ESTIMATION OF ALGAL GROWTH PARAMETERS FROM VERTICAL PRIMARY PRODUCTION PROFILES

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June 1981
CP-81-19

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PREFACE

One of the principal themes of the Task on Environmental Quality Control and Management in IIASA's Resources and Environment Area is a case study of eutrophication management for Lake Balaton, Hungary. The case study is a collaborative project involving a number of scientists from several Hungarian institutions and IIASA (for details see WP-80-187).

As part of the case study three different biochemical models of the lake's behavior are under development (results for two of these models have already been described in earlier working papers WP-80-139 and WP-80-149). In all these models the maximum algal growth rate plays an important role. This paper illustrates how this parameter can be estimated from measured vertical profiles of primary production. The procedure suggested provides not only a better understanding and explanation of the particularly high growth rate, compared to values quoted in the literature, but also decreases the number of parameters to be estimated in terms of the complex biochemical models.

ABSTRACT

Phytoplankton maximum growth rate and the saturation light intensity, I_s, can be estimated from vertical profiles of primary production by non-linear least-squares estimation. Solution through the normal equations leads to formula which are relatively simple and easy to implement. The computation of confidence contours is demonstrated, and the results are contrasted to the confidence limits on the parameters individually. These can be quite misleading due to model non-linearity and correlation between parameter estimation.

The procedure has been applied to primary production data from Lake Balaton, a shallow lake in Hungary. The growth rate-temperature relation is analyzed by separating the parameter set into two groups characteristic for 'warm' and 'cold' water phytoplankton, respectively. A bell-shaped curve is found for 'cold' water communities, with an optimum at about 7 - 9^{0}C, whereas the 'warm' water phytoplankton exhibits a strong exponential dependancy in the temperature range of interest (up to 25^{0}C). I_s appears also to be related to essentially constant. However, a roughly linear relation with considerably less scatter is obtained when I_s is plotted directly versus day-averaged solar radiation. This apparent fast adaptation is attributed to the extremely short overtime in Lake Balaton. Maximum growth rates of 10-20 day^{-1} have been found for temperatures between 20^0 and 25^{0}C. These results and a critical appraisal of available literature suggest that the common notion of maximum growth rates being in the order of 1-3 day^{-1} needs revision, at least for lakes with relatively high summer temperatures.

CONTENTS

INTRODUCTION

In situ measurement of photosynthetic activity or primary production is common practice in limnological research. Numerous examples can be found in the literature (e.g. Stadelman and Munawar, 1974; Jones, 1977; Findenegg, 1971; Megard and Smith, 1974). Among the characteristics calculated from the results yearly areal primary production is perhaps most frequently desired, because this quantity is considered to be an important indicator of trophic state (Rodhe, 1969). Much work has also been done to relate the instantaneous , the depth averaged or the depth and day averaged primary production to light (e.g. Talling, 1971; Ryther and Menzel, 1959), temperature (e.g. Stadelman et al, 1974; Verduin, 1956), or community composition (e.g. Findenegg, 1971; Jones and Ilmavirta, 1978). Generally the analysis focuses on such limnologically significant quantities as depth of optimal growth, photic zone depth, optimal light intensity and indicators of phytoplankton activity in the form of assimilation numbers and activity coefficients.

The vast majority of mathematical simulation models for lakes and reservoirs, on the other hand, deals with the rate of increase of biomass as a first order process, with a rate coefficient commonly expressed as a maximum growth rate attenuated by functions of temperature, light and nutrients. Clearly, parameters in this expression will have a distinct relation to the results obtained by limnologists, but, surprisingly enough, there appear to be very few publications in the open literature on the analysis of primary production results in terms of model parameters. Obviously, model parameters have been derived from primary production measurements but in a rather ad-hoc and intuitive fashion. Application of formal parameter estimation techniques in this field appears to be scarce. Fee (1973) used a non-linear least squares technique to fit the primary production depth profiles to one predicted by a relatively complicated light function. His principle aim was to use the mathematical model description to remove most of the approximations commonly used in limnology when deriving the daily aereal primary production from instantaneous depth profiles (Fee, 1969). No attention was given to the variances of the parameter estimates. Lederman et al. (1976) demonstrated the feasibility of non-linear estimation techniques for the analysis of phytoplankton batch-culture data for use in water quality simulation models, but the application was restricted to synthetical data only. In our own institute we applied simple computer programs for least squares parameter estimation from dark and light bottle tests.

The purpose of the present investigation is to apply an existing non-linear least squares parameter estimation technique to the analysis of primary production data, with the explicit goal of using the results in the framework of dynamical modelling. The paper comprises two parts:

i) Estimation of model parameters, including confidence bounds, from primary production measurements at different depths. By virtue of the relative simplicity of the expressions used in mathematical models the procedure turns out to be fairly simple and easy to implement. Consequently, the method is believed to be applicable in a great deal of commonly met situations.

ii) Correlation of the parameters obtained to environmental factors such as temperature and incident solar radiation. In the present application extensive information on the biomass composition was available. This allowed for a more detailed analysis than would otherwise have been possible. As a consequence, this part is probably somewhat more case-specific, but the results can be of interest for mathematical model building in general.

The data used originate from Lake Balaton in Hungary. The results are intended for use in the various phytoplankton dynamics and phosphorus cycle models developed for this lake (cf. Leonov and Vasiliev, 1980; Van Straten, 1980; Csaki and Kutas, 1980). The research reported herein was carried out as part of the Lake Balaton Eutrophication case study undertaken by the International Institute for Applied Systems Analysis, Laxenburg, Austria in close operation with the Hungarian Academy of Sciences and the National Water Authority of Hungary.

