Rev. Biol. Trop., 35(2): 183-193, 1987.

The application of calculation models for estimating primary productivity in two topical Mexican coastal lagoons

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(Received January 10, 1986)

Abstract: Data from detailed radiocarbon uptake studies of two turbid and highly productive Mexican tropical coastal lagoons with distinct ecological environments were used to evaluate and adapt calculation models for the integration of total daily ^{14}C productivity (Σp). For such environments, the precision of the conventional methodology does not permit reliable estimates of I_k from the low light regions of p/I curves. Since the widely used "Talling integral" was thus not directly applicable, alternative solutions which only require knowledge of the position and height of the subsurface productivity maximum were evaluated.One of these models was found to predict Σp to within 10% of planimetric measurements in all cases. Suggestions are given for practical application of this model and for its future development in association with the assimilation number concept.

Radiocarbon uptake experiments are widely employed for the estimation of primary productivity in the marine environment. Much attention has been given to the refinement of experimental details and assay techniques, particularly in the ocean and lake environments. The I.B.P. program handbook (Vollenweider 1974) provides an excellent practical résumé of these.

In order to apply conventional ^{14}C methods to highly productive and turbid environments such as coastal lagoons, some difficulties are encountered. The most significant of these result from the use of long incubation periods which give low estimates of productivity and from clogging of filters with suspended particulate material, making impracticable the use of Geiger-Müller counters. The refinements introduced by Fernández *et al.* (1979) avoid these pitfalls by employing several 1-hour incubation periods and utilizing the scintillation counting of small samples. Though this technique gives reliable *in-situ* estimates of daily productivity, it limits these measurements to one per day and requires a considerable effort in the field and an abundant supply of materials. The present study evaluates the use of productivity models in order to reduce to a minimun the time required for estimating ^{14}C productivity in highly productive and turbid environments.

METHODS

All radiocarbon uptake experiments were made in 1976 as part of a wider study of the chemistry and hydrography of the tropical coastal lagoons of Guerrero State, Mexico (Mee 1977). The data were obtained from centrally located stations in the Chautengo lagoon (station 3, Mee 1977) and the Mitla lagoon (Camelote basin). Full descriptions of these lagoons are given by Mee (1977, 1978).

RESULTS

Most productivity curves show significant surface mid-day light inhibition (Figures 1,2). The curves tend to be roughly symmetrical and any assymetry can usually be explained by one or more of the following criteria:

