Primary producers or autotrophs contain light-capturing pigments to carry out photosynthesis. Most photoplankton 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 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 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 or λ) is a particularly useful parameter for comparing underwater irradiance between water bodies, seasons, and wavelengths. Since 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 seagrass 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 Fig. 1b). Pierce et al. (1981) have 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 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.

²Often incorrectly termed extinction coefficient

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 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 due to 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 both 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 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). 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 differences in depth. These are, of course, highly idiosyncratic for specific systems (Burt, 1955; Scott, 1978).

LIGHT ATTENUATION IN THE CHESAPEAKE BAY

A comparison of diffuse downwelling spectral attenuation co-efficients reported for the Chesapeake Bay and its tributaries is presented in Figure 3 along with Jerlov's (1976) most turbid coastal water classification curve (Type 9). For the Chesapeake Bay, the earliest measurements of $K(\lambda)$ 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. 3a represent the range of values measured by Wetzel et al. (1981) 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 together with their specific site measurements in and near the mouths of the Sassafrass, Patuxent, Potomac and Chester Rivers in Fig. 3c. Their mean values fall within the upper ranges measured (Wetzel et al., 1981) 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 one at the mouth are plotted in Fig. 3b. The upriver station was found to be consistently more turbid; presumably due to 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 4π irradiance measurements in the Rhode River which generally agree with the measurements of Pierce et al. (1981) except in region 500-700 nm. Their measures fall within the observations made for the lower Bay (Wetzel et al., 1981). 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 Sassafrass River are the highest reported for the Bay. As noted there is nearly no available light below 500-600 nm. Wetzel et al. (1981) 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 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 illustrates the lower Bay sampling stations.

A summary of the recent Chesapeake Bay data on diffuse downwelling 2π irradiance attenuation coefficients indicates a severe attenuation of light energy in the photosynthetically important 400-500 nm (blue and 700-775 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 Sassafrass 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). 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., 1981).

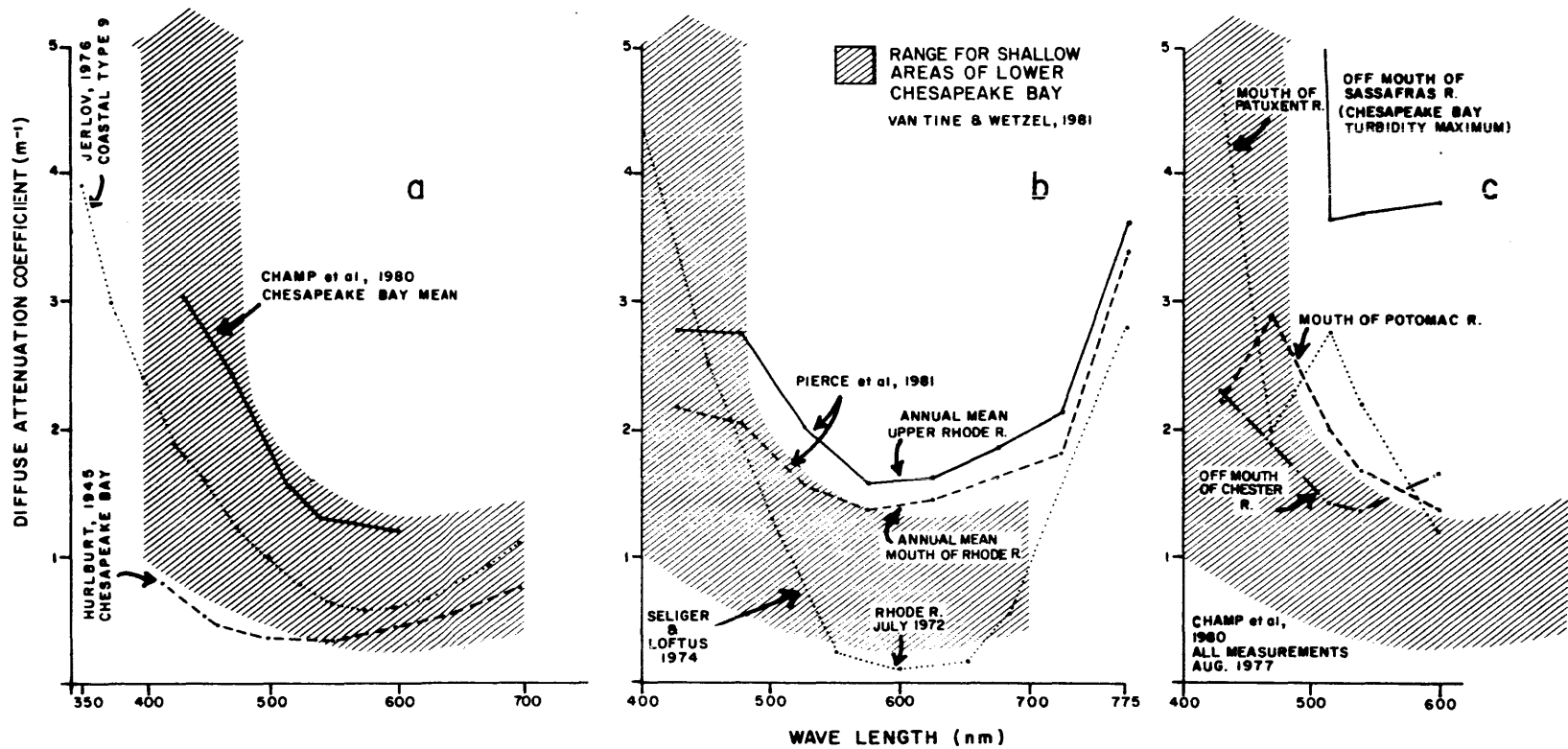


Figure 3. Comparison of diffuse downwelling spectral attenuation coefficients for Chesapeake Bay with Jerlov's most turbid coastal classification. (a) Plotted from tables in Jerlov, 1976; Hurlburt, 1945; Champ et al., 1980 (b) Plotted from table in Pierce et al., 1981 and calculated from 4π irradiance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

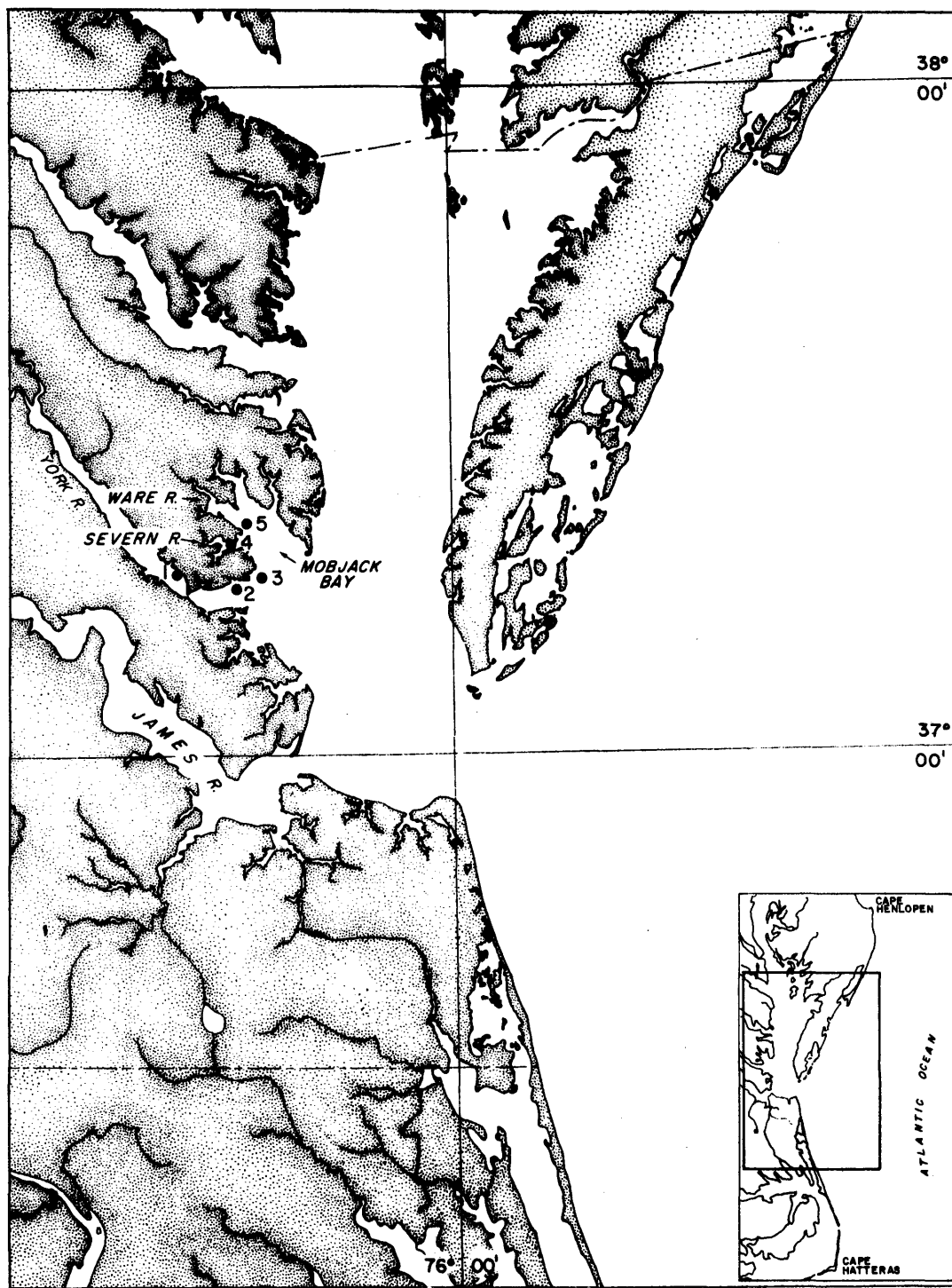


Figure 4. Locations of lower Bay stations (Wetzel et al., 1981).
 (1) Mumfort Is., York R., (2) Allen's Is., York R., (3) Guinea Marshes, (4) Mouth of Severn R., Mobjack Bay, (5) Four Point Marsh, Ware R., Mobjack Bay.

