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A Theoretical Comparison of the Attenuation of Light Energy and Quanta in Waters of Divergent Optical Properties

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With 5 figures and 1 table in the text

Abstract

The distinction between attenuation of light expressed as energy and as quanta is discussed on the basis of simulated sunlight penetration in freshwater and marine environments having a range of optical properties. For the 400—700 nm spectral band, attenuation of quanta is approximately equal to that of energy in water bodies having a Pt color of 5.5—6.5 (dissolved organic carbon ca. 5 ppm). In more transparent waters, energy is absorbed at a slower rate than quanta, while the opposite is true in more highly-colored waters. Simulated spectral distributions for quanta and energy at a number of depths in waters of various colors indicate that divergence in penetration of total energy and total quanta is always small on an absolute scale. Divergence relative to available quanta or energy at a particular depth, however, increases with depth to as much as 20 % at an optical depth of 5.0 in a highly-colored lake. Simulations also demonstrate that divergence of the energy and quantum attenuation over the integrated 400—700 nm range is damped by cancellation of the opposing gross effects of pure water and dissolved color in different parts of the spectrum. Divergence in penetration of quanta and energy can thus be much greater within specific portions of the 400—700 nm range, such as the action spectra of individual photosynthetic pigments.

Introduction

The classical studies of light penetration in aquatic habitats deal with the attenuation of energy in water columns having varied optical properties (e. g., James & Birge 1938). This approach is well suited to the older instruments for measuring light attenuation and also produces results that are directly applicable to studies of energy flow in food chains. It is well known, however, that rates of photosynthesis are more directly related to the number of quanta of light available in the photosynthetically-active wavelength range than to the amount of energy available within this range. The distinction between propagation of energy and quanta is of course inconsequential given constant spectral composition of light. Since the

spectral composition of light varies within and between habitats, however, several authors have advocated the expression of light intensity in terms of quanta (EDMONDSON 1956; CRAIG 1964; FEDERER & TANNER 1966; STEEMAN NIELSEN & WILLEMOES 1971). Quantum meters are now available to meet this need.

Although there is little doubt of the desirability of quantum meters and the use of quantum units in studies of photosynthesis, expression of irradiance in terms of energy will undoubtedly persist. This is partly justifiable on grounds of precedence (hence convenience), instrumentation, and particularly the conceptual significance of energy flow. The question therefore arises whether the interpretation of the physical and particularly the biological properties of aquatic environments will be significantly affected by differences in expression or measurement of light. This paper is intended to help resolve this question by comparison of the optical properties of a range of water bodies from the quantum and energy viewpoints. The important problem of uneven spectral sensitivity of sensors, which has been discussed by TYLER (1973) in relation to energy and quanta, is not of direct concern here. Attention is focused instead on the comparison between energy and quantum penetration with the assumption that total energy and quanta in a specified wavelength range can be measured without significant error.

Methods

Three lakes and two kinds of marine environments were selected as representative of the range of conditions that are encountered in aquatic studies. The three lakes are Helmet Lake, Adelaide Lake, and Crystal Lake, all of which are located in Wisconsin. Helmet Lake contains a high concentration of dissolved humic compounds (Pt color 236), Adelaide Lake is moderate in color (Pt color 28), and Crystal Lake is highly transparent (Pt color 0). These particular lakes were selected because complete optical data on them are available in the classical paper by JAMES & BIRGE (1938), and because they are used as illustrative material in HUTCHINSON's treatment of lake optics (1957, p. 366—425). Equivalence between Pt color and dissolved oragnic carbon is approximately linear at a rate of 1 ppm DOC per 10 Pt units, but there is some residual DOC (< 5 ppm) when the Pt color is 0 (JAMES and BIRGE, p. 54). Data for other lakes were also used, but since they produced results conforming to the pattern outlined by the three representative lakes they are not discussed in detail. The marine data include "average" ocean water as given in SVERDRUP et al. (1942) and "average" coastal water from the same source. These marine data, which are actually drawn from UTTERBACK's old but important work (1936), were spectrally incomplete owing to a lack of data at 400 and 700 nm. This deficiency has been remedied for present purposes by extrapolation based on more modern data (JERLOV 1968). Coastal water was considered to reduce irradiance by 49 %/m and oceanic water by 15 %/m at 400 nm. Corresponding values for 700 nm were set at 52 %/m and 44 %/m. The resulting "average" vertical attenuation coefficients for ocean water

