

RELATION BETWEEN TOTAL QUANTA AND TOTAL
ENERGY FOR AQUATIC PHOTOSYNTHESIS

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Relation between total quanta and total energy for aquatic photosynthesis¹

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Abstract

Measurements of underwater spectral irradiance have been used to investigate the behavior of the ratio of total quanta to total energy ($Q : W$) within the spectral region of photosynthetic activity. In data from a wide range of optical water types, the $Q : W$ ratio varies by no more than $\pm 10\%$ and is $2.5 \pm 0.25 \times 10^{18}$ (quanta $\text{sec}^{-1} \text{ watt}^{-1}$). Within this range $Q : W$ varies systematically and thus it may be predicted within $\pm 5\%$, if either the wavelength of maximum spectral irradiance or the chlorophyll concentration of the water under investigation is approximately known. The value of $Q : W$ may be used to determine the total quanta available for photosynthesis accurately from a measurement of the total energy and vice versa.

From a measurement of spectral irradiance, $dE(\lambda)/d\lambda$ (watt $\text{m}^{-2} \text{ nm}^{-1}$), the total quanta, E_Q (quanta $\text{m}^{-2} \text{ sec}^{-1}$), or total energy, E_W (watt m^{-2}), within a given wavelength region can be obtained using the following equations,

$$E_Q(\lambda_1, \lambda_2) = \int_{\lambda_1}^{\lambda_2} \frac{dE(\lambda)}{d\lambda} \times \frac{\lambda}{hc} \times d\lambda \quad (1)$$

and

$$E_W(\lambda_1, \lambda_2) = \int_{\lambda_1}^{\lambda_2} \frac{dE(\lambda)}{d\lambda} \times d\lambda, \quad (2)$$

where Planck's constant $h = 6.6255 \times 10^{-34}$ joules sec^{-1} and the velocity of light in vacuum $c = 2.9979 \times 10^{17}$ nm sec^{-1} . λ_1 and λ_2 give the lower and upper limits of the wavelength region under consideration. We have chosen $\lambda_1 = 400$ nm and $\lambda_2 = 700$ nm for the work reported here. This choice is discussed later.

For polychromatic radiant energy the number of quanta per unit of energy is given by the ratio of equations 1 to 2. To simplify notation we refer to this as the $Q : W$ ratio; i.e. the number of quanta per

unit energy (for the wavelength region specified). The $Q : W$ ratio will vary, for polychromatic radiant energy, with changing spectral energy distributions; i.e. with sun and sky conditions, with depth, and with changes from one optical water type to another.

For monochromatic radiant energy, $dE(\lambda)/d\lambda$ is a constant value and the $Q : W$ ratio becomes a simple function of wavelength,

$$\frac{Q(\text{quanta } \text{m}^{-2} \text{ sec}^{-1})}{W(\text{watt } \text{m}^{-2})} = \frac{\lambda}{hc} = \lambda(\text{nm}) \times 0.5035 \times 10^{16}, \quad (3)$$

using the above values for h and c .

It is of interest to study the behavior of $Q : W$ experimentally. That is, to examine, for a given total energy, the relative variability of the total quanta due to the natural changes in the spectral distribution of irradiance. For this purpose, it is necessary first to determine the variability of the $Q : W$ ratio above the sea and, if this variability is small, its average value, and second, to determine if the $Q : W$ ratio, as modified with increasing depth according to the optical properties of various water types, varies systematically and predictably.

The total quanta between 350 and 700

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nm have been recommended by Working Group 15 (1965) as a measure of the energy available for photosynthesis. On the basis of this recommendation quantum meters have been designed (Jerlov and Nygård 1969; Prieur 1970) and used for the study of primary productivity (Jitts 1963, 1973; Saijo 1973). Experimentally it has often been easier to build and accurately calibrate an instrument to measure total energy (Bethoux and Ivanoff 1970) rather than one to measure total quanta. Thus, if $Q : W$ could be predicted for a given water type, it would be possible to determine the total quanta available for photosynthesis accurately from a simple measure of the total energy. Before this can be done we must investigate the variability of the $Q : W$ ratio for atmospheric and oceanographic conditions.

Our cooperative work was made possible by SCOR Working Group 15 on photosynthetic radiant energy in the ocean. We especially acknowledge the assistance and encouragement of J. E. Tyler for securing much of the funding and coordinating the scientific efforts of this working group.