LAKE BALATON

Lake Balaton is a long-shaped shallow lake in western Hungary. With its 594 km^2 it is the largest lake in central Europe. The length is 77 km, the average depth is 3.14 m. In recent years cultural eutrophication has led to increased algal concentrations, especially in the south-western part (Keszthely Bay, see fig. 1) where the main tributary (the Zala River) carries approximately 30% of the total phosphorus load to the lake. The areal loading in this part of the lake is estimated to be about 3.1 g P/m^2 yr, whereas the whole lake estimate is close to 0.5 g P/m^2 yr. Due to its long shape, the uneven distribution of the loading and the considerable calcium precipitation along the axis of the lake, there is a remarkable west-to-east gradient for most water quality constituents, including biomass. A detailed description of the eutrophication problem of Lake Balaton and the role of mathematical modelling in research and management is presented in Van Straten et al. (1979).

PRIMARY PRODUCTION EXPERIMENTS

Primary production measurements were conducted in Lake Balaton in an annual rotation scheme at four locations (fig. 1) since 1972 (Herodek and Tamas, 1973,1974,1975,1978; Herodek et al., in press). Bottles were suspended at four depths and exposed for four hours around noon. The carbon uptake was determined by the ^{14}C-technique involving membrane filtration, fuming with hydrochloric acid and measurement of radioactivity by liquid scintillation (Herodek and Tamas, 1973). Simultaneously, algal counts were made for each sample, from which biomass fresh weight for each species was calculated by multiplication with the individual species cell volume, assuming a specific gravity of 1 g/cm^3. Water temperature, secchi disk depth, surface and underwater illumination were also measured. In addition global radiation over the day as well as over the

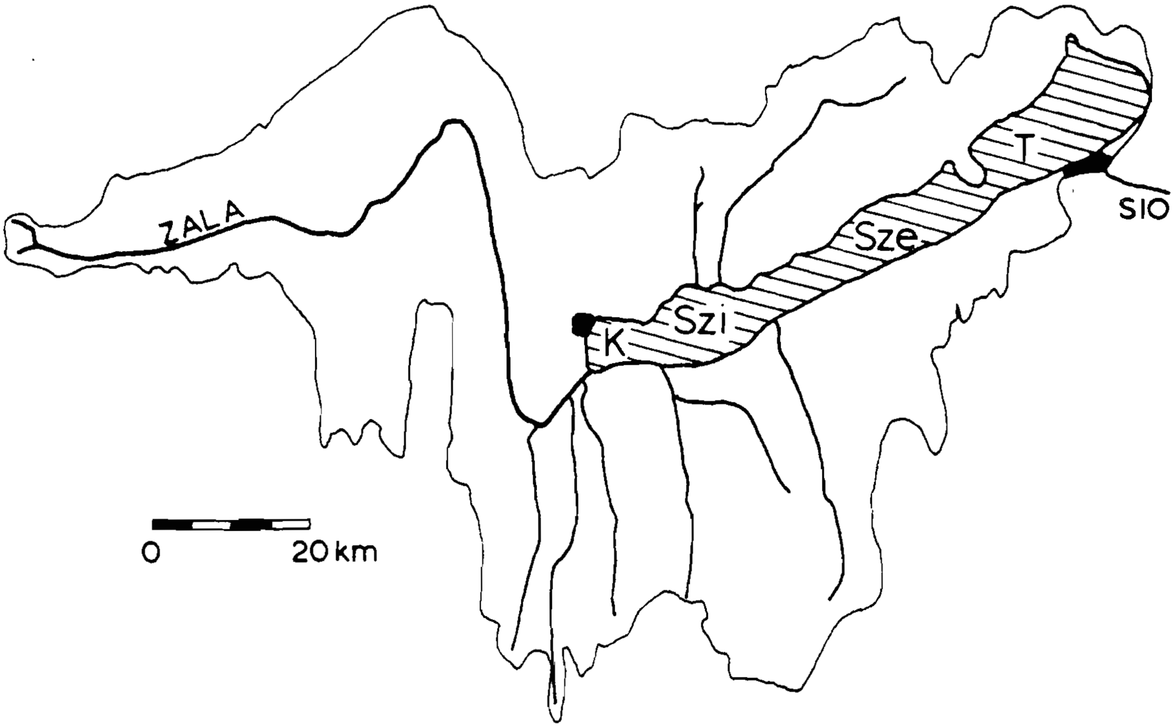

Figure 1. Lake Balaton and Measurement Sites,
K = Keszthely; Sri = Szigliget;
Sze = Szemes; T = Tihany

time of exposure were available from a nearby meteorological station.

Fig. 2 summarizes the results for three of the four measurement locations (Herodek, 1977). Note the difference in scale for the different basins. Generally, in Tihany, where resuspension of sediment deposits by wind action is governing the underwater light climate, a strong variability in the vertical patterns of primary production is observed. Frequently, inhibition occurs in the top layer as a consequence of the relatively high light levels. Transparancy is usually sufficient to allow for a markable production near the bottom of the lake. The observed maximum daily production was 0.6 g C/m^2 day in this part of the lake.

In the most polluted end of the lake, the Keszthely Bay, light transparency is generally much less, partly due to the self-shading of the algae. Hence, photoinhibition at the surface is rare, and no production is possible at the bottom. Here, very high daily productivities occured, up till 13.6 g C/m^2 day. The Szigliget basin takes an intermediate position, with a maximum daily productivity of 2.6 g C/m^2 day during the observation period.

A rough estimate of the annual production ranges from 95 g C/m^2 at Tihany, via 275 and 300 g C/m^2 for Szemes and Szigliget, to 830 g C/m^2 for Keszthely. From a productivity point of view Lake Balaton therefore falls in the category of eutrophic to hypertrophic lakes (cf. Rodhe, 1969). The difference among the basins is reflected in the biomass data as well. Maximal standing crops ranged from 5 g fresh weight/m^3 at Tihany through 6, 13 and 17 g fresh weight/m^3 for the Szemes, Keszthely and Szigliget basins, respectively. This will be discussed in greater detail later.