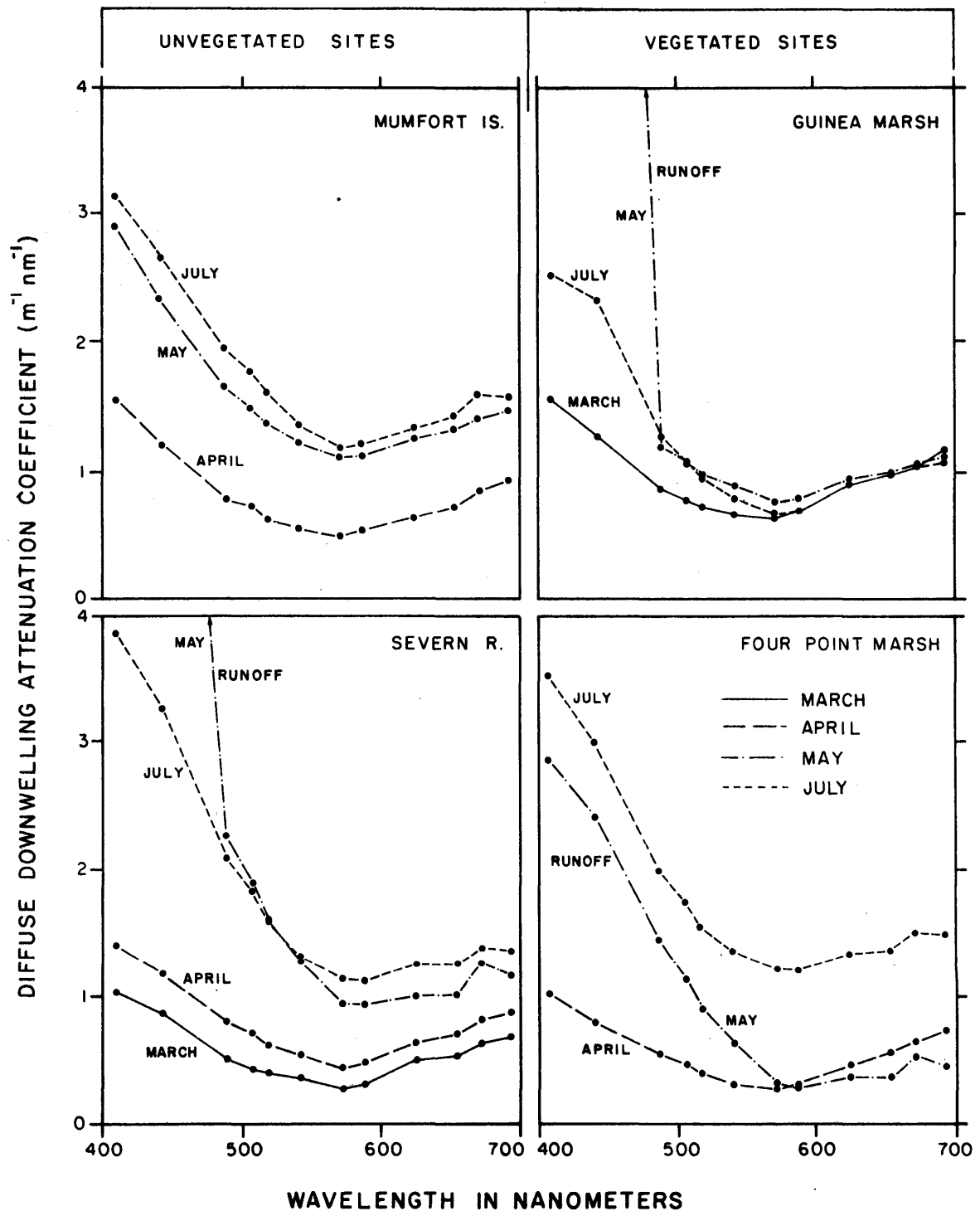


Figure 5. Mean monthly diffuse downwelling spectral attenuation coefficients for vegetated and unvegetated sites in the lower Chesapeake Bay. All coefficients calculated for the depth interval 0.1 to 0.5 m. Mumfort Island (York River) and Severn River sites: unvegetated. Guinea Marsh and Four Point Marsh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

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., 1981). 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 \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 $\text{nm}^{-1} \text{cm}^{-2} \text{s}^{-1}$, 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} (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 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) was grouped with the unvegetated sites having higher attenuation (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 analyses was the reduced attenuation in the 500-700 nm region at vegetated sites during May.

Kaumeier 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. The vegetated areas were 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.

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	$K_{\text{PAR}} (\text{m}^{-1})$
June	SAV	2.6 \pm 0.20
	Reference	2.5 \pm 0.75
July	SAV	2.5 \pm 0.30
	Reference	2.9 \pm 0.70

(continued)

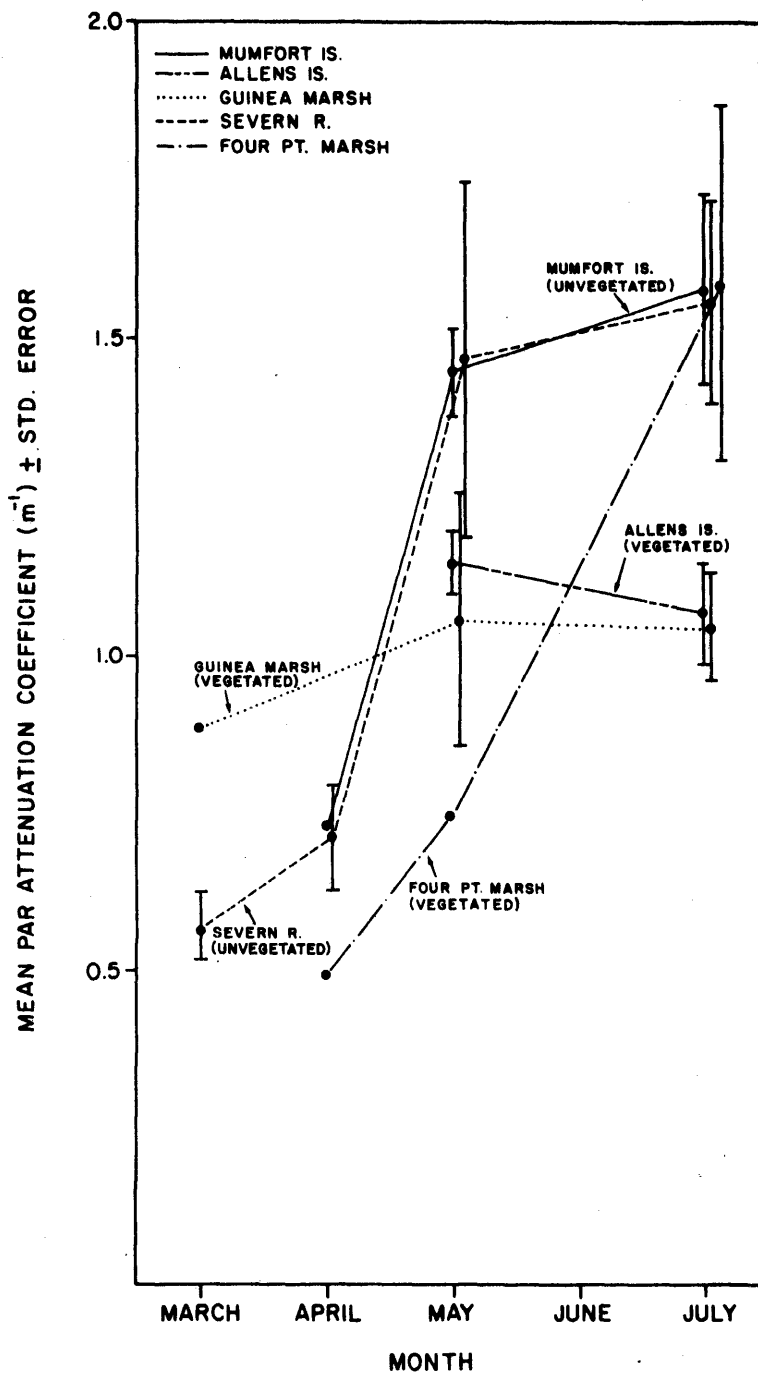


Figure 6. Mean monthly downwelling PAR attenuation coefficient ± 1 standard error of the mean for vegetated and unvegetated sites in the lower Chesapeake Bay (from Wetzel et al., 1981).

TABLE I. (continued)

Month	Location	K_{PAR} (m^{-1})
August	SAV	1.8 ± 0.56
	Reference	3.1 ± 0.33
September	SAV	1.9 ± 0.34
	Reference	3.8 ± 0.96

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 caused by increased nutrients can 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 $\mu g l^{-1}$ were not unusual. In contrast, lower Bay concentrations have not significantly changed (Fig. 8b).

TABLE III. RANGES OF CONCENTRATIONS OF CHLOROPHYLL *a* ($g l^{-1}$) 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

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.

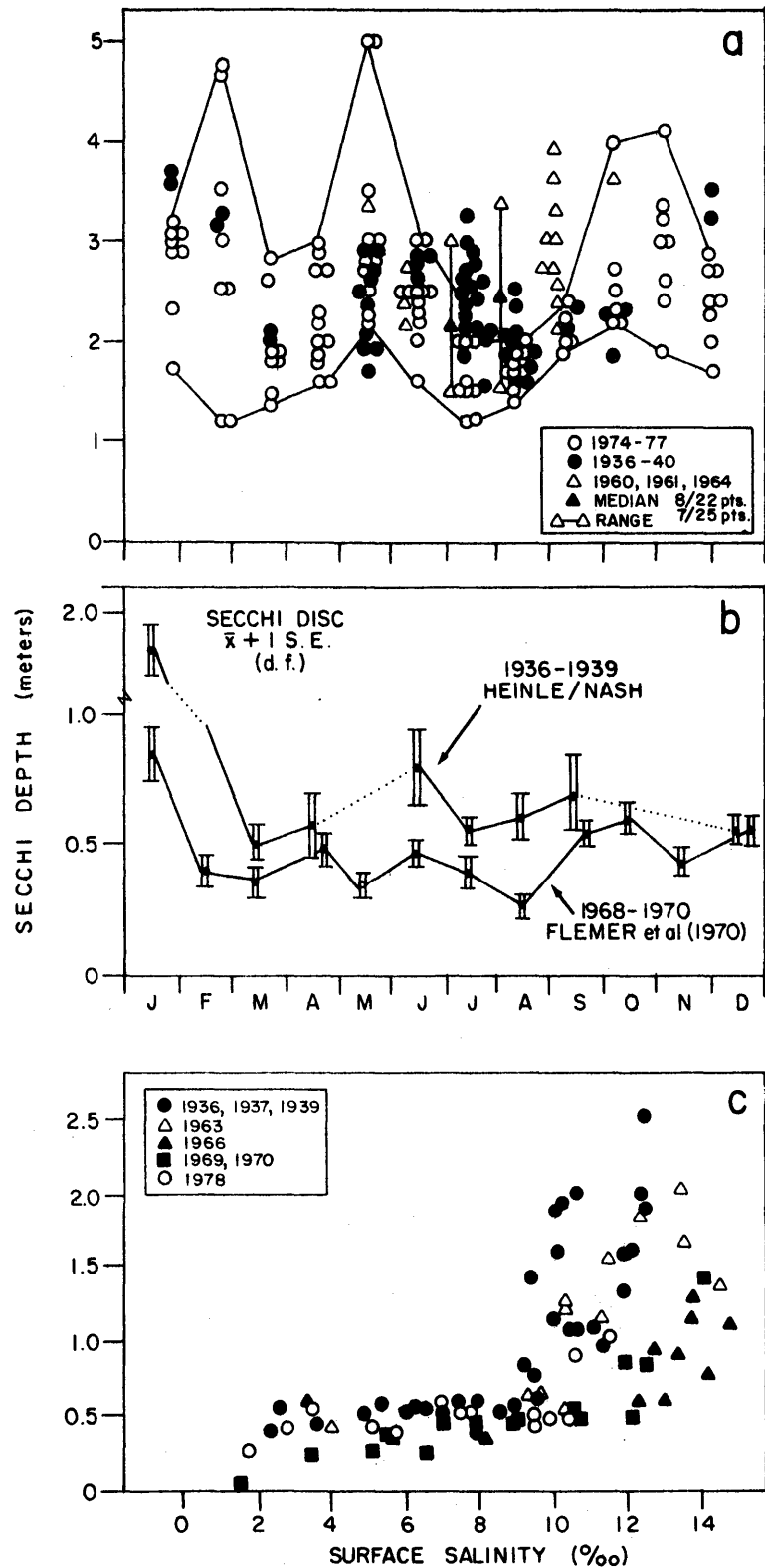


Figure 7. Historical Chesapeake Bay Secchi disc values (from Heinle et al., 1980 and references therein). (a) monthly mid-Bay means. (b) monthly means Patuxent River estuary. (c) Patuxent River Secchi depth vs. salinity, July.