Spectral irradiance data

The absolute values of spectral irradiance have been measured with two underwater spectroradiometers which were independently constructed and calibrated (Tyler and Smith 1966, 1970; Bauer and Ivanoff 1970). Both instruments use grating monochromators and multiplier phototubes to measure $dE(\lambda)/d\lambda$ (watt $m^{-2} nm^{-1}$) with a spectral resolution of about 5 nm. From the spectral irradiance data of the French and American instruments Q and W can be calculated using equations 1 and 2. Both instruments use properly designed underwater irradiance collectors and have been calibrated against absolute standards of spectral irradiance. In addition to a number of independent expeditions, the French and American instruments were used together during the SCOR Discoverer Expedition (Scripps Inst. Oceanogr. 1973). The instruments and a comparison of their data have been fully discussed elsewhere;

it is only necessary here to note that measurements using the two instruments give the ratio $Q : W$ with an absolute accuracy of a few percent and that independent measurements of this ratio made in the same waters agree within $\pm 1\%$. In addition, the spectral accuracy of the two instruments is within ± 1 nm.

Table 1 gives the expeditions, locations, and the number of published and unpublished spectral irradiance measurements used for this study of $Q : W$. The data cover a full range of optical water types from the clear waters of Crater Lake and the Sargasso Sea to very productive ocean waters. The chlorophyll a concentration in these waters ranged from less than 0.02 $mg m^{-3}$ to greater than 10 $mg m^{-3}$.

Results

Above surface

From the extraterrestrial solar spectral irradiance at the earth's mean distance from the sun given by Arvesen et al. (1969) or by Thekaekara and Drummond (1971), the computation of $Q : W$ leads to values of 2.742 or 2.731, respectively, for the wavelength region 400 nm to 700 nm. The spectral distribution of irradiance reaching the earth's surface depends on the sun altitude and the meteorological conditions of the intervening atmosphere. This can be seen, for example, in fig. 3 in Morel (1973) and in fig. 2 in Morel and Caloumenos (1973). These figures illustrate the well known experimental fact (Walsh 1961) that the spectral distribution of daylight, for different atmospheric conditions, varies around a hinge point near 560 nm. That is, as red light is relatively increased, the blue is relatively decreased and vice versa. Our experimental results show that, for the spectral region under consideration, the above water spectral distributions change, but $Q : W$ is only slightly modified.

The $Q : W$ values for 67 (Table 1) above surface measurements, with sun altitudes ranging from 22° to 90° and for meteorological conditions ranging from clear blue

Table 1. Cruises, general location, and number of spectral irradiance and chlorophyll *a* measurements used.

Cruises*	Location	Above surface measurements	Underwater measurements	Chl measurements†
(a) Baja, Ca. (1967)	Gulf of Calif.		16	
(b) WG-15 Sea Trials (1968)	Gulf of Calif.		49	32
(c) FRESNEL I (1968)	Gulf of Calif.	2	24	(h) 19
(a) FRESNEL II (1971)	Gulf of Calif.		32	(i) 23
(a) Visibility Laboratory	San Diego	3		
(c) Bimini (1967)	Gulf Stream	4	12	9
	Tongue-of-the-Ocean			
(d) Lakes (1969-1970)	Crater Lake	1	27	
	Lake Tahoe			
(a) Gosnold-145 (1969)	Georges Bank to Sargasso Sea	2	12	
(a) Alaminos 69-A-10 (1969)	Gulf of Mexico	4	17	
(e) Discoverer WG-15 (1970)	Sargasso Sea	3	96	(j) 84
	Gulf of Mexico			
	Galapagos - Cen. E Pacific			
(f) Discoverer WG-15 (1970)	Sargasso Sea	30	255	(j) 194
	Gulf of Mexico			
	Galapagos - Cen. E Pacific			
(g) Cineca II & Harmattan (1971)	Mauritanian upwelling area, Cen. E Atlantic	18	98	(k) 41
Totals		67	638	402

* (a) Smith and Tyler unpublished; (b) Smith and Tyler 1968; (c) Tyler and Smith 1970; (d) Smith et al. 1973; (e) Smith 1973; (f) Morel 1973; (g) Morel and Caloumenos 1973.