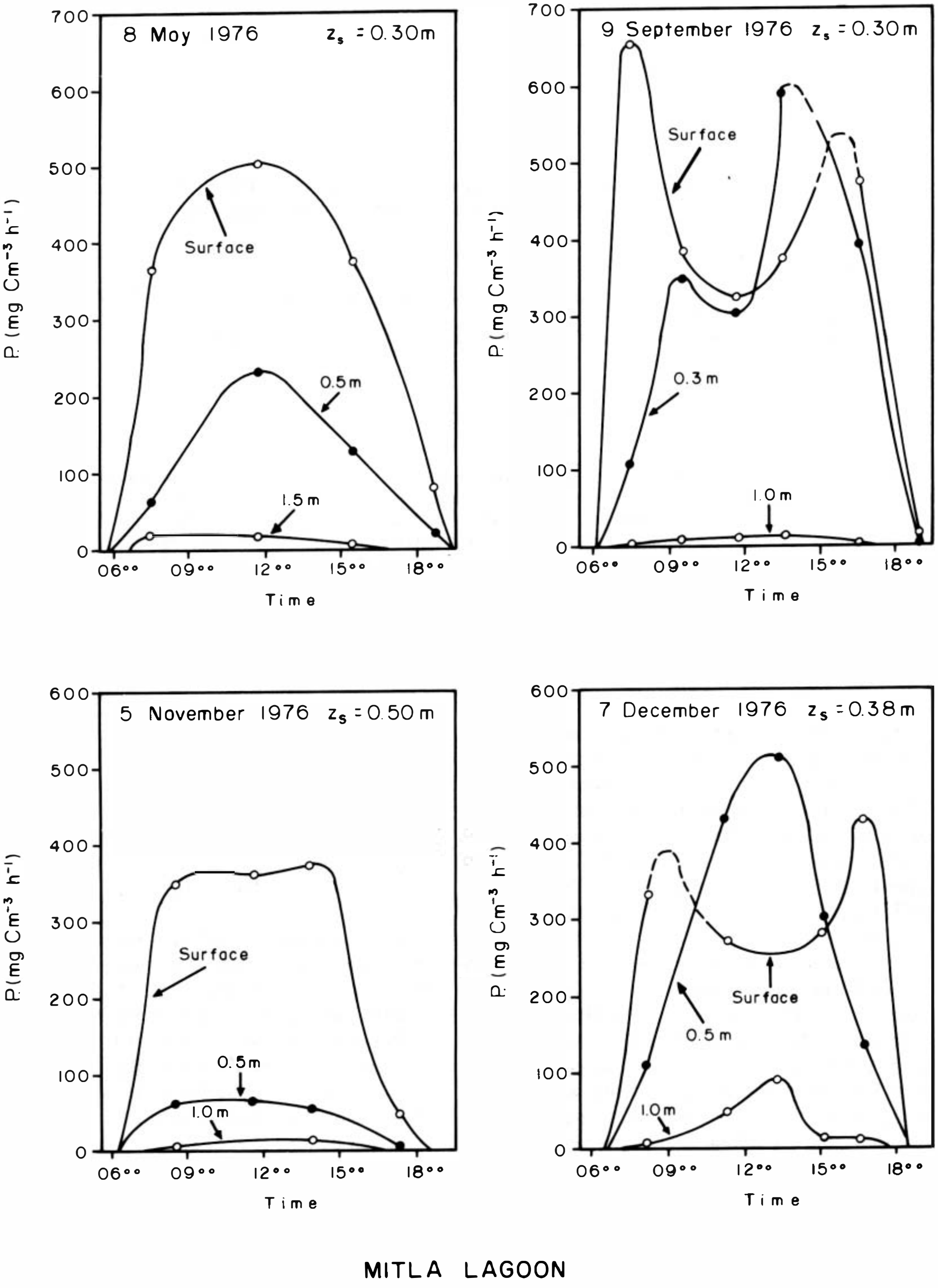
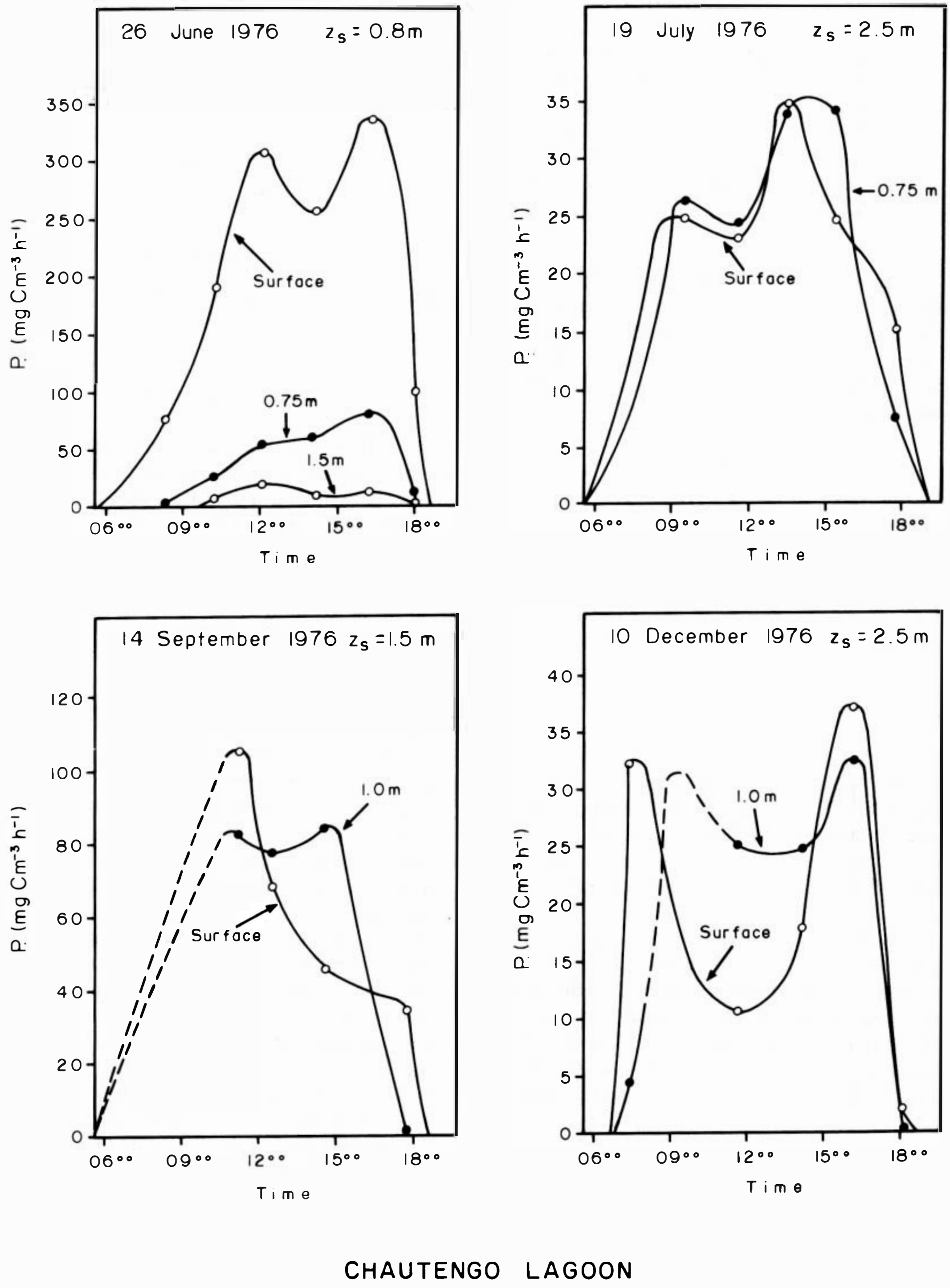