are intermediate between water types II and III and the coastal water corresponds closely to type 3 according to JERLOV's (1968) classification. Separation of scattering and absorbance is not attempted here, hence the older data, which ordinarily lump these effects, suffice in the simulations as well as more sophisticated modern data.

The initial data on each of the five water types consisted simply of the vertical attenuation rate (including absorbance and scatter) at all wavelengths between 400 and 700 nm as given in the sources cited above. An arbitrary amount of sunlight (200 cal/cm^2) was presumed to fall on the surface of each of the five waterbodies over an unspecified time period. Half of this light (100 cal/cm^2) was assumed to consist of photosynthetically-active radiation (400—700 nm; TALLING 1957 a, WESTLAKE 1965). The photosynthetically-active range may extend below 400 nm to wavelengths as short as 290 nm (HALLDAL 1967; D. F. WESTLAKE, pers. comm.), but the amount of subsurface irradiance available at the shortest wavelengths is so small that the lowest part of the range need not be considered here. The photosynthetically-active light was assigned a typical spectral composition for a clear day at sealevel (HENDERSON & HODGKISS 1963). These values compare closely with those computed by STRICKLAND (1958) from the data of LIST (1951). The penetration of the light was then simulated by means of a digital computer. No albedo or surface effects were introduced into the calculations, since these are not directly relevant to the questions posed here. Only downwelling radiation was considered due to the comparatively small importance of back-scattered light in most habitats.

The simulations were simplified by the assumption that all light would have an angle of incidence equal to 0°. The path length of light below the water surface is thus somewhat underestimated even for a sun at zenith. The term "depth", which is preserved here for simplicity, is thus more properly the mean path length of light in the water column.

The analysis in some instances makes use of the "optical depth" concept (TALLING 1957 a, b) to facilitate comparison of waters having greatly different optical properties. In accordance with TALLING's usage, one optical depth is here defined as the depth required to halve the irradiance at the most penetrating wavelength. For practical purposes the most penetrating wavelength is equated here with the 25 nm spectral block having the lowest extinction coefficient within the 400—700 nm band.

Results and Discussion

It is clear even without computation that radical changes in the spectral composition of light such as those occurring in natural waters are likely to alter the average quantum energy by selective removal of certain wavelengths. Two opposing tendencies are combined in natural waters. (1) In pure water, or water that contains some particulate material but little dissolved color, the long-wavelength portion of the 400—700 nm spectral block is selectively absorbed. This means that the average wavelength of the penetrating light decreases with depth. It follows from PLANCK's relationship that in such cases the average quantum will have a higher energy equivalent deep in the water column than near the surface.

Since the mean energy per quantum increases with depth, the attenuation of quanta must be more rapid than the attenuation of energy. (2) The opposite tendency is to be expected in lakes having a high amount of dissolved color, since such lakes absorb strongly in the shorter wavelength portion of the 400—700 nm band. The average energy per quantum is thus a decreasing function of depth, which means that energy must be attenuated more rapidly than the number of quanta.

It is not obvious how the opposing effects of pure water and dissolved color are combined in most natural waters, or what the magnitude of the resulting differences in quantum and energy penetration might be. The only energy-quantum comparison involving a number of water types appears to be that of SPENCE et al. (1971), which confirms the generalized deduction given above that transparent waters will be more transparent to energy than quanta, while lakes containing much dissolved color will be more transparent to quanta than energy. The following computational approach is intended to illustrate the range of conditions that can be expected and the possibility for approximating the quantum penetration from energy data obtained in the field.