† (h) Zeitzschel 1970; (i) Berman and Kiefer unpublished; (j) Baird 1973; (k) Groupe Mediprod 1973.

skies to completely overcast skies (incident irradiance, within 400–700 nm region, ranging respectively from 486 to 15 watts m^{-2}) have been calculated. For this wide range of conditions an average value of $Q : W = 2.77 \times 10^{18}$ quanta sec^{-1} $watt^{-1}$ was obtained; the standard deviation was $\pm 0.58\%$ and the maximum difference was $\pm 1.5\%$ for all the data. No statistically significant differences were found in the $Q : W$ ratio as a function of sun altitude or by comparing $Q : W$ ratios for blue skies, hazy skies, cloudy skies, and completely overcast skies. We conclude that, for marine atmospheres with sun altitudes

above 22° , the $Q : W$ ratio for the wavelength region between 400 and 700 nm can be taken as 2.77×10^{18} quanta sec^{-1} $watt^{-1}$ to an accuracy of plus or minus a few percent. Note that this value corresponds to monochromatic radiant energy at 550 nm (equation 3), which is the central wavelength of the spectral region considered.

Below surface

Below the water surface $Q : W$ is rapidly modified by the absorption and scattering of the water and its dissolved and suspended material. The behavior of $Q : W$

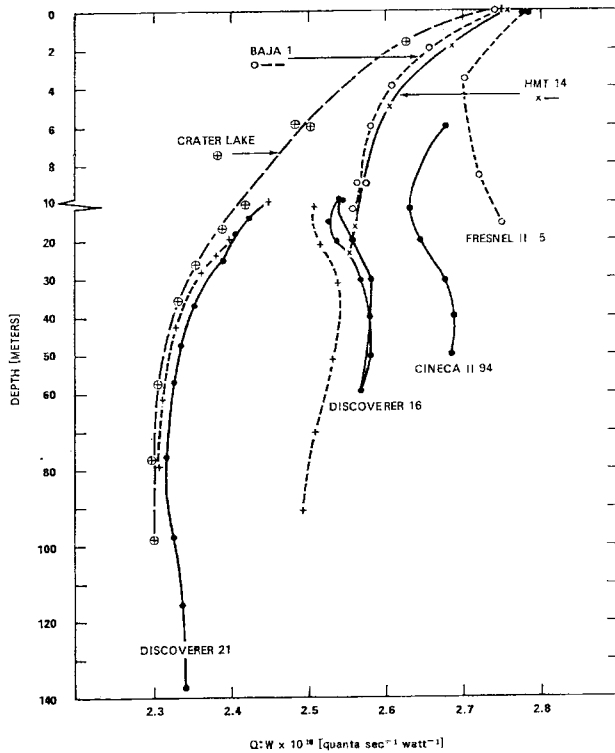


Fig. 1. Ratio of total quanta to total energy (both between 400 and 700 nm) vs. depth for several distinct optical water types. Note the change in the depth scale at 10 m. The range of λ_{Hmax} (defined in text) for each depth profile is from left to right: Crater Lake (448–461 nm); Discoverer station 21 (442–472 nm); Baja station 1 (495 nm); Harmattan station 14 (493–497 nm); Discoverer station 16 (481–506 nm); Cineca II station 94 (534–557 nm); FRESNEL II station 5 (557–566 nm). Solid lines denote French data, dashed lines denote American data.

as a function of depth, for several distinct optical water types, is shown in Fig. 1. The $Q:W$ ratio has a value near 2.77×10^{18} quanta sec^{-1} watt^{-1} just above the surface. Beneath the surface the long wavelengths are quickly attenuated and shift $Q:W$ to smaller values. With increasing depth $Q:W$ approaches a more or less constant value which is dependent on the optical properties of the water considered.

The wavelength for which the spectral irradiance, at a given depth z , has a maximum value, λ_{Hmax} , is also dependent on the water type. This maximum wavelength should not be confused with the wavelength of maximum transmittance, the value which λ_{Hmax} approaches with in-

creasing depth in uniform waters. The values of λ_{Hmax} , for each depth profile plotted in Fig. 1, are given in the figure caption.

For blue waters, where the wavelength for the maximum value of spectral irradiance, λ_{Hmax} , lies between 440 and 475 nm, the value of $Q:W$ is relatively low. As an example of clear natural waters the data from Discoverer station 21 in the Sargasso Sea and from Crater Lake are shown in Fig. 1. Note the sharp drop in $Q:W$ within the first 10 m, the close agreement between the two independent sets of data, and the nearly identical values for the clear fresh and the clear ocean water data. The slight increase in $Q:W$ below 100 m in the Sargasso Sea is due to a small chlorophyll *a* maximum at those depths (Baird 1973).

For blue-green waters, where λ_{Hmax} lies between 475 and 515 nm, the value of $Q:W$ is near 2.5×10^{18} quanta sec^{-1} watt^{-1} . As an example of these intermediate waters comparative data from Discoverer station 16, Harmattan station 14, and Baja station 1 are shown.