Fig. 1 Primary productivity curves for *in-situ* experiments in the Mitla lagoon. z_S is the Secchi depth.


26 June 1976 z_s = 0.8m

19 July 1976 z_s = 2.5 m

14 September 1976 z_s =1.5 m

10 December 1976 z_s = 2.5 m

CHAUTENGO LAGOON

Fig. 2 Primary productivity curves for *in-situ* experiments in the Chautengo lagoon. The vertical scale differs between diagrams. z_s is the Secchi depth.

(i) Cloudy sky conditions (26 June, Chautengo; 5 November, Mitla).
(ii) Increased afternoon vertical mixing by onshore breezes (introducing new nutrients but augmenting turbidity in shallow lagoons such as Chautengo).
(iii) Larger early morning (regenerated) nutrient supply (Vollonweider 1965).
(iv) Insufficient data points (eg. 8 May, Mitla).

Objectives of Productivity Calculation Models: If p_z is the production rate at a given depth z, for a small time interval ("instantaneous production rate", Vollenweider 1965) then the integrated productivity below a unit surface area through the time interval t_2-t_1 is:

$$\Sigma p_{(t_2 - t_1)} = \int_{t_1}^{t_2} \int_{0}^{\infty} (p_z \, dz) \, dt \qquad (1)$$

The general solution to this equation (Talling 1957) is:

$$\Sigma p = f(i) \frac{p_{opt}}{k} \qquad (2)$$

where P_{opt} is the production rate per unit volume at light optimum, f(i) is a function of the photosynthetically active incident light and k is the extinction coefficient of the photosynthetically active radiation (PAR) in the water column.

In order to perform the integrals in equation (1), expressions are thus required for the variability of production rates with light intensity, the change of light intensity with depth and through a daily solar cycle. For the latter two expressions Lambert's law and the equation given by Ikushima (1967) may be employed.

$$\text{Thus} \quad I_{zt} = I_{0t} \, e^{-kz} \qquad (3)$$

$$\text{and} \quad I_{0t} = I_0 \sin^3 (\pi/D) \qquad (4)$$

where I_0 is the maximum light energy available for photosynthesis (that which penetrates the surface at local apparent noon),

I_{0t} is the photosynthetically utilizable light energy penetrating the surface al time t,

I_{zt} is the photosynthetically utilizable light energy at depth z and time t,

D is the day length (as given by a nautical almanac)

and t is the time in hours (t_0 = dawn)

It follows that:

$$I_{zt} = I_0 \sin(\pi\, t\, D) e^{-kz} \qquad (5)$$

Since this equation adequately describes the light intensity at any point in a homogeneous water column on a cloudless day, the solution of the inner integral of equation (1) depends only upon the relationship between productivity and available light.

Production Rate/Light Intensity Curves: P/I curves are widely used by phytoplankton ecologists, particularly in laboratory culture (eg. Yentsch and Lee 1966; Steeman-Nielsen and Jorgensen 1968). They are used less commonly in field studies because there is a considerable difference between "instantaneous" production rates and those measured over a 3-6 hour period (Vollenweider 1965). Here, their production is possible given the very short incubation periods. It would normally be necessary to make accurate measurements of photosynthetically available light at each incubation depth (see Strickland 1958) but for the present purpose. use of the extinction coefficient derived from the Secchi depth, together with equation (5), is a tolerable substitute. In the highly turbid waters of Mitla and Chautengo, estimates from the relationship k = 1.44/Secchi depth (Holmes 1970) were found to correlate well with occasional measurements using a submersible irradiometer. This may not be true of other lagoon systems.