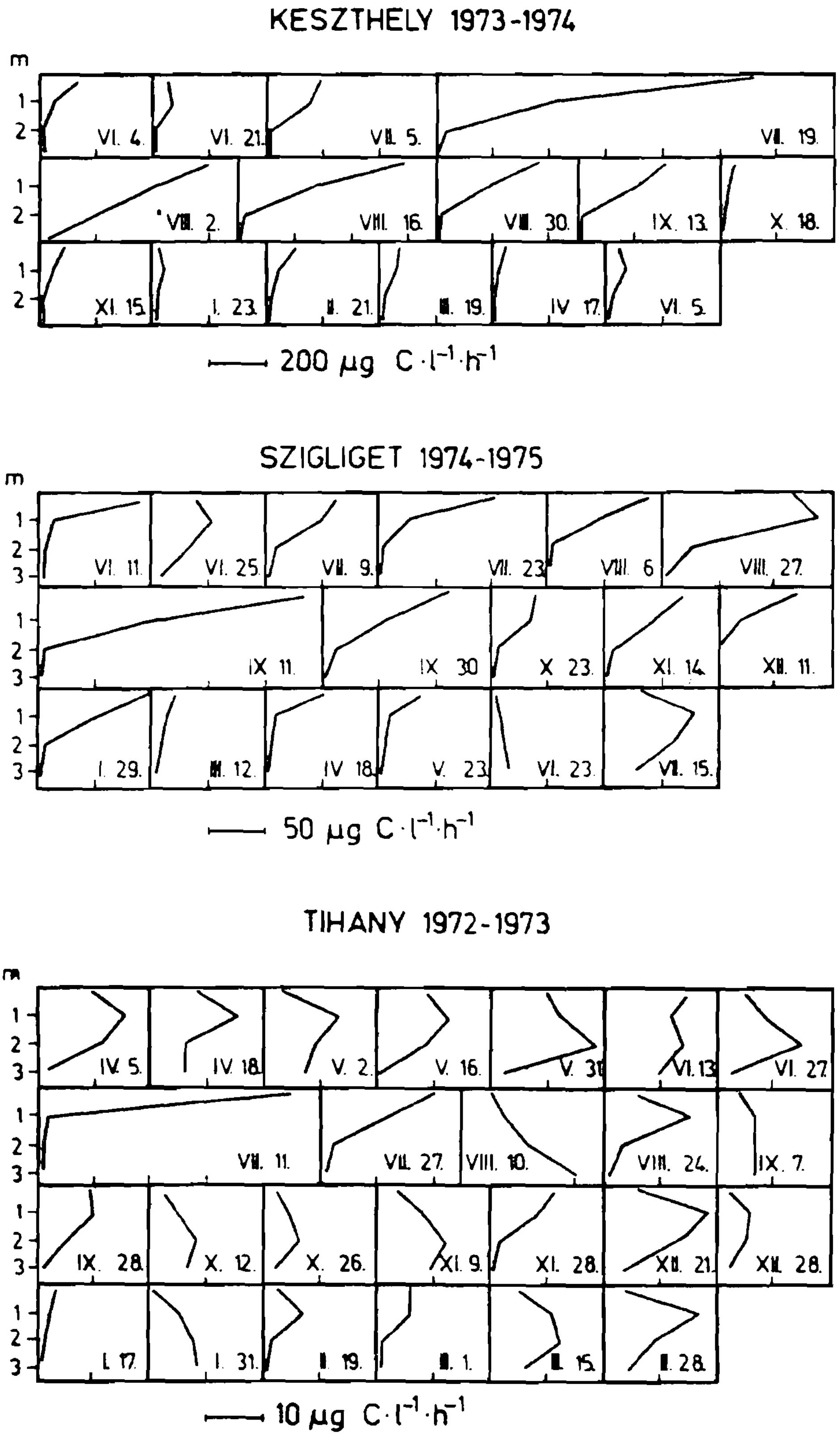

Figure 2. The Vertical Distribution of Production of Phytoplankton. (Note the difference in scale for the various basins.)

METHOD

ASSUMPTIONS

Practically all phytoplankton models use an algal growth term of the form

$$\frac{dA}{dt} = k_{max}(T)\ F_P F_L A + \ldots.. \qquad (1)$$

where A is the algal concentration (in suitable units), $k_{max}(T)$ the maximum unrestricted growth rate at temperature T, F_P a nutrient limitation factor and F_L some light attenuation factor, which may be derived from a depth and/or day averaged light-growth relationship, depending on the spatial and temporal detail of the model (cf. Kremer and Nixon, 1978). The latter two factors may be functions of temperature as well. The corresponding model for instantaneous carbon uptake rate in each bottle at depth z, as measured in the ^{14}C method, is given by

$$\Phi_z(t) = k_{max}(T(t))\ F_P(I_z(t))\ A(z,t) \qquad (2)$$

where the new symbols are

$\Phi_z(t)$ the instantaneous dissolved carbon uptake rate at time t and depth z

$F(I_z(t))$ the ratio of the actual growth rate at light intensity I_z at depth z to the growth rate at optimal light intensity, and

$A(z,t)$ the algal biomass in carbon units at depth z

Note that if A is measured in other units (e.g. chlorophyll-a) a conversion factor must be included in equation 2.

Equation 2 can be integrated over the time of exposure τ to yield a model estimate $\Phi_m(z)$ of the hourly averaged primary production during exposure, which can than be compared with the actually measured value $\Phi_e(z)$. Thus,

$$\Phi_m(z) = \frac{1}{\tau} \int_{to}^{t_o+\tau} k_{max}(T) F_P F(I_z) A(z) dt \qquad (3)$$

where for notational simplicity the time dependancy of the coefficients has been deleted. An essential implicit assumption inthe ^{14}C method is that there is no significant release of labeled carbon in dissolved form during growth. Naturally, the same assumption applies to the model equation 3. The ^{14}C method measures the total increase of particulate labeled carbon. Hence, internal transitions in the particulate carbon pool, such as excretion of particulate organic matter or grazing by zooplankton do not influence the result.