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 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
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

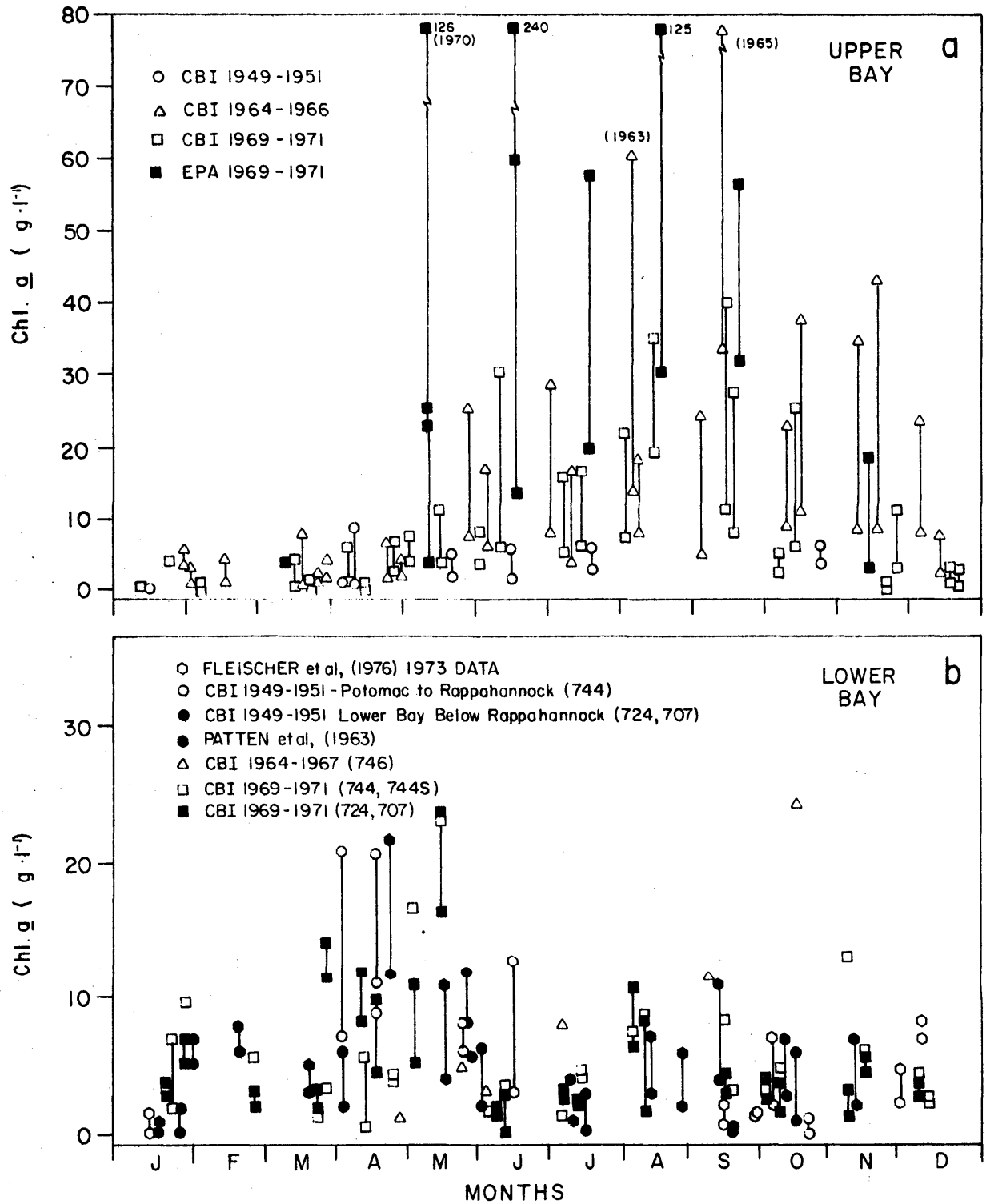


Figure 8. Summary of historical chlorophyll a data for the Chesapeake Bay. (a) upper Bay. (b) lower Bay (Redrawn from Heinle et al., 1980).

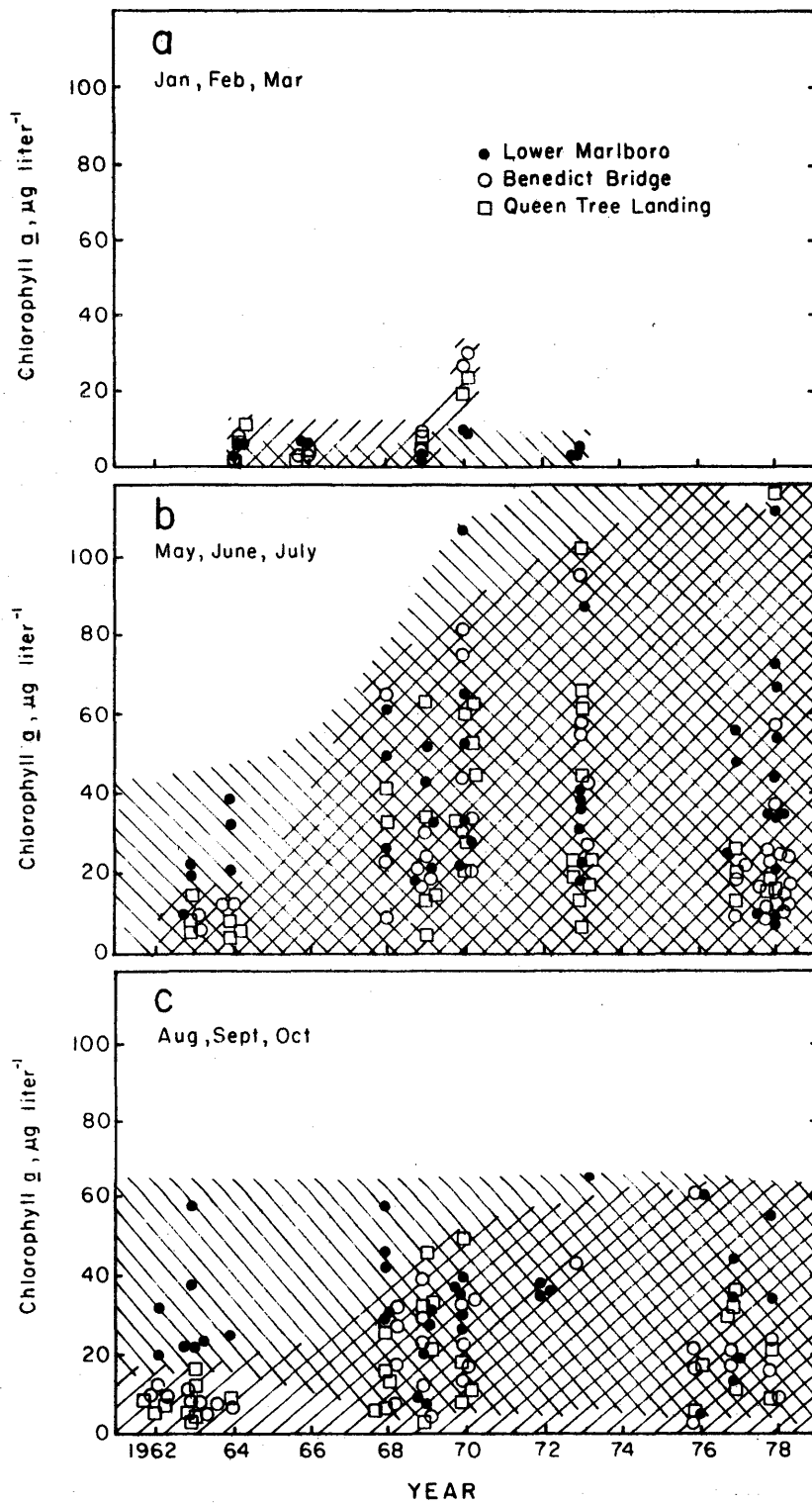


Figure 9. Summary of historical chlorophyll a data for three regions of the surface waters of the Patuxent R., Md. (a) January-March (b) May-July (c) August-October (Redrawn from Heinle et al., 1980).

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 shows the regions of the Bay which they categorized as moderately or heavily enriched. Many of these areas have experienced declines in Bay grasses on a time scale overlapping the enrichment.

TABLE IV. ANNUAL MEAN FRESHWATER FLOWS AND OCCURENCE 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

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 additional input due to 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 favoring phytoplankton blooms.