For the present P/I curves, light intensities were calculated for the mid-pont of each incubation period, except for the early morning and late afternoon incubations for which Ikushima's equation was integrated and divided by the exposure time (t_2 - t_1):

$$\overline{I_{0t}} = \frac{1}{(t_2 - t_1)} \int_{t_1}^{t_2} I_{0t}\,dt = \Big|_{t_1}^{t_2} \left[\frac{D}{3\pi}\cos^3\frac{\pi t}{D} - \frac{D}{\pi}\cos\frac{\pi t}{D}\right]\frac{I_0}{(t_2 - t_1)} \tag{6}$$

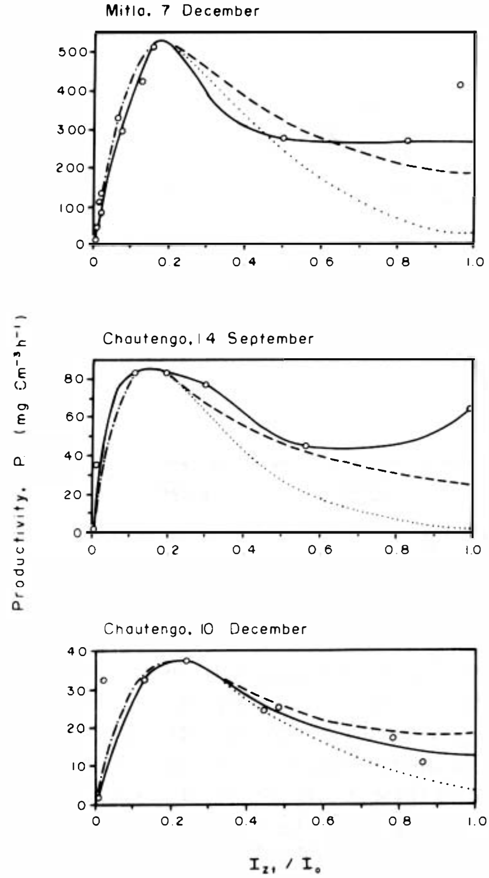


Fig. 3. p/I curves for three sets of experimental data. The continuous curve represents a visual "best fit" to the data. The hatched curve (------) was calculated using Equation 13 and the dotted curve (.......) using Steele's approximation (Equation 17).

Examples are shown in Figure 3. Despite the very different ecological conditions of the lagoons (Salinity: Chautengo = 8- $34^{0}/00$, Mitla = 2-$4^{0}/00$; productivity of Mitla is ten times higher than that of Chautengo, etc.), the general shape is similar with optimum productivity (P_{opt}) between 0.1 I_0 and 0.2 I_0 and considerable light inhibition of primary production at higher intensities. Light inhibition may be even greater than that measured by the ^{14}C technique as the borosilicate incubation bottles are opaque to much of the ultra-violet spectrum. On the ther hand, due to mixing processes, natural populations may only be exposed for very short periods to the deleterious effects of high light intensity, a factor as yet poorly studied.

For the initial experiments with calculation models for integrating the P/I curves it was decided to utilize the December Mitla data (Figure 3) owing to the higher density of data points at light levels below 0.2 I_0 and the Chautengo data for September and December where P_{opt} is very clearly located.

Integration of Productivity Curves: Most mathematical expressions for the photosynthesis-light relationship are based on the Smith (1936) equation:

$$p = p_{max} \frac{a I}{(1 + (aI)^2)^{1/2}} \tag{7}$$

where P_{max} is the maximum photosynthesis and a is a constant. Talling (1957) introduced the term I_k where $I_k = 1/a \cdot I_k$ represents the intercept between an extrapolation of the linear (light-dependant) slope of the P/I diagram and the height of saturation plateau (see Figure 4). The Smith equation has application only in cases where there is no light inhibition.

Talling (1957) has developed a practical integral of Smith's equation, based on planimetric measurements and considering $p = 0.5p_{max}$ for $I = 0.5I_k$:

$$\Sigma p_t = \frac{p_{max}}{k} \ln (2I_{0t}/I_k) \tag{8}$$

The analytical integral solution (Vollenweider, 1965) is:

$$\Sigma p_t = \frac{p_{max}}{k} . \operatorname{arc\,sinh} (I_{0t}/I_k) \tag{9}$$

Despite the disregard for light inhibition, these integrals fit most productivity data well and are