For green or discolored waters, where λ_{Hmax} lies above 515 nm, the $Q:W$ value remains relatively high, only slightly lower than for the values from above surface. Station 5 from the FRESNEL II cruise and station 94 from the Cineca II cruise are examples of these waters shown in Fig. 1.

In spite of the wide range of optical water types and their different underwater spectral energy distributions, the value of $Q:W$ varies only $\pm 10\%$ about the value 2.5×10^{18} quanta sec^{-1} watt^{-1} . Thus, for underwater measurements, this single value can be used to convert total energy to total quanta to within this accuracy. However, the trend of $Q:W$ values with λ_{Hmax} , as given in Fig. 1, suggests that a more accurate estimate of $Q:W$ may be obtained if it can be shown that this trend is systematic. Since both $Q:W$ and λ_{Hmax} are dependent on the optical properties of the water being considered, it is of interest to see if they are correlated.

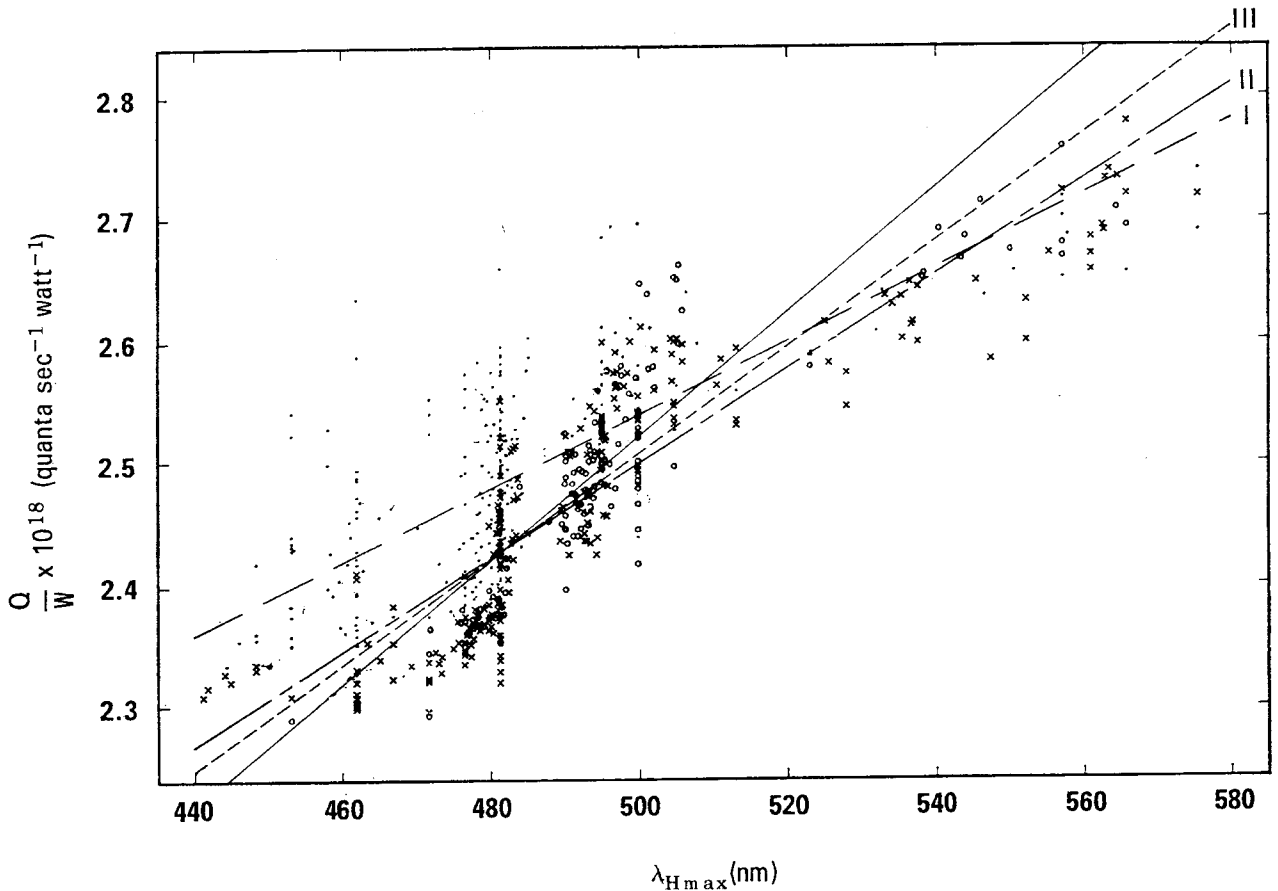


Fig. 2. $Q : W$ ratio vs. the wavelength for the maximum value of spectral irradiance (λ_{Hmax}) for all the underwater spectral irradiance measurements listed in Table 1. The data are separated into three classes depending on the Q value's percentage of surface quanta (between 400 and 700 nm). Dots represent $Q : W$ for Q values between 100 and 10% (number of data points, $N = 271$), cross signs for Q values between 10 and 1% ($N = 234$), and circles for Q value less than 1% ($N = 133$) of the total quanta above the surface. The solid straight line is the limiting value of $Q : W$ for monochromatic radiant energy, i.e. a graph of equation 3. A least squares fit to the three classes of data are shown by the straight lines. Line I is for Q values between 100 and 10% of above surface values, line II between 10 and 1%, line III less than 1%. Data fall into vertical columns because of the discrete wavelength steps of the spectroradiometer.

Figure 2 is a plot of $Q : W$ vs. λ_{Hmax} for the 638 underwater spectral irradiance measurements listed in Table 1. Since $Q : W$ varies with depth, as shown in Fig. 1, the distribution of $Q : W$ for a fixed λ_{Hmax} will not be a Gaussian distribution. Therefore, the use of a least squares fit to all the data would not be statistically valid. However by separating the data into three classes, dependent on the optical depth of the spectral irradiance measurement, we obtain distributions that are sufficiently Gaussian for our analysis because the influence of the variability with depth is reduced. It must also be noted that