It is convenient to consider first the penetration of all light in the 400—700 nm band without regard to changes in its spectral composition

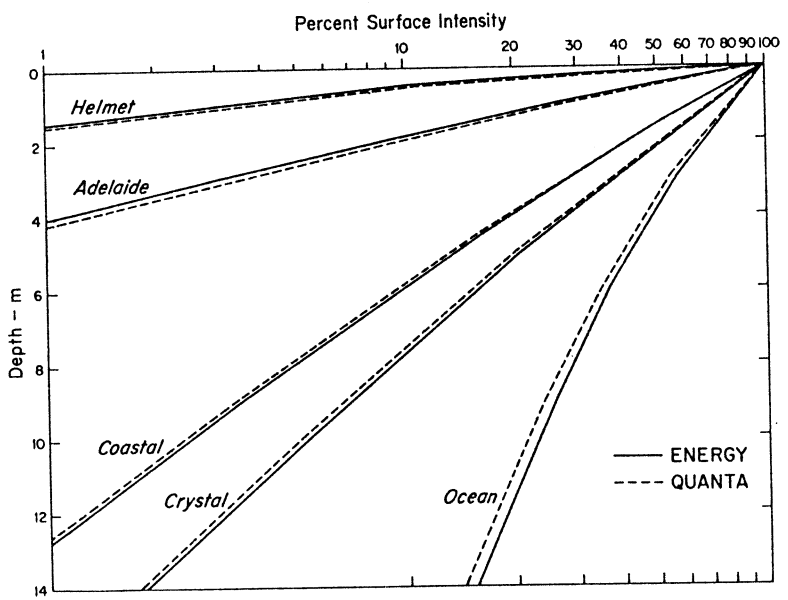

Fig. 1. Simulated penetration of photosynthetically-active radiation (400—700 nm) expressed as energy and as quanta for lakes of differing transparency, and for oceanic and coastal water.

with depth. The computations for each of the water types thus include (a) splitting the incident radiation between 400 and 700 nm into a number of wavelength blocks (25 nm per block), (b) simulating the attenuation of radiant energy from each spectral block by using the optical data for each water type, (c) using PLANCK's equation to convert the energy in each spectral block to quanta, (d) summing the energy and quanta over wavelength at each depth, (e) expressing the summed energy or quanta at each depth as a percentage of incident energy or quanta. The integrated results of the simulated penetrations are shown in Fig. 1. As expected, attenuation of