Theoretically, the evaluation of equation 3 is possible only if the functional relationships of T, F_p, $F(I_z)$ and A(z) with time during exposure are known. In most cases, however, measurements of temperature, radiation, nutrients and biomass during exposure are lacking, and, consequently, additonal assumptions have to be made. Doubtlessly, no large error will be introduced by assuming that temperature is constant throughout the experiments. Also incident radiation will be fairly time-invariant, (except perhaps on days with a strong variability in cloud cover), because the measurements have been carried out around the top of the daily sinusoid insolation curve. The situation with respect to variations in biomass is more delicate. As shown in figure 2 production rates can be as high as 1 mg C/l, h in extreme cases, which is in the same order of magnitude as the biomass itself. Thus, at first sight, one would expect a considerable increase of biomass during the 4 exposure hours. On the other hand, mortality processes will continue as well, and since in-lake biomass concentrations do not show strong increases within one day mortality must be quite significant, thereby mitigating the rise in biomass. Thus, the assumption of biomass varying only slightly in the course of a measurement is not unreasonable.

Perhaps the largest uncertainty exists with respect to the nutrient situation. In the last extremity, assimilation rates of about 1000 μg C/l h would have to be associated with a phosphorus uptake of roughly 10 μg P/l,h. At the prevailing orthophosphate levels in Lake Balaton (usually below 20 μg/l) this would imply that the concentration in the bottles would drop considerably during the 4 hours of exposure, unless ortho-phosphate is internally supplied or rapidly recycled. Admittedly such extreme assimilation rates rarely occur, but unfortunately no simultaneous measurements of the nutrient levels at the experimental days have been done, and thus the possibility of nutrient limitation can not be excluded. The best thing we can do is to incorporate the unknown factor F_p into k_{max}, and consider this new value as a lower bound to the true unlimited maximum growth rate.

Now equation 3 can be restated as

$$\Phi_m(z) = K(T)\ F(I_z)\ A(z) \qquad (4)$$

where, for convenience $\frac{1}{\tau} \int F_p dt$ has been incorporated in the parameter K. The next task is to estimate K and $F(I_z)$ from the experimental data. It should be noted that for each individual measurement day $F(I_z)$ can be determined from the vertical depth profile. If we would parameterize $F(I_z)$ with one single parameter, say I_f, (for example by the well known Smith ($I_f=I_k$) or Steele ($I_f=I_s$) formula), each measurement would provide one value for I_f in the array of values for all experiments together. As a final step one can then attempt to relate the variability in I_f with environmental factors such as temperature or incident radiation. A similar argument applies to the temperature dependancy of K.

ESTIMATION PROCEDURE

Introducing the simplified notation

$$\Phi_{mi}(K,I_f) = \Phi_m(z_i,K,I_f)$$

$$\Phi_i = \Phi_e(z_i)$$

for the model and experimental value of the hourly primary production at depth z_i, $i=1,...n$, a least squares estimate of K and I_f is obtained by minimizing the objective function

$$J(K,I_f) = \sum_{i=1}^{n} [\Phi_{mi}(K,I_f) - \Phi_i]^2 \qquad (5)$$

The light function F_I is non-linear in I_f and consequently linear least squares theory can not be applied here. Clearly, equation (5) could be readily solved by one of the existing non-linear least squares minimum search methods. However, since the problem has only two parameters and since equation 4 is linear in one of the two, (K), a more direct solution is obtained through examination of the 'normal equations', i.e. by setting $\partial J/\partial K$ and $\partial J/\partial I_f$ equal to zero (see Draper and Smith, 1966). Thus,

$$\sum_{i=1}^{n} [\Phi_{mi} - \Phi_i] \frac{\partial \Phi_{mi}}{\partial K} = 0 \qquad (6a)$$

$$\sum_{i=1}^{n} [\Phi_{mi} - \Phi_i] \frac{\partial \Phi_{mi}}{\partial I_f} = 0 \qquad (6b)$$

Substitution of equation 4 into equation 6a yields

$$K = \frac{\sum_{i=1}^{n} \Phi_i A_i F_i}{\sum_{i=1}^{n} (F_i A_i)^2} \qquad (7)$$

where, as before, F_i and A_i are simplified notations for the light attenuation factor and algal biomass at depth z_i. Equation 7 means that K can be expressed as an explicit function of I_f. Note that this result is valid for any functional relationship of growth-rate with light that can be characterized by one single parameter. Equation 7 also indicates that if the functional relationship and its parameter I_f are supposed to be known for some reason, the least squares estimate of the growth rate K can be computed by simple calculus.

Substitution of equation 4 in equation 6b, and dividing by K leads to

$$\sum_{i=1}^{n} (KA_i F_i - \Phi_i) A_i \frac{dF_i}{dI_f} = 0 \qquad (8)$$

which, together with equation 7 yields an implicit expression for I_f.

In the sequel we will now further evaluate equation (8) for the case of Steele's formula

$$F_i = \frac{I_i}{I_s} \exp\left(- \frac{I_i}{I_s} + 1\right) \tag{9}$$

where I_i is the light intensity at depth z_i and I_s is the equation parameter I_f (the light intensity for maximum growth). Differentiating with respect to I_s, substitution in equation 8 and dividing out non-zero, constant factors, finally results in

$$\sum_{i=1}^{n} (KA_i F_i - \Phi_i) F_i A_i \left(- \frac{I_i}{I_s} + 1\right) = 0 \tag{10}$$

The solution of this equation can be readily obtained by suitable existing zero-finding routines. Because of the light inhibition there might be two solutions for equation 10. In practice it turns out that there is hardly any problem because either the two I_s-values are very close, or the better solution can easily be selected by examining the sum of squared differences.