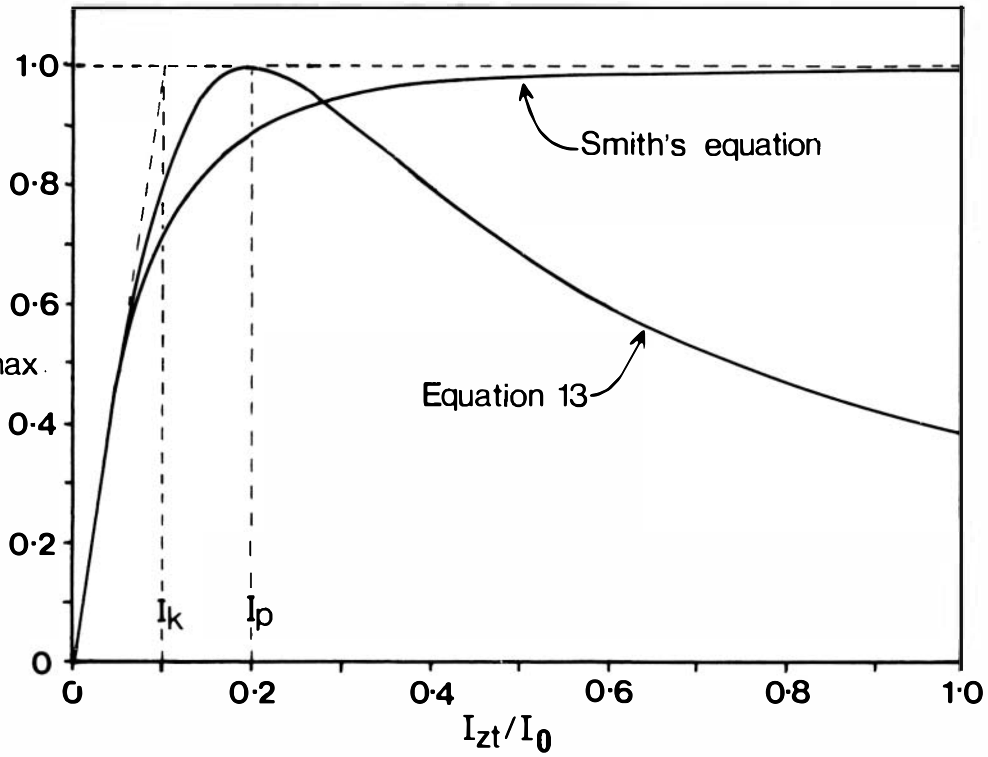


Fig. 4 Theoretical p/I curves given by the Smith equation (Equation 7) and Equation 13, assuming $I_k = 0.1\ I_0$.

thus widely employed. The I_k may be evaluated by plotting P_{zt} against I_{zt} and extrapolating the linear part of the P/I slope to the saturation plateau (Vollenweider 1974). This procedure, though effective in most marine environments has two serious drawbacks when applied to turbid tropical lagoons. First precision declines considerably at low values of p_{zt} and I_{zt}. As an illustration, an error of only 5cm in the collocation of a mid-day 1 metre incubation bottle in Mitla (December 1976) would result in a 20% relative error in the light intensity estimate for that measurement. Secondly in shallow lagoons where the bottom is illuminated most of the day, low light conditions are encountered only during the early morning and late evening and this light level usually varies considerably throughout even a 1 hour incubation period. It is apparent that any calculation model employing I_k values determined in this manner is unsatisfactory in such highly productive environments.

Another approach to estimating I_k is by solving Equation (7) for $p = p_{max}/2$ for which $I = 0.58 I_k$. Here p_{max} must be measured and data should be available in the region of $p_{max}/2$. In the present data set, only the Mitla, 7 December data is sufficiently complete for testing these procedures. A linear correlation of data points below $I_{zt} = 0.1\ I_0$ gives $I_k = 0.115\ I_0$ ($r = 0.97$). Alternatively, if $p_{max} = p_{opt} = 530$ mg C m^{-3} h^{-1}, then, by interpolation of Figure 3, I at $p_{opt}/2 = 0.06\ I_0$ and $I_k = 0.104$. This difference between the two I_k values generates only a 3% difference in the results of the modified Talling integral (9). For the Mitla, 7 December data (see Figure 5), the day-long integral is 2.81 g m^{-2} d^{-1}, very close (+ 4%) to the planemeter integral.