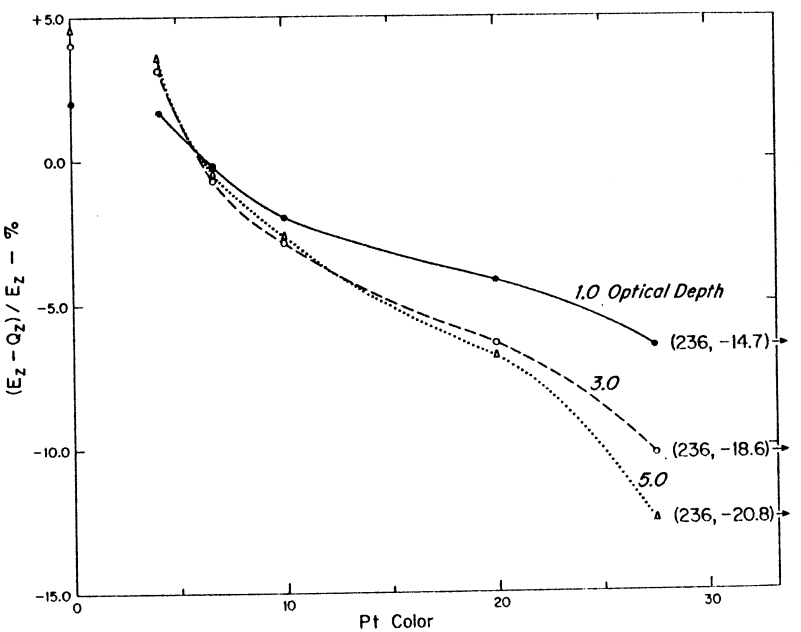

Fig. 2. Relationship between total energy and total quanta in Wisconsin lakes of high to moderate transparency. The abscissa gives the Pt color and the ordinate gives the difference between energy (E_z, percent of surface energy remaining at depth z) and quanta (Q_z, percent of surface quanta remaining at depth z) remaining at 1, 3, or 5 optical depth units below the surface. The difference between E_z and Q_z is expressed in relative terms as a percent of E_z at the indicated depths. Ordinate values were obtained by simulated penetration as described in the text. The trends between Pt color 0 and 4 are not marked owing to the greater importance of error in color judgement at such high transparencies. The data for Pt color 0 are from Crystal Lake, data for colors 4, 6, 10, and 20 are means for Wisconsin lakes reported by JAMES & BIRGE (1938, p. 132—135), and the data for color 28 are from Adelaide Lake. The off-scale positions of points for a highly-colored lake (Helmet Lake, Pt 236) are indicated in parentheses.

energy proceeds at a greater rate than attenuation of quanta in the highly-colored lake, while the reverse is true in the most transparent lake. Similar data for a number of water types indicate that the opposing effects of pure water and dissolved color would be approximately balanced in a waterbody with a Pt color of 5.5—6.5 (Fig. 2). The exact equilibrium point would of course depend upon the source of color and other factors such as particulate material.

Fig. 1 shows that the deviation between penetration of quanta and energy is small in absolute terms even for the most extreme cases. The difference between percent of surface energy and percent of surface quanta at a given depth (E_z—Q_z) does not exceed 5.0 % for any water type or depth. It is also obvious that the deviation develops most quickly in the upper layers of the water column and becomes virtually asymptotic at greater depths. This is of course due to the reduced rate of change in spectral composition of light at greater depths.

Divergence between attenuation of energy and quanta can assume considerable significance in a relative sense if the divergence is expressed as a percentage of available energy at the depth in question ($(E_z—Q_z)/E_z$). Fig. 2 shows that increasing dissolved color and increasing depth are both accompanied by an increase in the relative importance of the divergence.

The divergence of energy and quantum attenuation is much greater for certain portions of the spectrum than for the entire 400—700 nm spectral block, since factors causing divergence partly cancel each other when their effects are summed. The spectral distributions of quanta and energy for the 5 water types shown in Fig. 3 exemplify spectral variation in divergence between the two measures of light. In all natural waters, proportions of quanta are higher than those of energy in the uppermost portion of the 400—700 nm region. Conversely, in the short wavelength portion of the 400—700 nm region, energy is always available in greater proportions than quanta. Intersection of the quantum and energy spectral lines occurs between 525 and 675 nm depending on color. Figure 3 shows the shift in the intersection of the quantum and energy lines toward longer wavelengths with increasing dissolved color. In Crystal Lake, energy is present in greater relative proportions than quanta at wavelengths below 535 nm, while above 535 nm the opposite is true. Additional dissolved color forces the equilibrium wavelength from 535 nm in Crystal Lake to 600 nm in Adelaide Lake and to 650 nm in Helmet Lake.

The importance of the divergence in quantum and energy distributions could obviously be substantial if specific photosynthetic pigments are individually considered, as indicated in Table 1. The long-wave action spectrum of chlorophyll a, for example, falls in the spectral segment