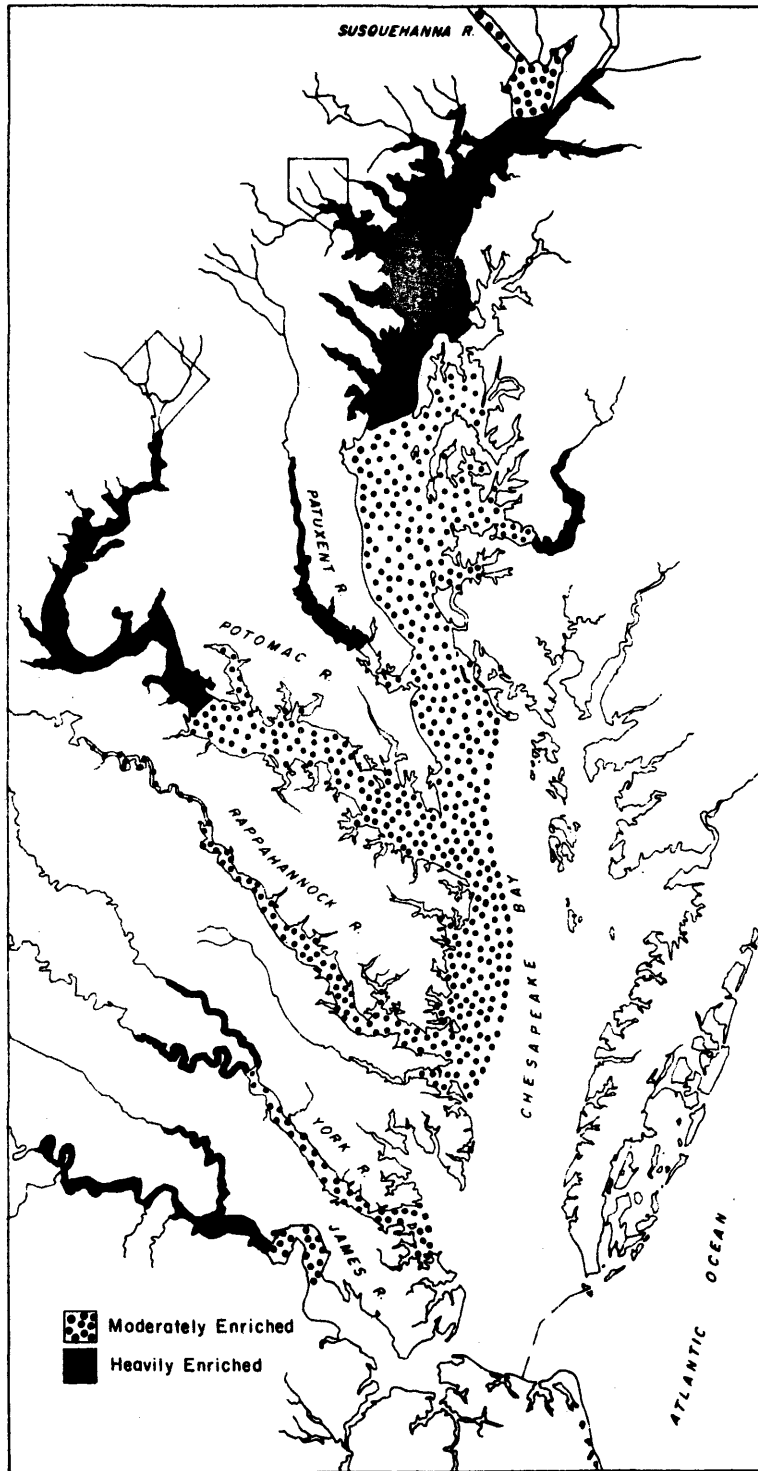


Figure 10. Portions of the Chesapeake Bay considered enriched by Heinle et al., 1980. Enrichment is defined as increase in chlorophyll a levels from historic, natural periods of stability.

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

TABLE V. 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 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.

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 IV) 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 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 the general climatic regime being the principal driving forces.

SECTION III

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 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, 400-720 nm. Chlorophyll a absorbs light more effectively at higher wavelengths (>600 nm) while 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 it is used directly for biochemical reactions.

The photochemical reactions are driven by units of light energy termed photons (quantum energy). The quantum energy is a function of wavelength; quanta of shorter wavelengths contain more energy than quanta of higher 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. 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 termed 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 since it reflects the ability of a species to adapt to various light spectral 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 material, dissolved organic compounds and other water column constituents as discussed in Section II.

A general approach to the investigation of photosynthesis 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 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). 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 Michaelis-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 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.

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 9-month period. Biomass and photosynthesis 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, Neinhuis 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.

In situ light manipulation experiments provided evidence of the importance of light to seagrass production. For example, at the end of a 9-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, primarily due to shading of the macrophytes by the epiphytes. Both Kiorbe (1980) and Phillips et al. (1978) provided data to indicate that epiphytic development suppressed macrophyte growth. Sand-Jensen

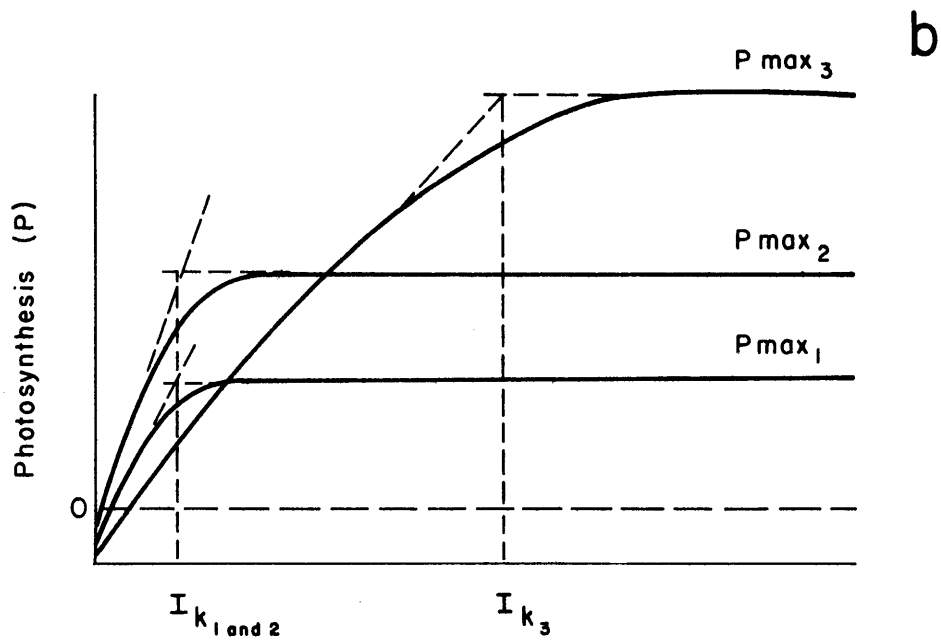
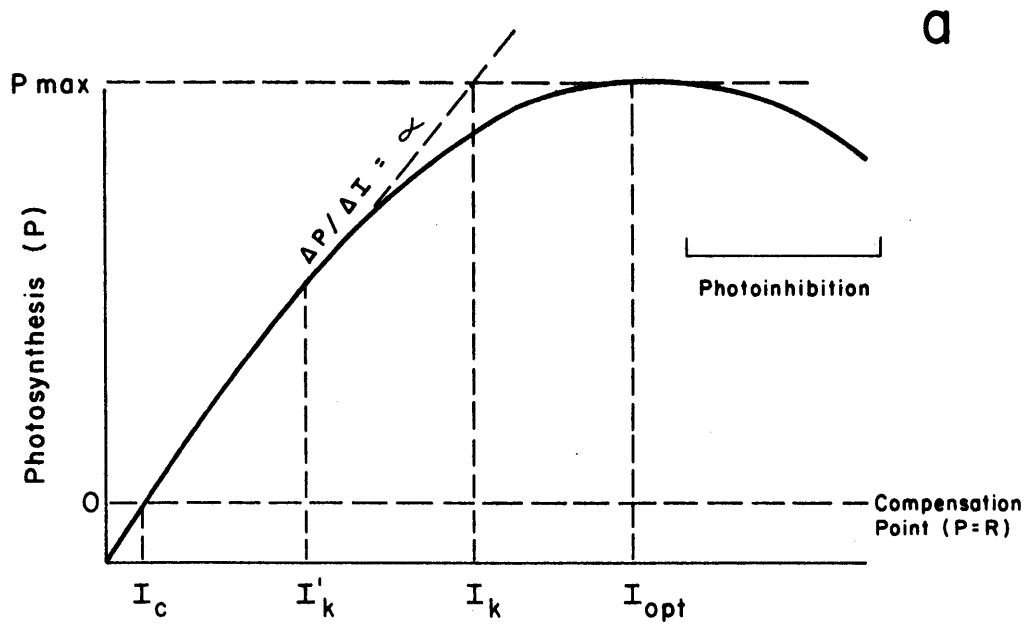


Figure 11. Diagrammatic photosynthesis-light relationships. See text for description of parameters.

(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. In contrast, 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 reduced 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 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 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 α 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, 1970 a, b; Titus and Adams, 1979). Sun species generally exhibit higher P_{max} values than shade species which exhibit greater α 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 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; 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 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) 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 and Zostera marina and Ruppia maritima in the lower Bay. These experiments utilized whole plants or leaves subjected to various light intensities (created through the use of neutral density screens) and various temperatures.

The second approach utilized microcosms in which the effects of various concentrations of phytoplankton and suspended solids on light penetration and 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. (1981) and Wetzel et al. (1981).

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 to light with light saturation occurring between 600 and 800 $\mu\text{E m}^{-2} \text{s}^{-1}$. 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 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., 1981). Since these species co-exist in the lower Chesapeake Bay, an evaluation of

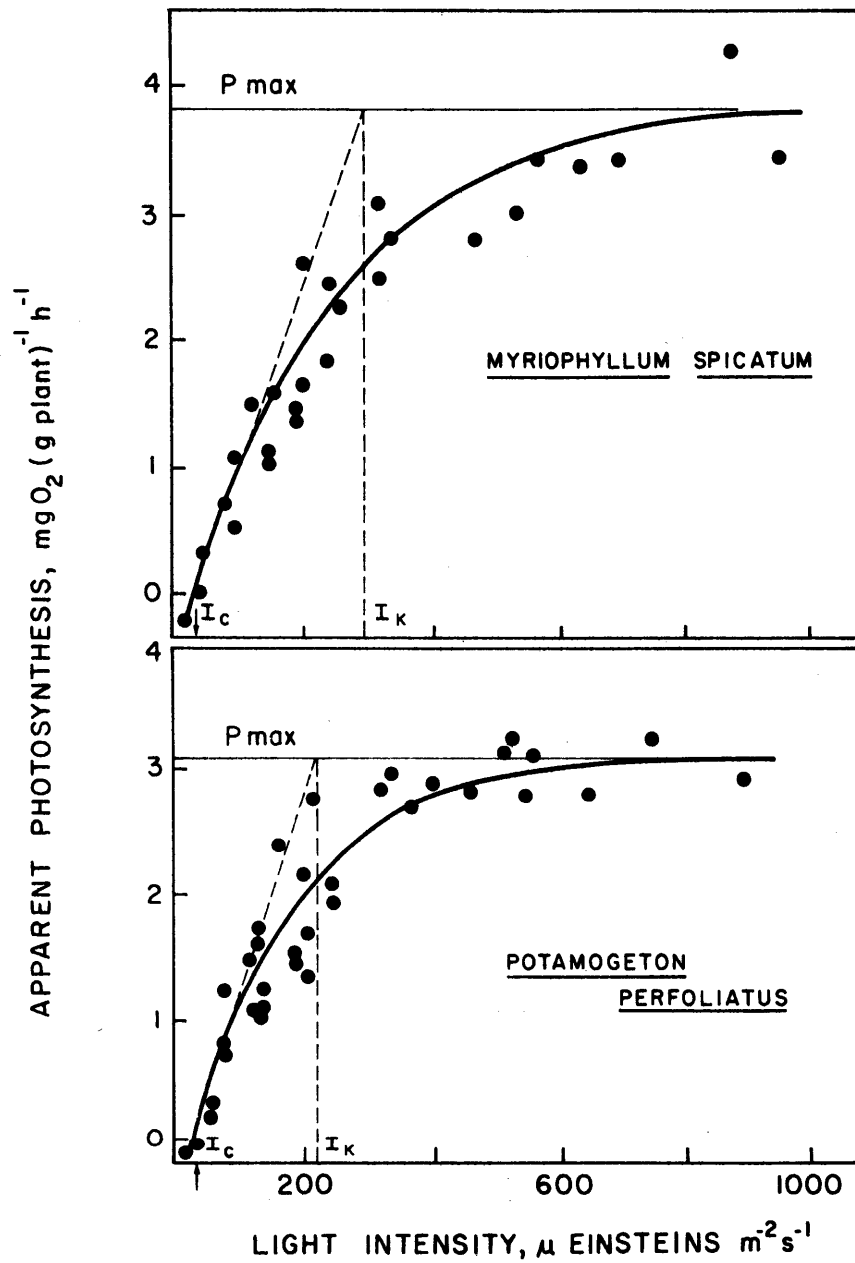


Figure 12. Photosynthesis-light curves for two species of upper Chesapeake Bay submerged vascular plants (from Kemp et al., 1981).