λ_{Hmax} cannot exhibit a strictly continuous spectral variation because of the presence of Fraunhofer lines. In Fig. 2 the data have therefore been divided into three classes. The first corresponds to total quanta values between 100 and 10% of the surface total quanta values, the second to Q values between 10 and 1% of the surface values, and the third to data from depths where the Q values are less than 1% of the surface values. The solid line shows the limiting case for monochromatic radiant energy. Figure 1 indicates that $Q : W$ values approach a constant value with increasing depth, and it is known (Ty-

ler 1959) that spectral distributions become increasingly monochromatic with depth. Since $Q : W$ values from greater depths ($< 1\%$) are calculated from increasingly monochromatic radiant energy, we can expect that these $Q : W$ values will lie closer to the monochromatic line than values from nearer the surface (100–10%).²

Linear least square fits to the three classes of data are shown as lines I, II, and III, $Q : W$ being considered as a dependent variable of $\lambda_{H_{\max}}$. The tendency for the $Q : W$ ratios from the greater optical depths (increasing from class I to class III) to approach the graph of the monochromatic limit is clearly demonstrated. The sample linear correlation coefficients, r , for classes I to III are 0.72, 0.89, and 0.87, respectively; assuming Gaussian distributions within each class, these values yield a high probability that $Q : W$ and $\lambda_{H_{\max}}$ are correlated and that our fit to a straight line for each class is justified. A quadratic fit to the three classes was poorer than the linear fit shown.

These three least square fits show that the $Q : W$ ratios for blue waters approach the monochromatic limit from above this limit. On the other hand, the $Q : W$ ratio for green waters approaches the monochromatic limit from below. Blue-green waters have $Q : W$ ratios near the monochromatic limit. This is because measurements from blue-green waters exhibit a more or less symmetrical spectral energy distribution about the associated $\lambda_{H_{\max}}$ and hence $Q : W$ remains relatively close to the monochromatic limit at all optical depths. The spectral distribution for blue waters, on the contrary, is skewed toward long wavelengths. Thus, in near surface blue waters, $Q : W$ has a relatively large value, due to the presence of a high proportion of long wavelength quanta. With increasing depth, the spectral distribution of these blue waters becomes more symmetric and $Q : W$

approaches the monochromatic limit because of the preferential absorption of the longer wavelength quanta. The converse is true in green waters, which is skewed toward short wavelengths near the surface, where short wavelength quanta are preferentially absorbed with depth.

The $Q : W$ data (Fig. 2) and the least square fit to those data indicate that $Q : W$ is correlated with $\lambda_{H_{\max}}$. Thus, if $\lambda_{H_{\max}}$ is known, or can be estimated, a more accurate value for $Q : W$ can be chosen than just the average value for all the data.