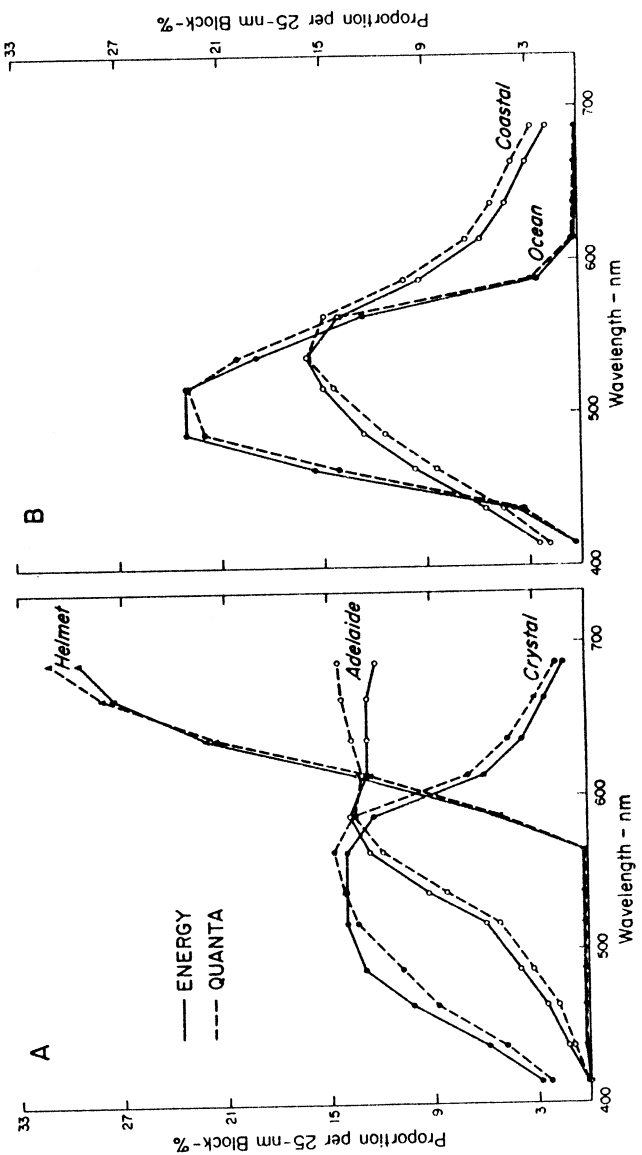

Fig. 3. A. Amounts of energy and quanta in successive 25 nm spectral bands centered as indicated on the abscissa. Amounts on the ordinate are expressed as percent of the total energy or quanta between 400 and 700 nm. The depth represented for all three lakes is 2.0 optical depth units. For Helmet Lake, one optical depth is 0.35 m, for Adelaide Lake, 0.75 m, and for Crystal Lake, 3.0 m. B. The same information for oceanic and coastal water. For oceanic water, one optical depth is 9.60 m, and for coastal water, 2.56 m.

650—700 nm. In lakes of intermediate to moderate color, this segment of the spectrum accounts for a substantial percentage of the light available for photosynthesis and the divergence between quantum and energy distributions is maximal in this region. In Adelaide Lake, for example, the proportion of quanta is 13 % higher than the proportion of energy in this part of the spectrum.

Table 1. Summary statistics for simulated light penetration in 3 lakes of different transparency and 2 marine environments. The first two columns indicate the depth to which 10 % and 1 % of the surface light penetrates. The last column gives the percentages of energy and quanta falling in the red peak of the chlorophyll *a* action spectrum at an optical depth of 3.0.

1 % I_0, m	10 % I_0, m	650—700 13 O.D. ÷ 400—700 13 O.D. %
Helmet Lake		
Energy 1.46	0.53	48.41
Quanta 1.54	0.59	53.04
Adelaide Lake		
Energy 4.07	2.11	25.70
Quanta 4.19	2.19	29.11
Crystal Lake		
Energy 16.5	7.67	2.99
Quanta 16.3	7.55	3.90
Average Coastal		
Energy 12.8	5.90	4.10
Quanta 12.7	5.81	6.33
Average Ocean		
Energy 46.5	18.9	0.11
Quanta 45.5	17.9	0.21

The exact proportion of energy or quanta in any portion of the 400—700 nm wavelength range can be most easily determined from a graphical representation of the distribution functions (cumulative frequency distributions) corresponding to such probability density functions as those illustrated in Fig. 3. Representative distribution functions are shown in Fig. 4. The proportion of energy or quanta in any wavelength interval can be obtained by subtraction of the appropriate cumulative frequencies. Distribution function graphs are of course more useful for computational than for interpretive purposes.