As previously mentioned, the Smith equation does not contemplate light inhibition. Vollenweider (1965) and Fee (1969) present a modified equation which should fit most experimental data:

$$p = p_{max} \frac{aI}{(1 + (aI)^2)^{1/2}} \frac{1}{(1 + (\beta I)^2)^{n/2}} \quad (10)$$

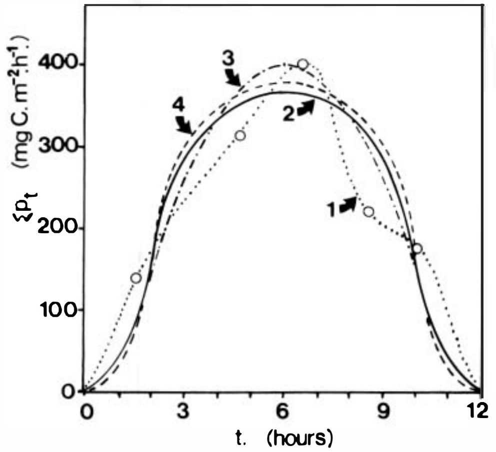


Fig. 5 Variation of integrated water-column productivity with time for the December Mitla data. Curve (1) represents raw experimental data integrated by planimeter. Curve (2) was calculated from planimetric integration of data from the "visual best-fit" p/I curve. Curve (3) was calculated using Talling's integral (Equation 9) and curve (4) was calculated using Equation (14).

and in which β and n are constants.

This equation generates a family of curves which fit most productivity data with the limitation that they reach a maximum at values different from p_{max} and are thus difficult to relate to experimental data. Mommaerts (1982) has introduced a proportionality constant, b, to allow the observed productivity maximum (p_{opt}) to take the same value as p_{max}. Thus:

$$p = p_{opt} \frac{I/I_k'}{(1 + (I/I_k'b)^2)^{1/2}} \frac{1}{(1 + (\beta I/b)^2)^{n/2}} \quad (11)$$

(where I_k' is the I_k value (defined in Equation 7) for this equation).

This equation, except in its simplest forms, is difficult to integrate analytically. For the case where n = 1 and $\beta = 1/I_k'$, b has the numerical value of 2 and:

$$p = p_{opt} \frac{I/I'_k}{1 + (I/2\ I_k')^2} \quad (12)$$

Mommaerts (1982) has shown by differentiating (11) that the light intensity at p_{opt}, $I_p = 2\ I_k'$. From Equation (12), and using the full notation:

$$p_{zt} = 2p_{opt} \frac{I_{zt}/I_p}{1 + (I_{zt}/I_p)^2} \quad (13)$$

By substituting dz = -dI/kI, from Lambert's Law, in the depth integral of (12), this integral may be written in a convenient form:

$$\Sigma p_t = 2 \frac{p_{opt}}{k} \arctan (I_{0t} / I_p) \quad (14)$$

Use of this integral only requires knowledge of the position and height of the productivity maximum given by the P/I curve and is thus less subject to the methodological imprecision described earlier.

Equation (13) was applied to each of the examples shown in Figure 3. As can be seen from the figure, the model gave a satisfactory fit in all cases. Its application on the December Mitla data is shown on Figure 5. For this example, total daily primary productivity was estimated at 2.79 g m^{-2} d^{-1}, only 3.9% greater than the planimetric measurement.

Substitution of Equation (4) in the time integral of expression (14) yields a general solution of Equation (1):

$$\Sigma p = 2 \frac{p_{opt}}{k} \int_0^D \arctan \left[\frac{I_0 \sin^3 (\pi t/D)}{I_p} \right] dt =$$

$$2 \frac{p_{opt}}{k} \int_0^D f(I, t)\, dt \quad (15)$$

By dividing the light day into ten equal parts, a simplified Simpson's Rule expression may be devised in order to estimate this integral. Thus:

$$\Sigma p = 2 \frac{p_{opt}}{k} \frac{4D}{30} [\ 2 f(I, t_1) + f(I, t_2) +$$

$$+ 2 f(I, t_3) + f(I, t_4) + f(I, t_5)\ ] \quad (16)$$

where $t_n = n\ D/10$ and f(I,t) is as defined in (15).

This expresion is relatively simple and programmable on many pocket calculators.

An Alternative non Smith-equation approach to calculation models is the empirical relationship given by Steele (1962):

$$p_{zt} = \frac{I_{zt}}{I_p} \; p_{max} \exp\left(1 - I_{zt}/I_p\right) \tag{17}$$

Following Lambert's Law substitution, this expression may be integrated (Vollenweider, 1965):

$$\Sigma p_t = \frac{p_{max}}{k} \; e \; [\, 1 - \exp\left(-I_{0t}/I_p\right)] \tag{18}$$

By use of equation (4) for I_{0t}, a Simpson's rule expression can be derived for the daily integrated productivity as in (16). Expression (17) was applied to the present data and, as may be seen in Figure 3, the resulting fit was poorer than that of the modified Smith equation model (expression 13). The generally poor fit of Steele's model was previously noted by Vollenweider (1965) and Parsons and Takahashi (1973).