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 $300 \mu\text{E m}^{-2} \text{s}^{-1}$ while Ruppia light saturation requires about $700 \mu\text{E m}^{-2} \text{s}^{-1}$ to become light saturated. 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 $>8^{\circ} \text{C}$ (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.

TABLE VI . PHOTOSYNTHETIC PARAMETERS FOR RUPPIA MARITIMA AND ZOSTERA MARINA LEAVES AT VARIOUS TEMPERATURES. THE LIGHT IS THE TOTAL LIGHT FLUX DURING THE 4h ^{14}C INCUBATIONS. (FROM WETZEL et al., 1981).

TEMP $^{\circ}\text{C}$	LIGHT E m^{-2}	P_{max} ($\text{mg C g}^{-1} \text{h}^{-1}$)		INITIAL SLOPE α	
		<u>Ruppia</u>	<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 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 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 $3.7 \text{ mg C g}^{-1} \text{hr}^{-1}$. I'_{k} ranged from 110 to $225 \mu\text{E m}^{-2} \text{s}^{-1}$ and I'_{k} from 70 to $350 \mu\text{E m}^{-2} \text{s}^{-1}$.

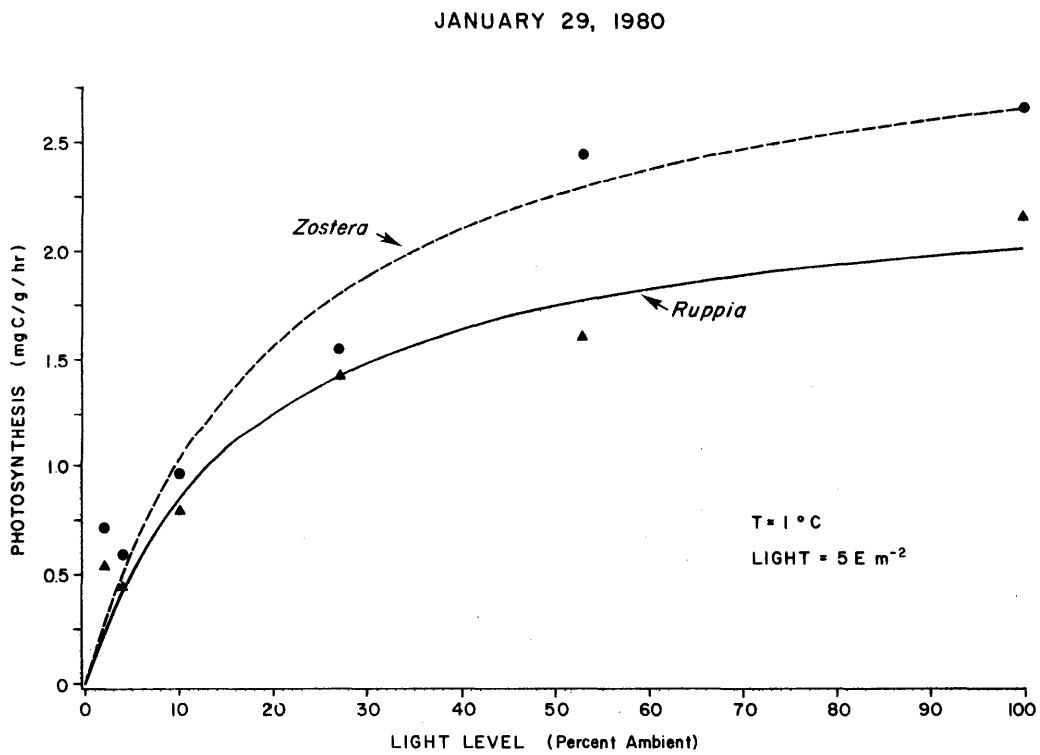
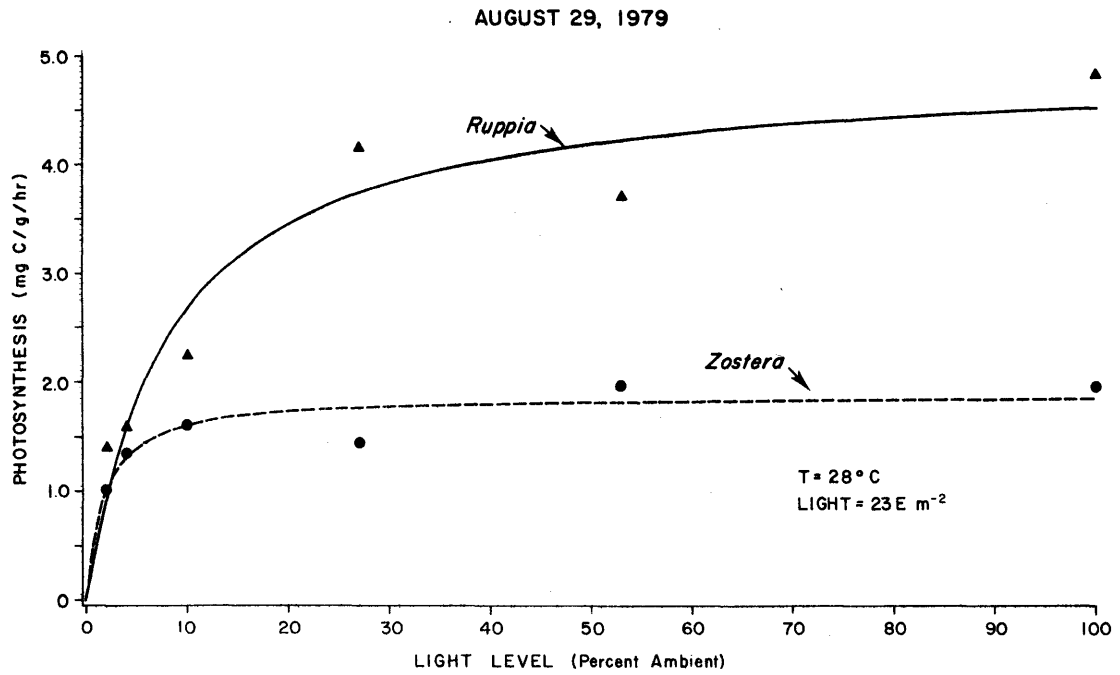


Figure 13. Photosynthesis-light curves for Ruppia and Zostera from a mixed bed site on the Eastern Shore, Virginia. Light is total light flux during 4 h ¹⁴C incubations (from Wetzel et al., 1981).

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	
<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 & Waisel 1979
" "	1.5	130	175	40	Drew 1978
<u>Halodule uninervis</u>	1.6	140	220	50	Bear & Waisel 1979
<u>Syringodium filiforme</u>	3.7	225	290	120	Buesa 1975
<u>Ruppia maritima</u>	1.9	123	236	30	Nixon & Oviatt 1973
<u>Vallisneria americana</u>	2.2	130	100	--	Titus & 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 & Adams 1979
" "	1.9	110	70	25	Van et al. 1976
" "	1.3	200	290	30	Kemp et al. 1981
<u>Potamogeton pectinatus</u>	0.9	195	350	60	Westlake 1967
<u>P. perfoliatus</u>	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 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 (μE m⁻² s⁻¹) assuming 1 mW cm⁻² = 2360 Lux = 0.86 cal cm⁻² h⁻¹ = 46 μE m⁻² s⁻¹ (Hansen & Biggs, 1979).

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

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., 1981). 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. 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., 1981). Ruppia also showed a higher total chlorophyll concentration than Zostera. This higher chlorophyll concentration in combination with its canopy structure are adaptations 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 suspended sediments 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.