Divergence between distribution of energy and quanta depends on water depth as well as water type. Figure 5 shows the effect of depth on the quantum and energy distributions in a moderately-colored lake. The graph shows the expected shift in spectral composition toward the most penetrating wavelengths and a concomitant shift in the intersection of quantum and energy lines. With increasing depth there is increasing divergence of the quantum and energy lines, but the rate of divergence declines with increasing depth.

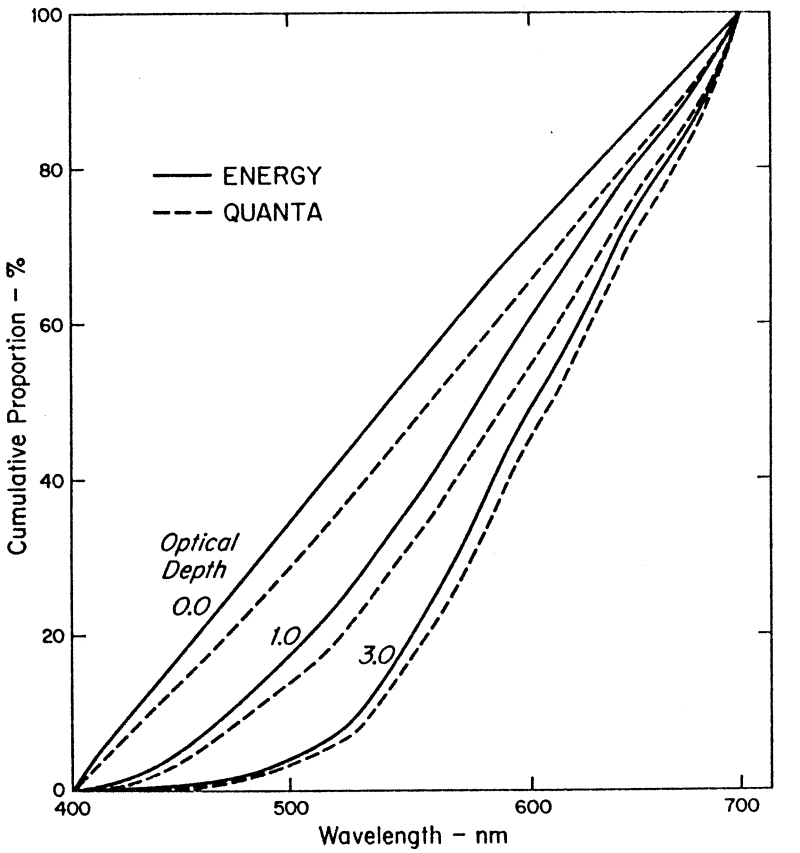

Fig. 4. Distribution functions for light at optical depths 0.0 (incident light), 1.0 (0.75 m), and 3.0 (2.25 m) in Adelaide Lake expressed as energy and as quanta.

The simultations clearly indicate the validity of a conceptual separation between penetration of energy and quanta in marine and freshwater environments. For practical purposes it is safe to ignore the distinction if the phenomenon under study is to be integrated over depth and has a broad action spectrum. Significant quantitative errors could result from energy-based interpretations of quantum phenomena, specifically photosynthesis, if attention is focused on particular portions of the spectrum or if efficiency of a process at various depths is of interest. The magnitude of potential errors can be approximated very simply, even with a desk calculator, by means analogous to those used above if the optical properties of the waterbody are known.