An alternative technique for selecting a more accurate value for $Q : W$ is suggested by the data shown in Fig. 3. $Q : W$ and $\lambda_{H_{\max}}$ are plotted vs. \log_{10} (average Chl *a* concentration in the water column above the instrument). We have plotted \log_{10} (Chl *a*) because it is known that the spectral effects of increased chlorophyll concentration are nonlinear (Yentsch 1960; Clarke et al. 1969). When chlorophyll is added to clear water the band of minimum absorption, and hence $\lambda_{H_{\max}}$, approaches asymptotically to the wavelength region near 560–570 nm where chlorophyll *a* has minimum absorption and where absorption due to water begins to increase rapidly. Consequently a relatively large shift in $\lambda_{H_{\max}}$ occurs for a relatively small addition of chlorophyll to clear seawater. By plotting \log_{10} (Chl *a*), this nonlinearity is reduced to a convenient scale for comparison with our other variables of interest.

The minimum absorption of chlorophyll *a* and the rapid increase in the absorption due to water also places an upper boundary ($\sim 2.7 \times 10^{18}$) on $Q : W$ in natural, nonsilty waters. The lower limit of $Q : W$ ($\sim 2.3 \times 10^{18}$) is found in the clearest waters. Thus, the upper and lower limits to $Q : W$ in natural waters are determined primarily by the absorption properties of water and of chlorophyll *a*.

There are several reasons why a correlation between chlorophyll *a* and $\lambda_{H_{\max}}$ is expected to be rough. First, consideration of only chlorophyll *a* neglects all other absorbing and scattering substances (particulate or dissolved) within the water column;

² Upwelling spectral irradiance, not considered in this paper, is much less polychromatic than downwelling spectral irradiance and hence gives $Q : W$ values close to the monochromatic curve (equation 3).