CONFIDENCE REGIONS

The approximate 100(1-q)% confidence contours around the estimated point K, I_s can be calculated by finding points K, I_s which satisfy

$$J(K,I_s) = J(\hat{K},\hat{I}_s)[1 + \frac{p}{n-p}\mathcal{F}(p,n-p,1-q)] \tag{11}$$

where $\mathcal{F}(p,n-p,1-q)$ denotes the upper 100q% points of the $\mathcal{F}$-distribution for P parametrs and n observations. The evaluation of the contours in this case is particularly straightforward. If we call the right-hand side of equation 11 Q (a known quantity once the minimum has been found) we can write

$$\sum_{i=1}^{n} [\Phi_{mi} - \Phi]^2 = Q \qquad (12)$$

Substitution of equation (4) leads to

$$aK^2 - 2bK + C - Q = 0 \qquad (13)$$

where

$$a = \sum_{i=1}^{n} (A_i F_i)^2 \qquad \text{a function of } I_s \text{ alone} \qquad (14a)$$

$$b = \sum_{i=1}^{n} A_i F_i \Phi_i \qquad \text{a function of } I_s \text{ alone} \qquad (14b)$$

$$c = \sum_{i=1}^{n} \phi_i{}^2 \qquad \text{a constant} \qquad (14c)$$

Hence, if we select a value for I_s the two K values on the contourline follow simply from

$$K = \frac{b \pm \sqrt{b^2 - a(c-Q)}}{a} \qquad (15)$$

As pointed out by Draper and Smith (1966) the contour lines calculated this way represent exact confidence contours, but the confidence level is only approximate because of the non-linearities of the model. In the case of the measurements in Lake Balaton we have n=4 and F(2,2,0.95) = 19.00, and so the confidence region with an approximate level of confidence of 95% is given by

$$J(K,I_s) \leq 19.00\, J(\hat{K},\hat{I}_s) \qquad (16)$$

VARIANCE-COVARIANCE MATRIX

An alternative way of examining the quality of the parameter estimates is to calculate the variance-covariance matrix for the parameters. Again, this can only be calculated approximately because of the model non-linearities:

$$V_a(\hat{K},\hat{I}_s) = (\hat{G}^T \hat{G})^{-1} s^2 \qquad (17)$$

with

V_a the approximate variance-covariance matrix at the minimum

G the Jacobian matrix of the residuals:

$$\hat{G}_{ji} = \left\{\frac{\partial \phi_{mi}}{\partial \underline{\theta}_j}\right\}_{\underline{\theta}=\underline{\hat{\theta}}}$$

$\theta_1 = K$

$\theta_2 = I_s$ and,

s^2 an estimate of the residual error variance

$s^2 = J(\hat{K},\hat{I}_s)/(n-p)$

The variances can be used to provide a confidence interval on the parameters individually and are, therefore, somewhat easier to use than the full confidence regions. However, it should be emphasized that the results can be quite misleading if the parameters are correlated. Thus, the covariances should always be checked in this case.

EXAMPLE

In order to demonstrate the concepts outlined in the previous section an example is presented for one of the measurement points, February 21, 1974 in Keszthely Bay. Table I presents the observed data and the parameter estimation. The confidence regions are shown in Fig. 3a.

TABLE I: Calculation Example

Location: Keszthely; *Date*: 21-2-1974; *Daylength*: 10.1 h; *Exposure*: 10.00-14.00; *Global radiation during exposure*: 78 cal/cm^2; *Global radiation over whole day*: 167 cal/cm^2; *Water temperature*: 7°C; *Secchi transparency*: 0.42 m; *Biomass*: 5.23 mg fresh weight/l (~ 523 µg C/l)

depth m	% of surface illumination	Φ_e (µg C/l h)	Φ_m µg C/l h	F_i (eq. 9)
	measured		calculated	
0.25	34.7	90.1	90.1	0.999
1.0	4.4	28.6	28.2	0.313
2.0	0.6	2.8	4.3	0.048
2.75	0.3	0.9	2.2	0.024

Estimated parameters

K: 0.173 h^{-1}; standard error: 0.003 h^{-1}; coefficient of variation: 2%; I_s: 6.53 cal/cm^2 h; standard error: 0.38 cal/cm^2 h ; coefficient of variation: 6%; correlation coefficient: 0.18