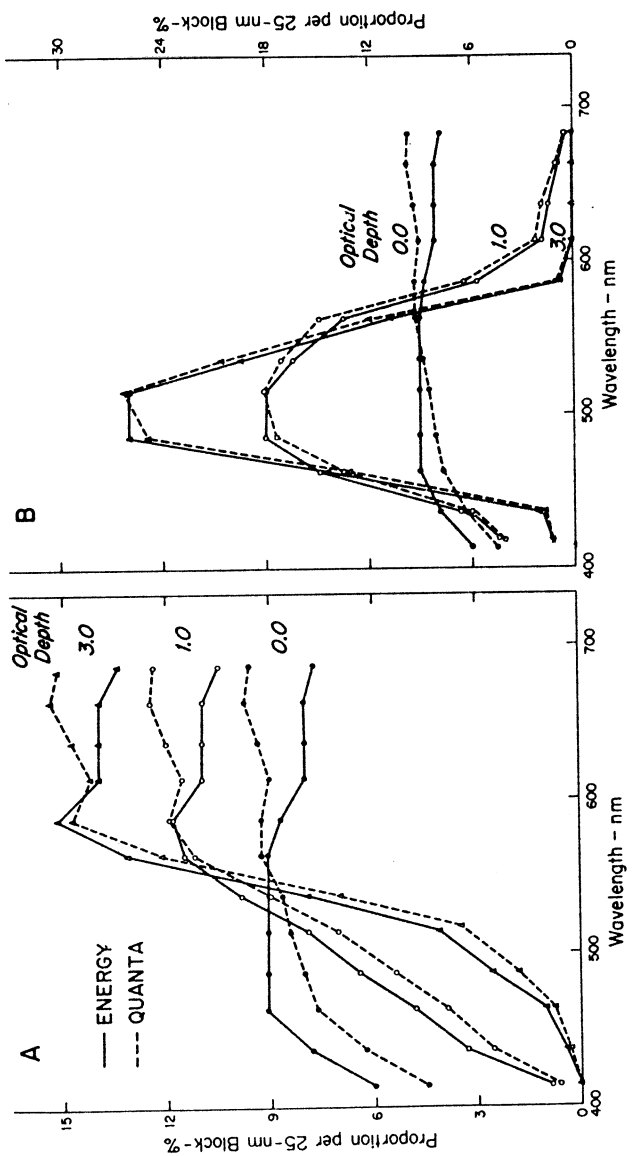

Fig. 5. A. Simulated penetration of light into Adelaide Lake, Wisconsin. The ordinate indicates percent of the total photosynthetically-available radiation (400—700 nm), as quanta and as energy, found in a 25 nm spectral block centered as indicated on the abscissa. Spectra for three depths are shown: optical depth 3.0 (2.25 m), 1.0 (0.75 m), and 0.0 (incident light). B. The same simulations for ocean water. Optical depths are: 3.0 (28.80 m), 1.0 (9.60 m) and 0.0 (incident light). Note scale change from A to B.

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Zusammenfassung

Der Unterschied zwischen der als Energie und als Quanten bezeichneten Lichtdämpfung wird besprochen, und zwar auf Grund des Eindringens von Sonnenlicht in Süßwasser und ins Meer mit unterschiedlichen optischen Eigenschaften simuliert. Für den spektralen Bereich von 400—700 nm stimmt die Quantendämpfung ungefähr mit der Energiedämpfung in Wässern überein, die eine Gelbfärbung entsprechend 5,5 bis 6,5 mg Pt/L haben (gelöster organischer Kohlenstoff ca. 5 mg/l). In lichtdurchlässigeren Gewässern wird die Lichtenergie schwächer als Lichtquanten absorbiert, während das Gegenteil in stark gefärbten Gewässern eintritt. Durch Simulierungen ist nachzuweisen, daß der Unterschied in der Eindringung von Gesamtenergie und Gesamtquanten, gemessen im absoluten Maßstab, immer gering ist. Divergenz in relativen Einheiten aber vergrößert sich mit der Tiefe bis auf 20 % in einer optischen Tiefe von 5,0 stark gefärbten Sees. Simulierungen beweisen auch, daß die Divergenz in verschiedenen Spektralbereichen durch Gegenwirkungen von reinem Wasser und Humusstoffen aufgehoben und im Bereich von 400—700 nm ganz unterdrückt wird. In spezifischen Teilen dieses Spektralbereichs, wie z. B. in den Aktionsspektren einzelner photo-synthetischer Pigmente, kann also die Divergenz wesentlich größer sein.

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