AUGUST 1980

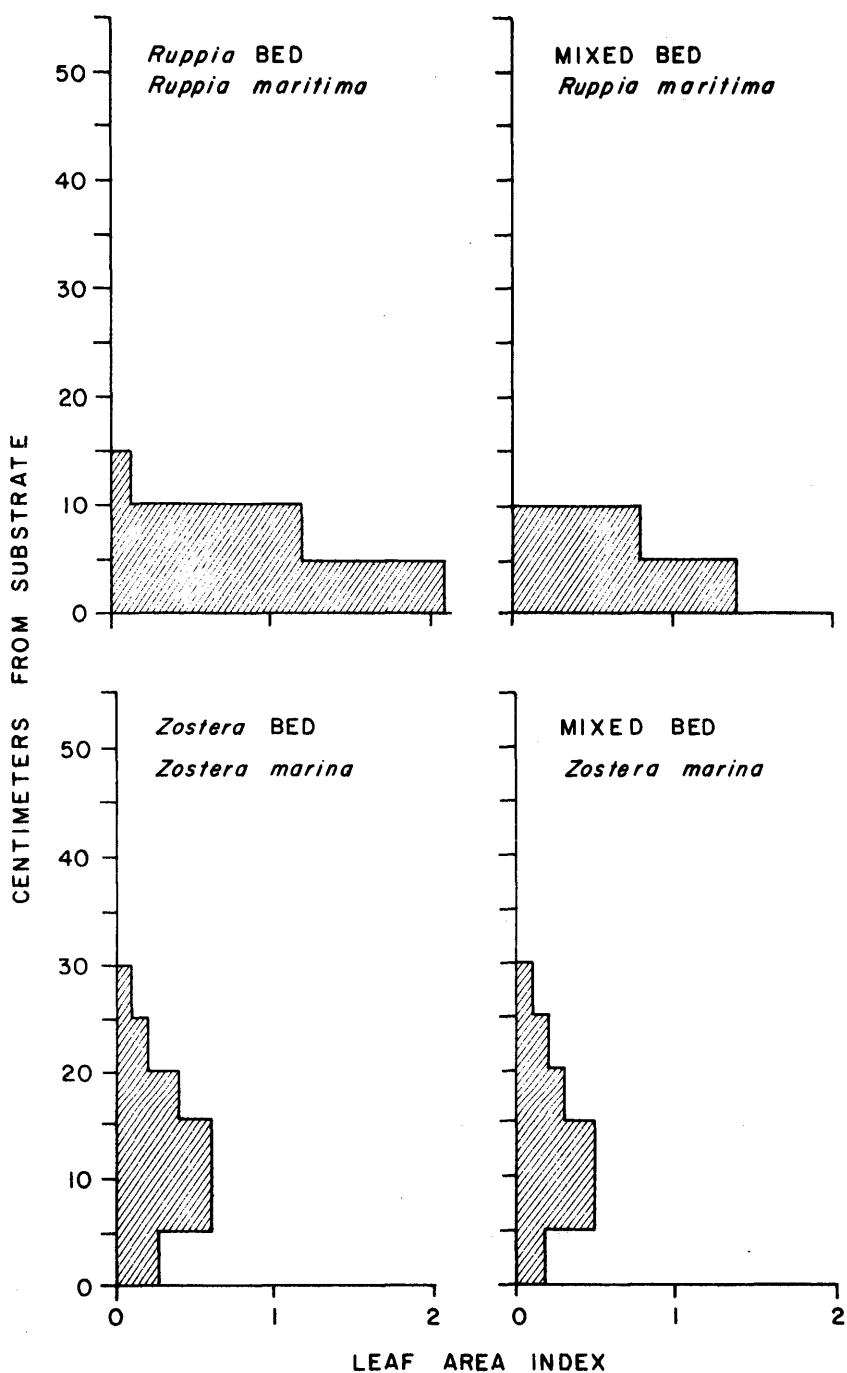


Figure 14. Vertical distribution of one-sided leaf area index (m^{-2} plant m^{-2} substrate) for *Ruppia* and *Zostera* at three vegetated sites on the Eastern Shore, Virginia (from Wetzel et al., 1981).

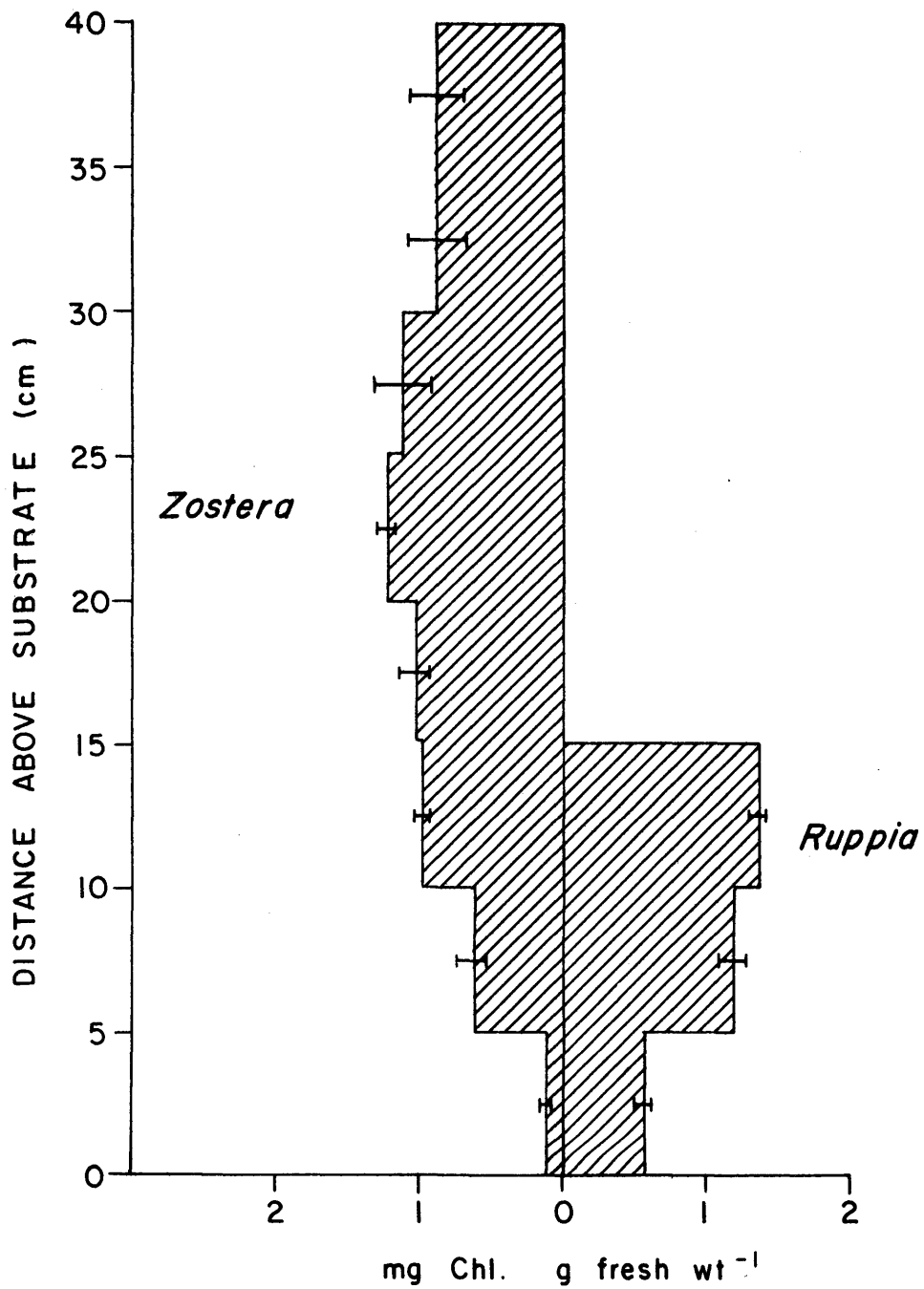


Figure 15. Vertical distribution of total chlorophyll for *Ruppia* and *Zostera* from a mixed bed area on the Eastern Shore, Virginia. Values \pm standard error, n = 3 (from Wetzel et al., 1981).

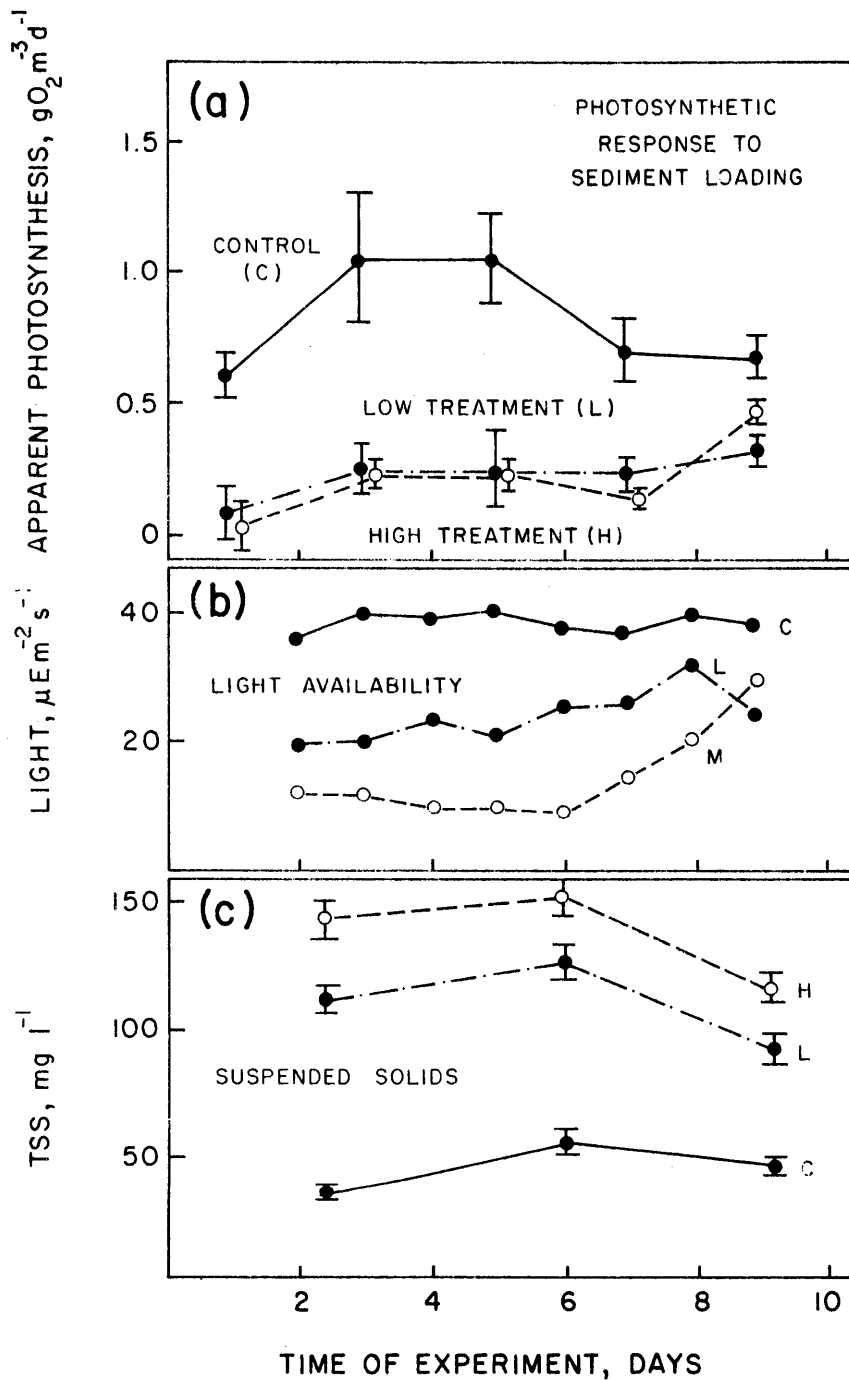


Figure 16. Effect of (c) total suspended solids (TSS) on (b) light availability and (a) rate of photosynthesis of Potamogeton perfoliatus (from Kemp et al., 1981).

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 $200 \text{ E m}^{-2} \text{ s}^{-1}$ 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 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., 1981). These studies were conducted under a wide range of in situ light regimes 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 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 (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.