Several other models have been formulated to describe the P/I relationship (for example; Parker 1975, Jassby and Platt 1976, Webb *et al.* 1974), and Platt *et al.* (1977) have reparameterized 5 of these models in terms of the initial slope and the assimilation number. Unfortunately these models do not fit the requirements of the present data set given the difficulty in evaluating the initial slope and the need for a simple description of light inhibition. Interestingly, Lederman and Tett (1981) have shown that, for light values below I_p, most models give similar results particularly considering the generally poor precision in productivity measurements.

Estimation of p_{opt} and I_p: Both p_{opt} and I_p may usually be estimated from a P/I diagram by describing the productivity maximum. For the December Mitla data total daily productivity was calculated for a variety of I_p values in order to examine the tolerable error in the estimation of this parameter. For present purposes, values of Σp within ± 10% of the planimetric integrals were considered as tolerable. Results are shown in Figure 6 together with corresponding values for the Steele integral (18) and the Talling integral (9) applied to (16) and utilizing $I_k = 0.5\ I_p$. In the three integrals a wide margin of error in the measurement of I_p is acceptable. In the case of equation (16), tolerable values of I_p would be from 0.148 I_0 to 0.243 I_0. In terms of depth, this would represent a 17 cm margin of acceptable error in the positioning of a mid-day incubation bottle. This perhaps explains why the present approximation works so well. In the case of equation (9), the range is slightly smaller (0.176 I_0 to 0.278 I_0) and for the Steele integral (18) the range is slightly larger (0.16 I_0 to 0.35 I_0). The "best fit" I_p value (zero apparent error), varies very slightly from model to model (I_p (16) = 0.202 I_0, I_p (18) = 0.222 I_0).

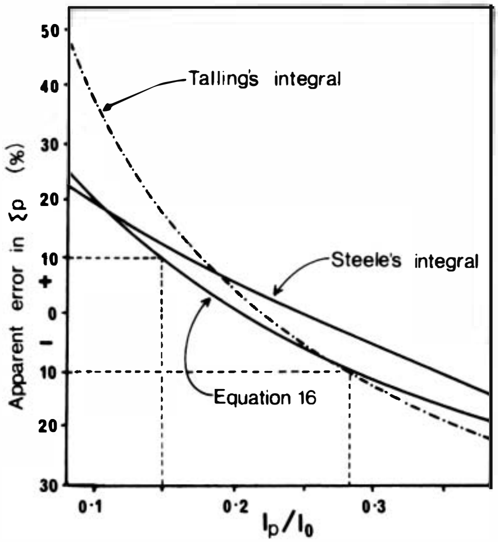


Fig. 6 The effect of assigning different values of I_p upon the daylong integral estimate for 3 calculation models. The data used here is the December Mitla data and apparent error is that measured with respect to the planimetric integral. For Talling's integral it is assumed that $I_k = I_p/2$.

In both lagoons the I_p values were close to 0.2 I_0. This value is somewhat lower than that of Rodhe (1965) for temperate lakes (I_k = 0.18 I_0) but the light and ecological conditions are not readily comparable. For cases where insufficient data for measuring p_{opt} are available, this can be estimated by rearranging Equation (13):

$$p_{opt} = \frac{p_{zt}}{2} \left[\frac{I_p}{I_{zt}} + \frac{I_{zt}}{I_p} \right] \tag{19}$$

If a value is assumed for I_p (*e.g.* 0.2 I_0) p_{opt} is easily estimated. In practice, unless (13) is an exact description of P/I, this equation is only useful for data reasonably close to I_p.

DISCUSSION AND CONCLUSIONS

Equation (16) and Steele's integral (18) were applied to all of the productivity measurements made in the Mitla and Chautengo lagoons except for the two experiments carried out during overcast sky conditions (26 June Chautengo;. 5 November, Mitla). In the Chautengo lagoon, the bottom was generally within the euphotic zone. In this case, the equations were applied for surface values of I_{0t} and subsequently for bottom values off $I_{zt}(= I'_{0t})$, calculated using (3), and the two results were subtracted. All productivity estimates are shown in Table 1. For the May (Mtla) and July (Chautengo) experiments, Equations (19) was employed to estimate p_{opt}, assuming $I_p = 0.2\ I_0$. From the table it can be seen that, for the range $\Sigma p = 0.32 - 2.8$ g m^{-2} d^{-1}, the modified Smith's equation model (16), gives values of Σp within 10% of the planimetric measurements for all of the experiments. This precision is within the limits considered as reasonable by Vollenweider (1974). The Steele integral was found to be less reliable for the present data, especially in the case of measurements made in Chautengo lagoon.