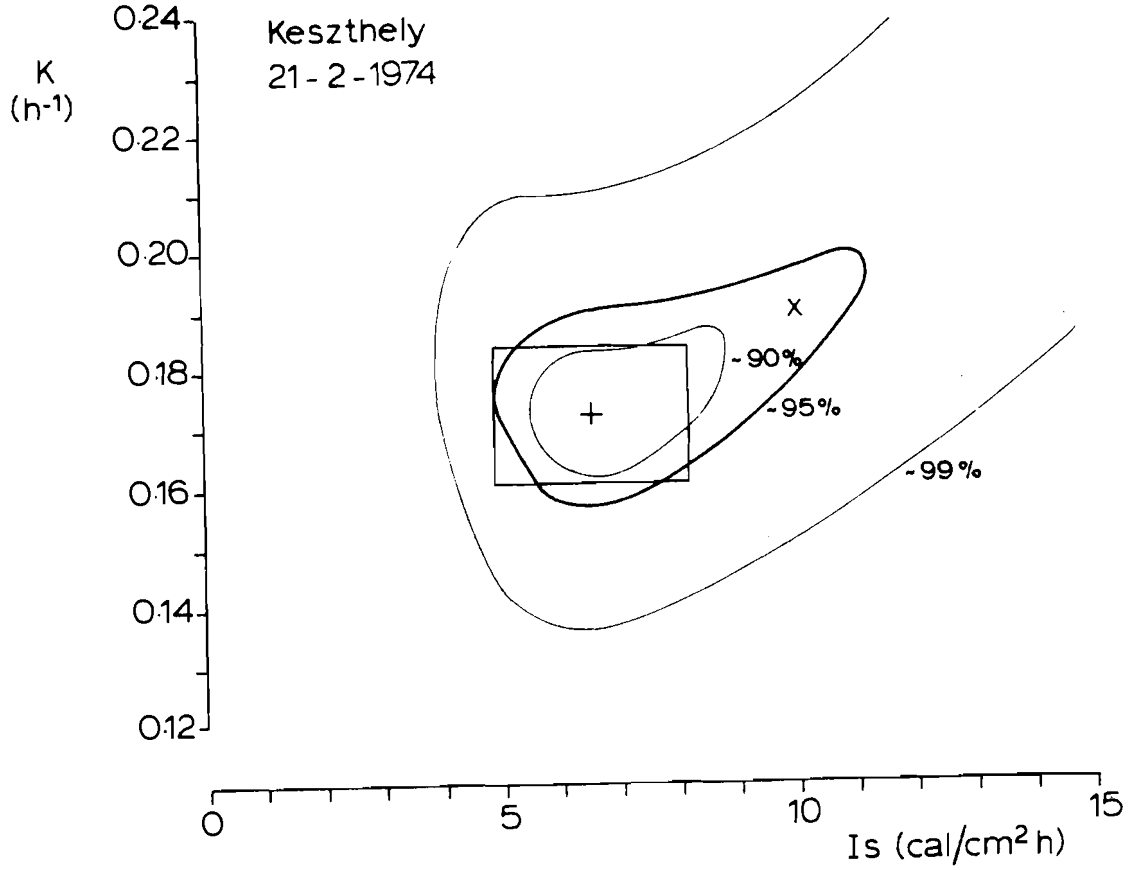

Figure 3a. Confidence Regions in Parameter Space (growth rate K and light saturation parameter I_s). The rectangle respresents individual confidence limits for each of the parameters separately.

The interpretation is that parameter combinations within, for example, the 95% line, are considered, on the basis of the data, as not unreasonable estimates for the true parameter values at an approximate 95% level of confidence. The rectangle in the figure indicates the confidence limits for each of the parameters separately calculated from the variance-covariance matrix (2 degrees of freedom: ± 4.303 * standard error from table I). The figure clearly illustrates the biased view obtained when using the individual parameter confidence limits. Figure 3b gives an impression of the quality of the fit. Also shown is the primary production curve belonging to the point marked x in figure 3a (dashed line). The shaded area around each of the observation points indicates the range of prediction when using all reasonable parameter combinations, that is all points within the confidence limit region.

RESULTS

Table II summarizes the results of the estimation for all experimental days. Confidence limits and bounds are presented also. It should be stressed that these refer only to the uncertainty associated with the estimated observation error. Other errors may also exist. In particular, the assumption that the carbon content of the algae is 10% of the fresh weight directly affects the level of the growth rate estimate (but not I_s). A larger value for the ratio proportionally decreases the estimate.

Generally, the Steele equation fits the data quite well, although sometimes there is a tendency of slightly overestimating the production in the deeper layers. Only in few cases there was a serious lack of fit. The calculations were based on the assumption of a vertically homogeneous biomass distribution, except for the Tihany where more detailed data were available. Lack of fit could arise in case of strong vertical inhomogeneities in biomass.

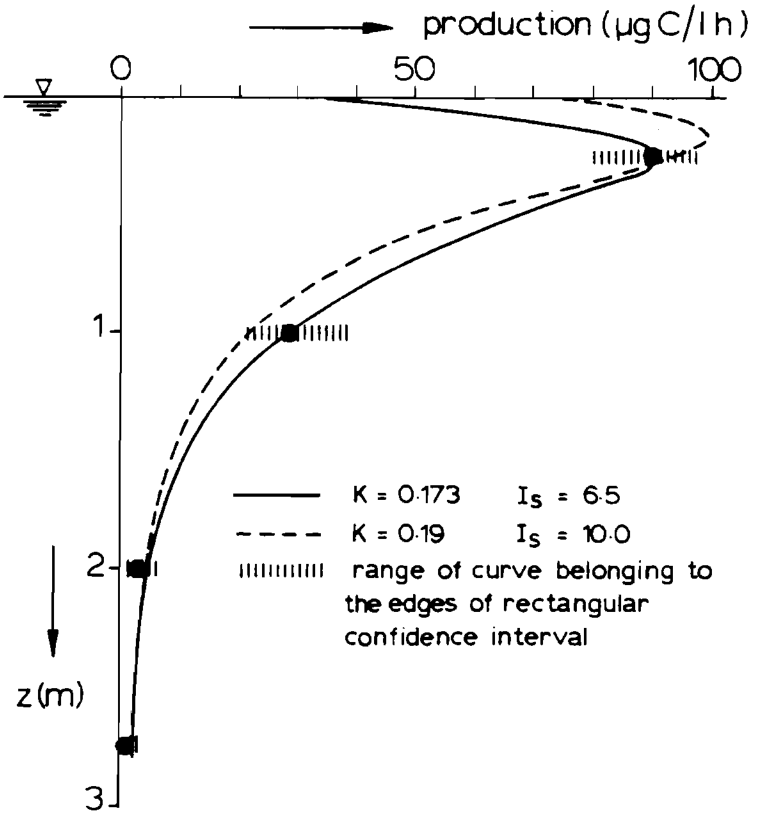

Figure 3b. Primary Production Curves for the Optimal Point (indicated by + in fig. 3a, solid line) and the Point marked x in fig. 3a (dashed line). Shaded Areas indicate the production ranges of all parameter points within the rectangular confidence interval in fig. 3a.