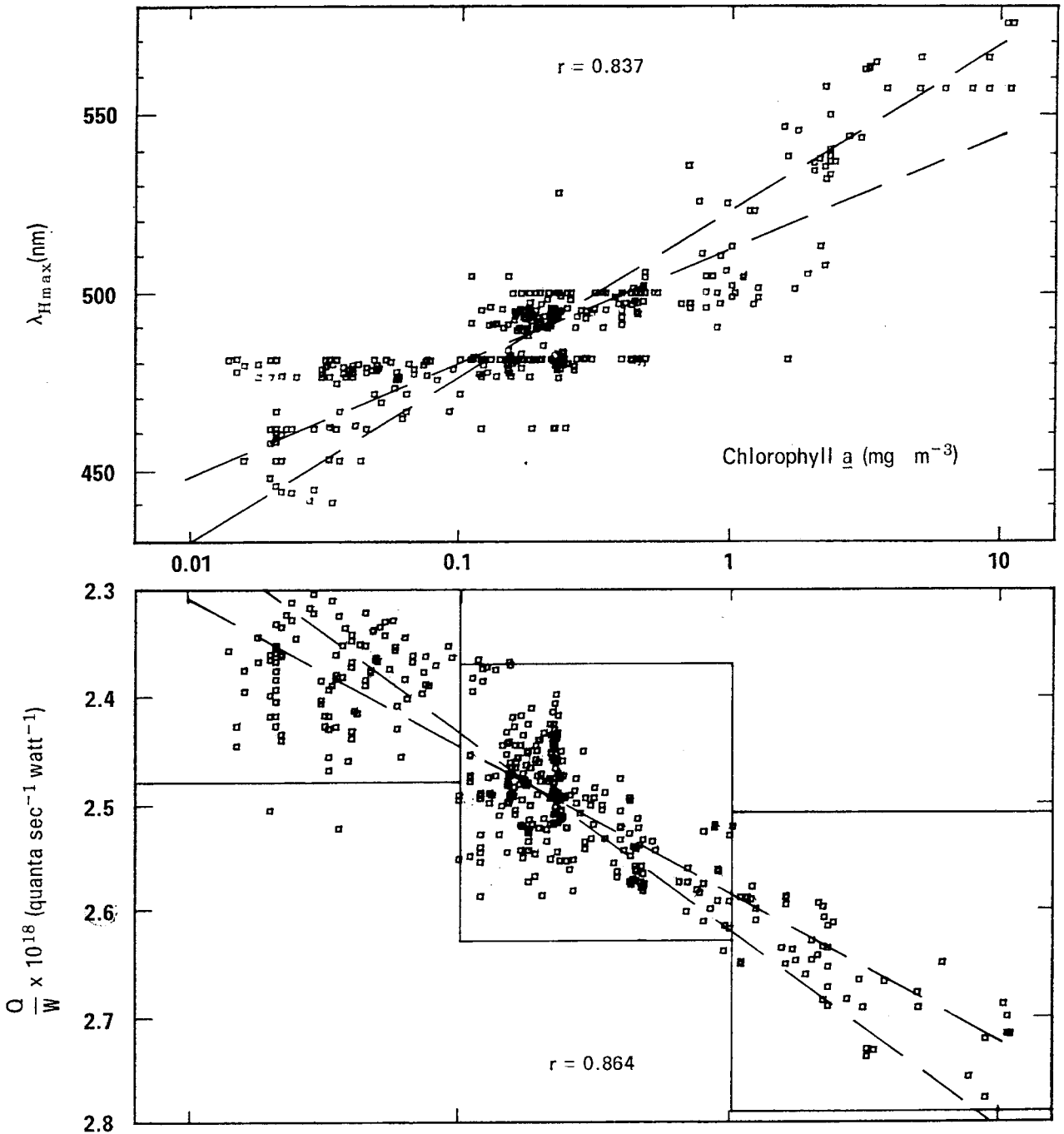


Fig. 3. Average chlorophyll *a* concentration above irradiance meter on a log-scale vs. $Q : W$ and $\lambda_{H_{max}}$ for the 402 chlorophyll data listed in Table 1. Regression lines and the sample linear correlation coefficient, r , are given for both sets of data. The solid lines in the lower half of the figure separate data into waters with low ($< 0.1 \text{ mg m}^{-3}$), medium ($0.1\text{--}1.0 \text{ mg m}^{-3}$), and high ($> 1 \text{ mg m}^{-3}$) average chlorophyll *a* concentrations corresponding to blue, blue-green, and green waters and to $Q : W$ ratios of 2.35 , 2.50 , and $2.65 \times 10^{18} \text{ quanta sec}^{-1} \text{ watt}^{-1}$.

in particular, it does not take into account the spectral affects of accessory pigments or of dissolved "yellow" substances. The chlorophyll *a* concentration is used because it is a commonly measured parameter and because it can be considered, on average,

as representative of the total pigment concentration (Yentsch 1960). That a correlation exists at all implies that there is some correlation between chlorophyll *a* and these other substances (Morel and Caloumenos 1974). Second, for our

Table 2. Recommended values for the $Q : W$ ratio.

	$Q : W \times 10^{18}$ ($\frac{\text{quanta}}{\text{sec watt}}$)	Chl a (mg m^{-3})	$\lambda_{H\text{max}}$ (nm)
Above surface avg	2.77 ± 0.02		
Below surface	2.50 ± 0.25		
"Blue" water	2.35 ± 0.13	<0.1	440-485
"Blue-green" water	2.50 ± 0.13	0.1-1	475-510
"Green" water	2.65 ± 0.13	>1	500-570

comparisons we have used an average value for chlorophyll a in the water column above the instrument. Since chlorophyll a vs. depth typically shows a non-constant profile, the averaging process tends to reduce any existing correlation. If not for the first problem, it would be profitable to replace the average values with weighted values based on the known chlorophyll a profile and the known diffuse attenuation coefficients for irradiance; however for present purposes this more exact procedure is not justified.

Figure 3 shows a rough correlation of \log_{10} (Chl a) with both $\lambda_{H\text{max}}$ and $Q : W$. The sample linear correlation coefficient being 0.84 and 0.86 for the two cases. We use this rough correlation to demonstrate that a more accurate ($\pm 5\%$) value of $Q : W$ can be estimated if either $\lambda_{H\text{max}}$ or the chlorophyll a concentration for the water under consideration is known. By dividing the data in Fig. 3 into three zones corresponding to low, medium, and high chlorophyll a concentration and to blue, blue-green, and green waters, respectively, a value for $Q : W$ can be estimated to within $\pm 5\%$.³ Values of $Q : W$ for these three zones are given in Table 2.

³ The late J. D. H. Strickland once remarked that an experienced marine biologist could estimate the chlorophyll concentration of ocean waters within an order of magnitude merely by looking at them. Steemann Nielsen (1963) also noted that, to a first approximation, oceanic production could be estimated by simply estimating the color of the sea. Figure 3 provides data and quantitative values of $\lambda_{H\text{max}}$ and \log_{10} (Chl a) justifying these astute observations. With an experienced eye, $\lambda_{H\text{max}}$ and thus \log_{10} (Chl a) and $Q : W$ can be roughly estimated.