Tentative application of Equation (16) is thus possible in high-productivity, turbid waters under the following conditions:

(i) Measurement during a clear, sunny day.
(ii) There should be no major changes in the hydrochemical or light-extinction characteristics of the water column during the day.

Under these circumstances, one set of incubation bottles should be placed at 0.01 I_0, 0.05 I_0, 0.1 I_0, 0.2 I_0, 0.3 I_0, 0.5 I_0, 0.8 I_0 and I_0, or calculated as fractions of Secchi depths. Incubation time should be one hour and incubations should not be carried out in the first or last fifth of the daylight period (in order to avoid the highly variable early morning or late afternoon light and nutrient conditions). In this manner, 6 or more different productivity experiments can be carried out during one day, each at a distinct location within the same lagoon. The p_{opt} and I_p should be determined from either a p/I or p/z diagram (applying Equation (3) in the latter case). All other methodology is similar to that described by Fernández *et al.* (1979).

Equation (15) is the same as the general solution presented in expression (2) when:

$$f(i) = 2\int_0^D f(I, t)\ dt \tag{20}$$

This expression may also be shown in terms of the assimilation number (θ) which is the optimum productivity (mg m^{-3} h^{-1}) divided by the chlorophylla concentration, Cl_a (mg m^{-3}) (see Parsons and Takahashi 1973; Platt and Subba Rao 1975).
Thus:

$$\Sigma p = \frac{\Theta\ Cl_a}{k}\ f(i) \tag{21}$$

If θ, Cl_a and k are measured and a value is assumed for I_p (as in Equation 18), Σp may be estimated for any water column in a homogeneous phytoplankton population using equations (16) and (21). In Table 1, assimilation numbers are shown for the present data. These values, which will be fully discussed in another paper, are quite different for the Mitla (3.75 – 4.1 g gCl$_a^{-1}$ h^{-1}) and Chautengo (13.2 – 25.3 g gCl$_a^{-1}$ h^{-1}) lagoons and, in the case of Mitla, are remarkably constant. If the comportment of θ were known, no further uptake measurements would be required to apply equation (21) to any point in a lagoon, provided that Cl_a and k estimates are available. Whilst this approach to "whole lagoon" primary productivity estimation seems promising, more detailed studies of the variation of θ in these water bodies are required before it may be generally utilized.

The productivity calculation model adapted for this study appears to offer a viable alternative to the conventional planimeter-integration techniques. The model should by no means be regarded as a universal and precise description of P/I curves in coastal lagoons but appears to provide a reasonable approximation of this relation for integration purposes and as such,

Table 1

Lagoon	Date	P_{opt}	θ	$\Sigma\rho$	$\Sigma\rho$-Solution (15)		$\Sigma\rho$ -Steele's equation	
		mgC m^{-3} h^{-1}	gC gCl_a^{-1} m^{-3} h^{-1}	(planimeter) gC m^{-2} d^{-1}	gC m^{-2} d^{-1}	Apparent Error %	gC m^{-2} d^{-1}	Apparent Error %
Mitla	May 8	540*	3.75	2.65	2.54	–4.2	2.64	–0.5
Mitla	Sept. 9	595	3.72	2.80	2.61	–6.7	2.73	–2.5
Mitla	Dec. 7	512	4.10	2.69	2.79	+3.9	2.87	+7.1
Chautengo	July 19	38*	19.0	0.32	0.301	–5.7	0.29	–10.2
Chautengo	Sept. 14	84	13.2	0.98	0.92	–6.2	0.87	–11.4
Chautengo	Dec. 10	38	25.3	0.33	0.32	–1.8	0.29	–11.7

* Calculated from equation (18)

may have wide application in highly productive and turbid aquatic environments.

ACKNOWLEDGEMENTS

I thank Hugo Fernández for his help with the fieldwork, Enrique Mandelli for stimulating this research, Eric Jordan for his supply of ^{14}C, and Ricardo Tapia for use of his scintillation counter.

RESUMEN

Se hizo un estudio detallado de la fijación de carbón radiactivo en dos lagunas costeras tropicales de la costa del Pacífico mexicano, con el propósito de estimar la tasa diurna de productividad primaria (Σp). Los datos así obtenidos fueron utilizados para evaluar y adaptar modelos de cálculo para la integración de las curvas de p/I (Productividad/Intensidad luminosa). Las integrales comúnmente empleadas en estudios oceanográficos requieren datos precisos de p en la región de baja iluminación y no contemplan los efectos de la fotoinhibición y, por lo tanto, no son aplicables al caso actual. Se desarrolló un modelo que solamente requiere conocimiento de la altura y posición del máximo subsuperficial de p y que permite el cálculo preciso de Σp.

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