Table II. Results

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Tihany 72-73

DATE			PHYSICS			BIO	EXTINCTION		PARAMETERS					PRIM.PROD.
yr	mn	dy	phot	Rtot	temp	biomass	ext	cv	Kmax	cv	Is	cv	corr.c	
			h	cal/cm2	c	mugC/l	1/m	%	1/h	%	cal/cm2h	%	-	mgC/m2day
72	4	18	13.7	294	13	319.7	2.07	43	.051	19	6.3	20	-0.45	252
72	5	2	14.3	519	15	247.3	1.44	11	.082	9	7.2	9	-0.42	476
72	5	16	14.9	189	16	135.0	1.44	22	.092	13	7.2	16	-0.39	249
72	5	31	15.5	226	19	226.9	1.85	6	.080	41	5.5	51	0.18	334
72	6	13	16.0	485	23	378.9	1.40	32	.053	32	32.4	64	0.78	336
72	6	27	16.1	538	19	446.9	1.76	36	.036	23	7.9	22	-0.25	347
72	7	11	15.7	269	22	558.1	3.68	3	no parameters found					
72	7	27	15.2	221	23	380.9	2.28	14	.053	6	3.9	6	-0.56	318
72	8	10	14.5	550	24	216.1	.62	5	.068	17	12.0	28	-0.63	519
72	8	24	13.8	306	17	132.7	2.18	18	.232	11	9.5	11	0.38	417
72	9	7	12.9	399	20	173.7	.81	10	.049	4	10.9	5	-0.45	249
72	9	28	11.4	217	14	180.6	2.15	5	.055	17	9.5	23	-0.05	108
72	10	12	10.4	308	12	38.3	1.18	14	.181	11	7.4	18	-0.10	134
72	10	26	9.6	181	9	33.6	1.14	10	.134	47	6.6	67	0.24	80
72	11	9	8.9	177	10	48.3	.82	5	.215	5	6.5	10	-0.09	208
72	12	21	8.3	141	1	46.0	1.81	3	.450	23	2.1	28	-0.40	239
72	12	28	8.2	128	0	29.4	1.71	15	.154	49	4.8	63	0.15	50
73	1	17	8.5	53	0	53.7	*******		.081	101	2.1	158	0.98	****
73	1	31	9.0	108	0	56.4	1.77	79	.115	6	5.4	15	0.85	69
73	2	19	10.0	261	1	69.7	3.36	11	.122	6	4.3	5	0.01	63
73	3	1	10.6	137	3	104.0	2.61	5	.081	6	6.1	7	0.02	72
73	3	15	11.5	148	5	108.9	1.14	9	.129	22	4.9	29	-0.28	295
73	3	29	12.4	303	11	143.7	1.93	16	.085	11	6.7	18	0.11	184

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Table II. Results (continued)

Keszthely 73-74

DATE			PHYSICS			BIO	EXTINCTION		PARAMETERS					PRIM.PROD.
yr	mn	dy	phot	Rtot	temp	biomass	ext	cv	Kmax	cv	Is	cv	corr.c	
			h	cal/cm2	c	mugC/1	1/m	%	1/h	%	cal/cm2h	%	-	mgC/m2day
73	6	4	15.8	360	21	207.6	4.25	20	.653	4	9.5	11	-0.32	1088
73	6	21	16.2	161	21	156.2	4.41	24	.485	6	3.4	6	-0.24	629
73	7	5	15.8	482	24	282.8	2.86	6	.893	5	11.1	5	-0.37	3102
73	7	19	15.6	504	25	624.9	3.75	11	1.906	0	16.1	0	-0.52	10177
73	8	2	14.9	618	22	1049.4	1.90	9	.656	10	27.6	16	-0.23	9941
73	8	16	14.2	522	24	881.0	2.59	7	.757	2	21.6	2	-0.55	7107
73	8	30	13.4	258	20	1264.0	4.05	20	.310	2	7.6	4	-0.41	2835
73	9	13	12.5	325	20	782.7	3.69	12	.407	5	12.1	13	-0.38	2265
73	10	18	10.1	61	13	420.3	2.70	9	.050	16	5.6	28	0.99	126
73	11	15	8.6	55	7	194.1	3.20	31	.408	8	3.2	20	0.24	434
74	1	23	8.6	118	4	378.4	1.70	15	.076	1	5.5	1	0.14	312
74	2	21	10.1	167	7	522.6	4.18	19	.173	2	6.5	6	0.18	477
74	3	19	11.8	295	9	213.0	4.66	36	.409	7	6.2	10	-0.26	524
74	4	17	13.7	398	11	716.3	3.67	0	.097	1	9.1	1	-0.69	594
74	6	5	15.8	510	20	257.7	2.01	9	.276	7	15.4	9	-0.12	1158

Table II. Results (continued)

Szigliget 74-75

DATE			PHYSICS			BIO	EXTINCTION		PARAMETERS					PRIM.PROD.
yr	mn	dy	phot	Rtot	temp	biomass	ext	cv	Kmax	cv	Is	cv	corr.c	
			h	cal/cm2	c	mugC/1	1/m	%	1/h	%	cal/cm2h	%	-	mgC/m2day
74	6	11	15.8	420	17	395.3	4.24	1	.221	3	10.1	9	-0.83	718
74	6	25	16.0	594	20	227.2	1.94	14	.325	9	17.6	9	-0.03	1265
74	7	9	15.8	425	20	1705.3	2.43	8	.054	2	11.1	2	-0.37	1296
74	7	23	15.4	163	17	655.1	4.79	15	.153	0	5.3	2	0.09	682
74	8	6	14.7	281	24	1114.4	4.35	19	.095	1	7.4	2	-0.50	784
74	8	27	13.6	388	22	1273.3	1.80	12	.140	2	14.6	2	-0.18	2722
74	9	11	12.6	491	18	961.1	3.67	1	.323	2	13.5	2	-0.78	2398
74	9	30	11.3	76	12	772.4	2.07	3	.145	3	7.1	8	0.14	912
74	10	23	9.8	263	8	399.4	2.67	12	.182	3	9.0	2	-0.43	605
74	11	14	8.7	167	5	834.0	3.43	24	.094	2	7.1	3	-0.27	443
74	12	11	8.4	25	5	981.0	1.86	11	.083	12	4.6	23	0.97	444
75	1	29	8.6	155	3	670.8	2.24	2	.140	3	11.5	7	0.08	683
75	3	12	11.3	172	7	525.4	1.86	32	.028	8	8.2	15	0.21	181
75	4	18	13.7	617	9	494.8	3.99	2	.095	14	37.9	41	0.98	272
75	5	23	15.3	215	21	158.4	2.36	1	no parameters found					