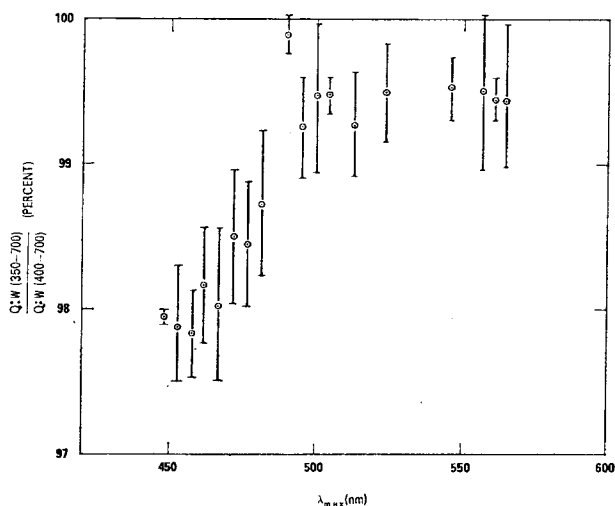


Fig. 4. Comparison ratio $Q : W$ (350-700 nm) to $Q : W$ (400-700 nm) vs. $\lambda_{H\text{max}}$ based on American data listed in Table 1. The dots represent the mean value of this ratio for all data at a given $\lambda_{H\text{max}}$ and the bars indicate 1 SD from this mean.

Limitations

The above results are applicable to natural waters whose concentration of suspended material is small or primarily of biological origin. All data from river effluents or otherwise silty waters have been excluded from consideration. It is likely that silty waters, with high $\lambda_{H\text{max}}$, will have relatively high $Q : W$ ratios independent of chlorophyll concentration. Thus, no reliable inference with respect to chlorophyll a can be made for such waters.

For experimental reasons and in order that the French and American data could be used in a consistent manner, we used the wavelength region from 400-700 nm for the results reported here. Working Group 15 (1965) recommended using the wavelength region from 350-700 nm when considering the energy available for photosynthesis. In blue waters the wavelength range from 350-400 nm may contain as much as 10% of the total quanta in the range from 350-700 nm. For blue-green and green waters the contribution from the wavelength region between 350 and 400 nm to the total irradiance becomes less and tends toward zero as $\lambda_{H\text{max}}$ increases. Even though this far blue region is rich in

quanta, it has relatively little effect on $Q : W$.

The maximum effect of neglecting the region from 350–400 nm is seen in the values from above surface. From the ratio $Q : W$ (350–700 nm) to $Q : W$ (400–700 nm) for these data we find that the region from 350–400 nm causes at most a 2% decrease in $Q : W$.

For underwater data the ratio $Q : W$ (350–700 nm) to $Q : W$ (400–700 nm) is plotted vs. λ_{Hmax} in Fig. 4. A value of 100% for this comparison ratio would indicate that addition of the region from 350–400 nm would have no effect on $Q : W$. Figure 4 shows that the maximum effect of neglecting this far blue region is –2% for blue waters and reduces to about –0.5% for blue-green and green waters. Consequently, the $Q : W$ values recommended here, leading to an accuracy of $\pm 5\%$, can be used for either spectral range, 350–700 nm or 400–700 nm.

Conclusions

We have investigated the experimental behavior of $Q : W$ (between 400 and 700 nm) using measurements of spectral irradiance from a number of locations covering a wide variety of optical water types. The $Q : W$ ratio behaves predictably within given limits. Above the surface $Q : W$ is $2.77 \pm 0.16 \times 10^{18}$ quanta sec^{-1} watt^{-1} , a value independent (within $\pm 0.6\%$) of sun elevation (above 22°) and meteorological conditions.

Below the surface $Q : W$ exhibits greater variability ($\pm 10\%$) but is predictably dependent on the optical properties of the water under investigation. The average $Q : W$ is $2.5 \pm 0.25 \times 10^{18}$ quanta sec^{-1} watt^{-1} . Greater accuracy ($\pm 5\%$) for $Q : W$ can be obtained by choosing this ratio according to the ranges of λ_{Hmax} or of the average chlorophyll *a* concentration of the water under consideration (Table 2) or, less reliably, even on visual observation of the optical water type.

A practical consequence is that total quanta can be estimated within $\pm 5\%$ from the relatively easier measurement of total

energy or vice versa. Thus, despite the fact that photosynthesis is a quantum process, the relations of photosynthesis to irradiance, in natural waters, can be studied on the basis of energetic values (watts, joules) as well as of quanta values without significant error.

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