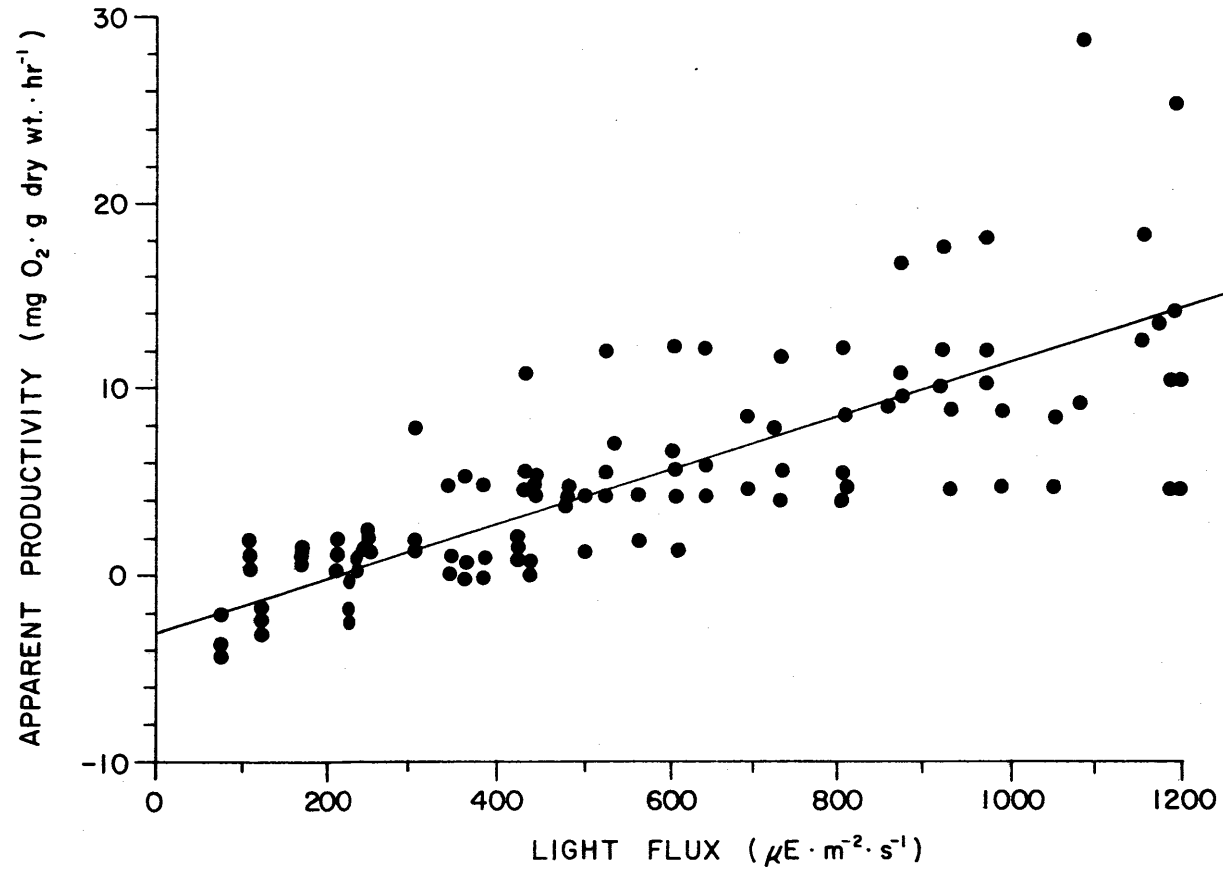


Figure 17. Response of upper Chesapeake Bay submerged vascular plants to light flux (from Boynton, unpublished data).

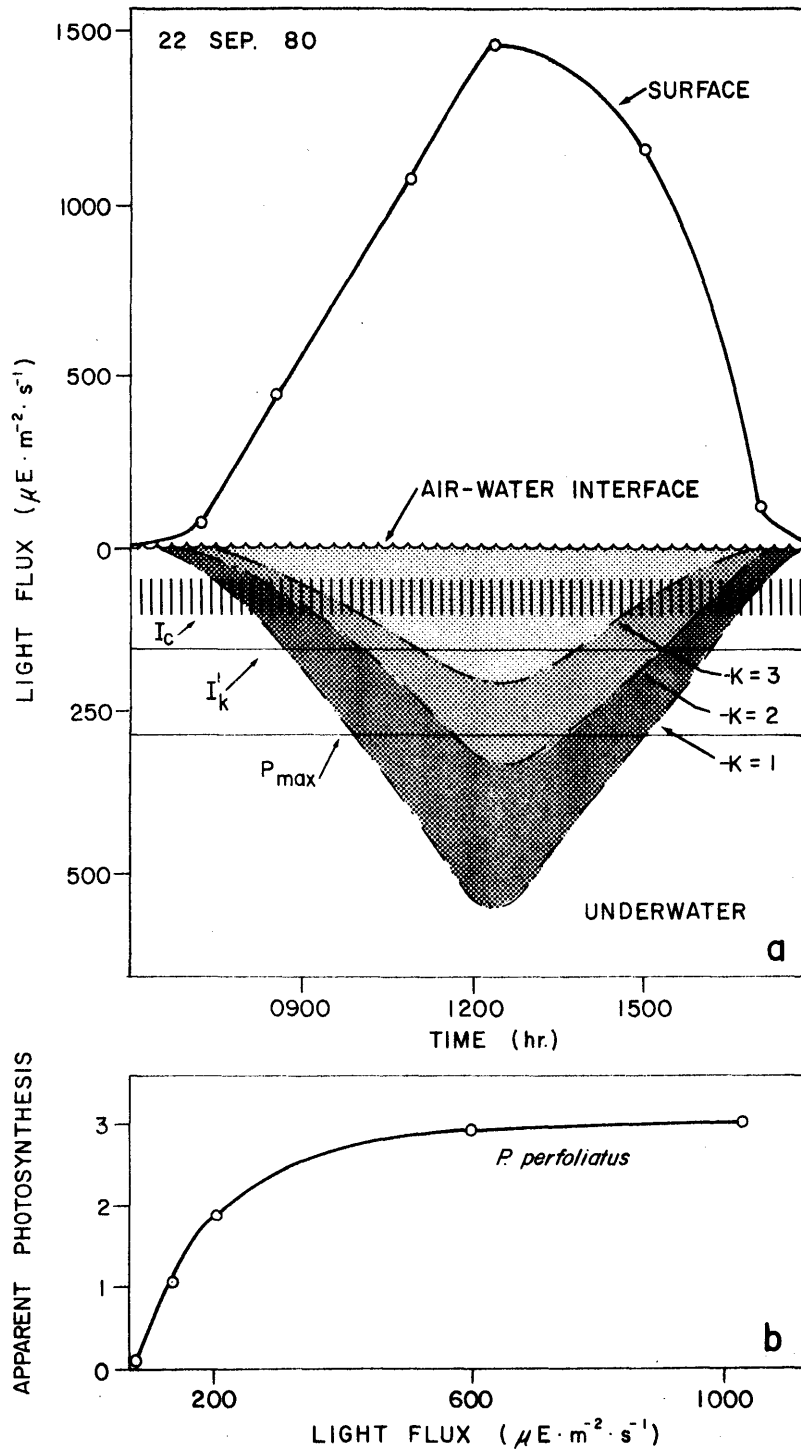


Figure 18. Diagrammatic representation of surface (a) and underwater (b) light flux at Todd's Cove, upper Chesapeake Bay calculated for three light extinction (K) coefficients. I_c , I'_k and P_{max} calculated from $P - I$ curve of Potamogeton perfoliatus (c). (from Kemp et al., 1981).

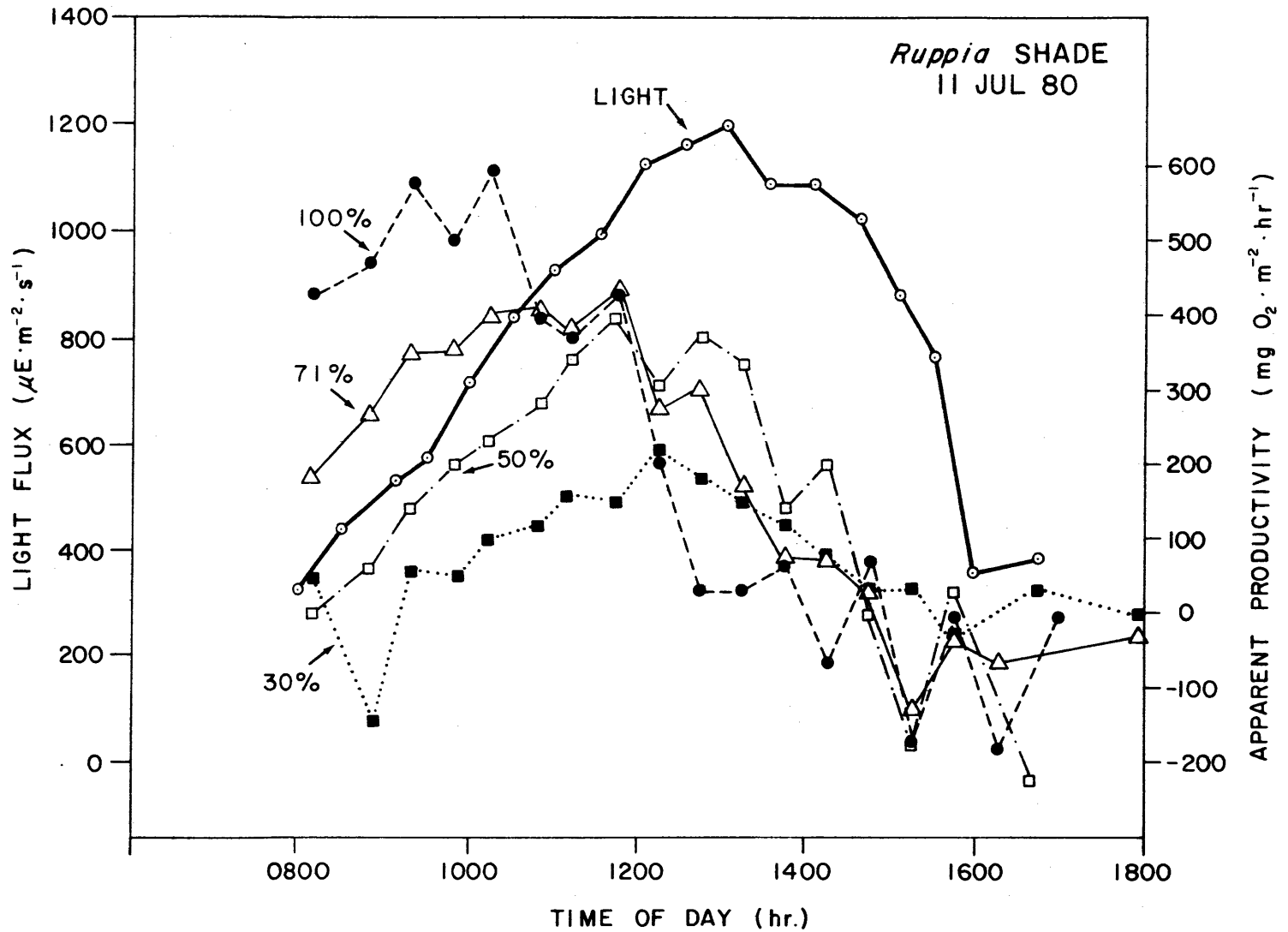


Figure 19. Apparent productivity and light flux at the canopy top vs time of day for *Ruppia* experiments at 100, 71, 50 and 30% of ambient light at the canopy top (from Wetzel et al., 1981).

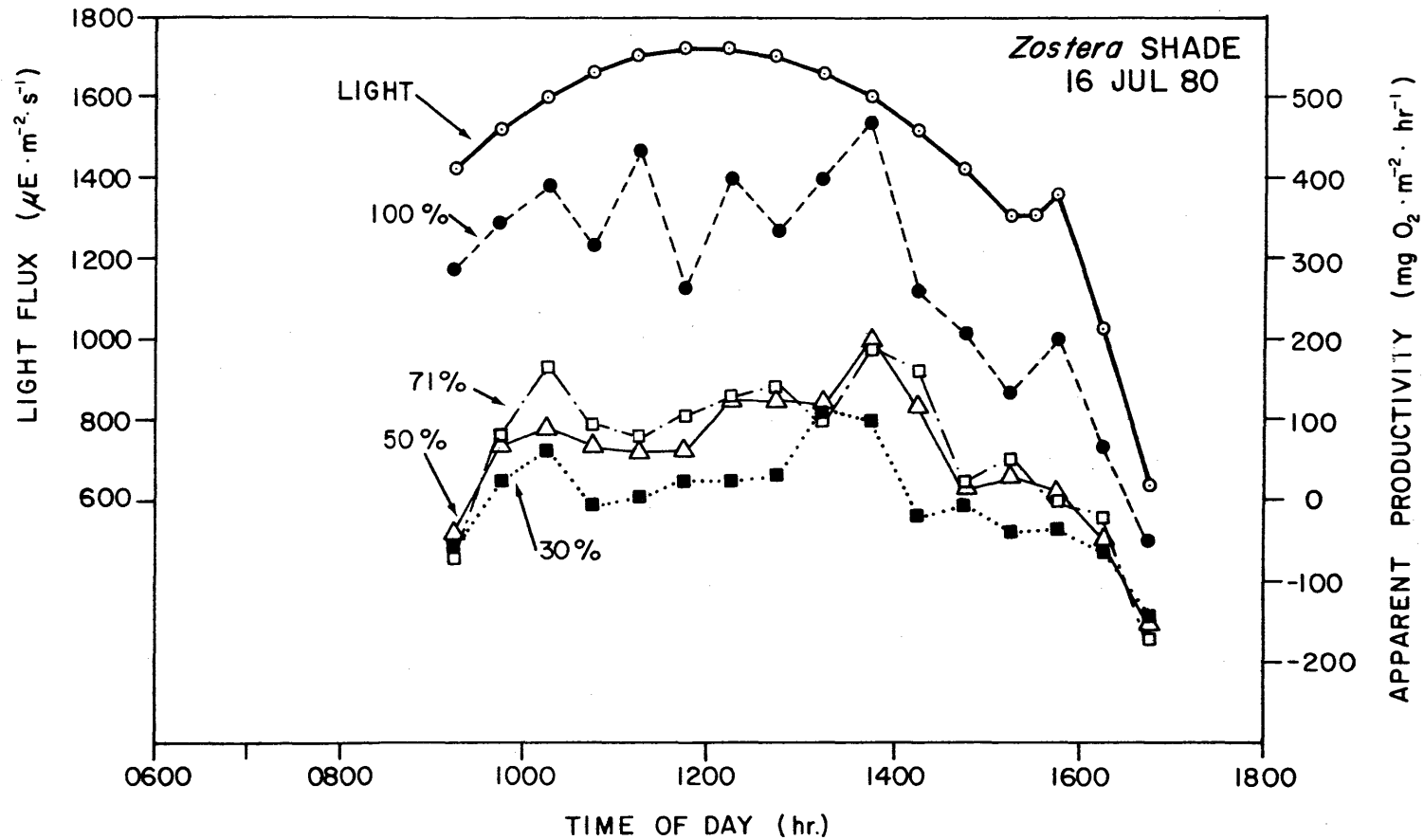


Figure 20. Apparent productivity and light flux at the canopy top vs time of day for *Zostera* experiments at 100, 71, 50 and 30% of ambient light at the canopy top (from Wetzel et al., 1981).

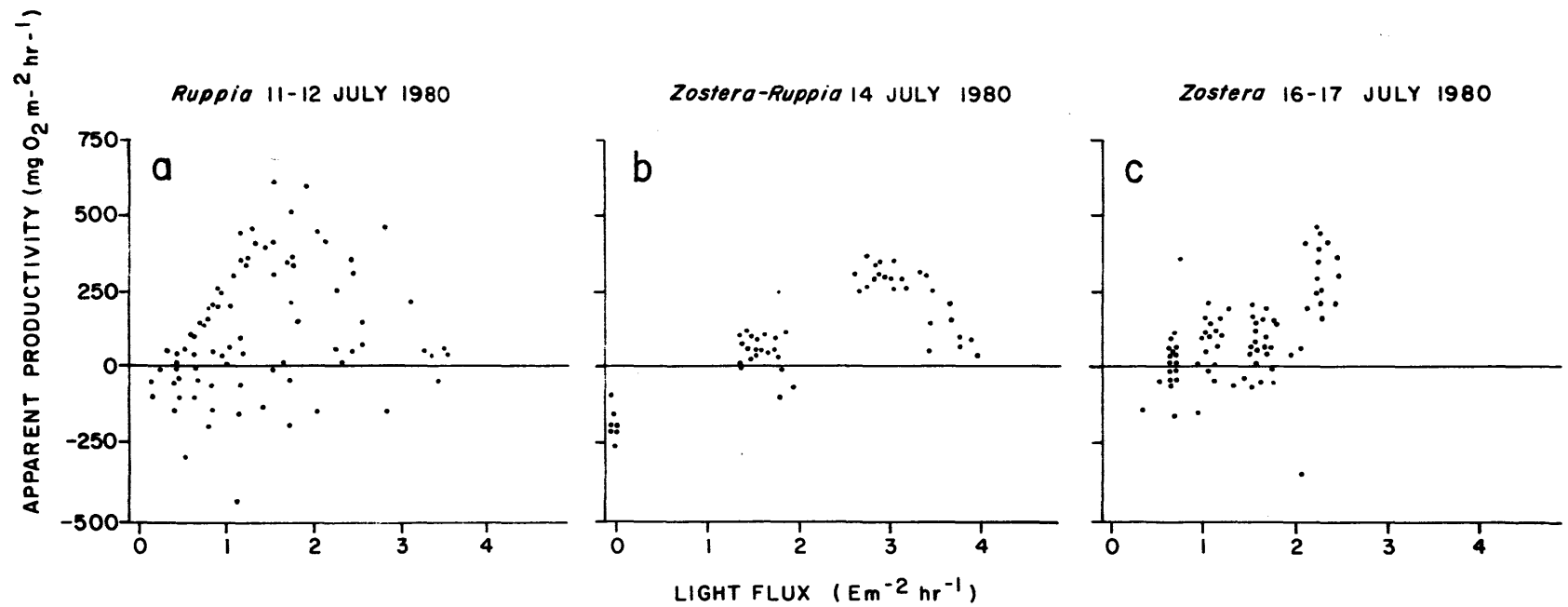


Figure 21. Apparent productivity vs light flux for Ruppia (a), mixed Ruppia-Zostera (b) and Zostera (c) areas, Eastern Shore, Virginia (from Wetzel et al., 1981).

The erratic pattern of data points and greater number of negative rates for Ruppia strongly suggest different community behavior. At the community level, the differences may be due to differences in community respiration rates or 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 for specific rate asymptotically approaches P_{max} . Therefore the linear relationship does not adequately describe the photosynthetic response. This is true for all measures taken at or near P_{max} .

TABLE VIII. APPARENT O_2 PRODUCTIVITY AND LIGHT: LINEAR REGRESSION ANALYSIS FOR LOWER BAY STUDIES (FROM WETZEL et al., 1981)

{MG O_2 m^{-2} HR^{-1} vs. E m^{-2} HR^{-1} (AT CANOPY TOP)}								
DATE	AREA	N	m	b	r	E m^{-2} HR^{-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
5 May 80	<u>Mixed</u>	28	89.7	-189	0.607	2.11		585
14 Jul 80	"	50	77.9	- 48.9	0.553	0.627		174

- ¹ N = number of observations
 m = slope
 b = y-intercept
 r = correlation coefficient
 I_c = estimated light compensation point (x-intercept)

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., 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 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 in the Vacluse Shores study area.

For the 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 IV

SUMMARY

The apparent optical properties of estuarine water create in general a light-limited environment for the process of photosynthesis. Water, suspended particles and dissolved compounds all interact to both attenuate total photosynthetically active radiation as well as spectrally shift (i.e. 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. In at least one documented case, a spectral shift created by pulp mill effluents caused an extensive decline and die-off in turtle grass (Thalassia testudinum) communities in northern Florida (R. J. Livingston, pers. comm.).

However, data on spectral characteristics and specific waveband attenuation in estuarine and coastal environments are lacking. Our summary of available data, Section II, 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 autotrophic production in the Chesapeake Bay as well as other estuaries. The current data base is neither extensive nor intensive enough to draw conclusions. It has only been within the past decade that submarine spectral irradiance studies have become technologically feasible and this is reflected in the general paucity of information.

Studies in the 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 II) in lower Bay communities indicate a severe attenuation of light energy in the photosynthetically important 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 the Chesapeake Bay with regard to light quality and quantity suggests some improvement (i.e. lower attenuation) in the vegetated areas although the data are quite variable. Kaumeyer et al. (1981) in the upper Bay reported significant differences for one site and not for another while in the lower Bay, comparison of four sites (two vegetated and two non-vegetated) does not indicate consistent

differences in either light quantity or quality. There may be, at these lower Bay sites, some improvement in attenuation in the 400 to 500 nm region in spring months. The only definitive light quality differences between the sites was reduced attenuation in the 500 to 700 nm region in vegetated areas during May. At the present, we do not have a very good estimate of daily variability in order to evaluate point measurements such as these. However, even with these rather limited data, diffuse downwelling attenuation in 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 stressed.

There is much larger data base on plant response to total available light energy (PAR) 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 $\mu\text{E m}^{-2} \text{sec}^{-1}$ 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 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 are in general operating under sub-optimal 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 the majority of its growing seasons and 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 as a whole are light-stressed.

Historical data relative to light (turbidity and indirectly nutrients) and past distribution and abundance on submerged aquatics indicate progressive Baywide 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) concluded for roughly the same time scale that the general pattern of disappearance of submerged plant communities followed 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 suggests 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 that at present 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 (i.e. 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 the 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 the vegetation to both qualitative and quantitative measures of available light and the implicit assumption that over the past several decades water quality throughout the Bay and particularly in the tributaries has progressively declined. Further changes in these parameters can only affect Bay grasses in an adverse way.

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