Table II. Results (continued)

Szemes 76-77

DATE			PHYSICS			BIO	EXTINCTION		PARAMETERS					PRIM.PROD.
yr	mn	dy	phot h	Rtot cal/cm2	temp c	biomass mugC/1	ext 1/m	cv %	Kmax 1/h	cv %	Is cal/cm2h	cv %	corr.c -	mgC/m2day
76	4	7	13.1	92	11	482.6	2.15	19	.067	7	5.2	14	0.09	349
76	4	21	13.9	446	13	465.6	2.02	5	.067	15	7.8	23	0.23	515
76	5	6	14.6	544	15	235.6	1.00	4	.063	13	13.3	15	-0.14	437
76	5	19	15.2	538	20	122.6	1.09	9	.150	4	7.2	6	0.13	555
76	6	1	15.7	411	18	181.8	1.45	12	.186	2	16.9	3	-0.16	680
76	6	15	16.0	620	20	129.9	1.76	24	.340	3	13.4	4	-0.28	898
76	6	29	15.9	617	25	238.4	1.15	7	.207	8	16.9	11	-0.04	1385
76	7	13	15.7	549	23	208.0	1.50	12	.346	4	20.5	6	-0.12	1449
76	7	27	15.1	581	21	256.3	1.59	8	.330	1	18.5	2	-0.21	1653
76	8	10	14.4	448	20	259.9	1.58	16	.246	10	12.2	14	-0.21	1256
76	8	24	13.7	477	19	269.5	1.46	11	.185	8	13.5	11	-0.16	1009
76	9	7	12.8	297	16	306.8	1.72	20	.182	5	7.4	7	-0.10	940
76	9	21	11.9	193	15	161.9	1.83	7	.329	7	6.7	8	0.02	742
76	10	5	10.9	128	17	186.9	1.29	8	.157	8	6.1	12	-0.11	488
76	10	19	10.0	74	12	92.4	1.91	15	.288	1	3.7	2	-0.08	284
76	11	2	9.3	72	10	94.3	1.36	8	.201	3	2.9	5	-0.10	278
76	11	16	8.6	87	9	75.0	2.67	2	.264	3	2.6	3	-0.24	151
76	12	1	8.5	20	4	109.8	1.68	32	no parameters found					
76	12	14	8.3	77	3	115.0	1.06	8	.087	5	3.5	7	-0.07	159
77	2	15	9.8	114	3	56.7	1.57	27	.121	20	3.7	24	-0.39	96
77	3	30	12.5	110	10	428.0	4.37	3	.176	1	4.4	2	-0.80	447
77	4	7	13.0	348	9	648.1	2.62	18	.127	10	7.6	12	-0.04	951

Table II also presents an estimate for the extinction coefficient. It should be noted that this quantity was not needed for the parameter estimation, because the radiation at every depth was directly computed from the measured light attenuation. However, extinction values would be needed when calculating the depth averaged and day averaged primary production with the help of the model. Again, on some days, considerable inhomogeneities occur, and, consequently, an estimate for the daily areal primary production could be in error.

The optimal light intensities in table II are in units of global radiation. When using global radiation as indicator of light intensity, as was the case in our data and is the case in most mathematical models, this is the correct form to use, because according to equation 9 only the ratio is important. If desired I_s can be recalculated in terms of Photosynthetically Available Radiation (PHAR) by multiplication by about 0.5 (cf. Talling, 1971).

ANALYSIS

Now that the parameters have been obtained the next step is to see whether a further data reduction is possible, by looking for factors which could explain part of the variation in the results. For example, algal growth rate is a function of temperature, and a plot of the growth rates of all experiments versus the respective temperatures would probably enable the derivation of a suitable empirical relationship for modelling purposes. In the present case a slightly more sophisticated analysis was worthwhile because of the availability of detailed algae counts.

BIOMASS COMPOSITION

Inspection of the biomass data revealed a clear distinction in biomass composition throughout the seasons. Therefore, an attempt was made to separate the data set on the basis of temperature preference. Algal species that preferentially seemed to appear at the lower end of the temperature scale were labeled 'cold', at the higher end 'warm'. Species for which no decision could be made, as well as those biomass fractions not counted by name were called 'mixed'. The 'cold' water group consisted of the Chrysophyta (diatoms), with the exception of the Melosira species, and some benthic diatoms occasionally occuring during stormy weather. To the 'warm' water algae counted the Cyanophyta, the Euglenophyta and the Pyrrophyta with the exception of the Cryptomonas species. The latter were placed in the 'mixed' group, together with the Melosira species and the Chlorophyta. It should be noted that each group still covers a broad spectrum of temperature preferences, and the terms 'cold' and 'warm' have only a relative meaning.

The time courses of the so split biomass, as well as the total are shown in Figure 4. The temperature cycle is associated with a clear succession of 'cold and 'warm' water algae during the year, even when total biomass does not show a spring and a summer peak. Note that the plots refer to different years. Of course, part of the variation is not explained by just a separation in 'cold' or 'warm' water algae. Peaks may be due to different species in different years and different basins. For example, the peak in November-December 1974 in Szigliget Bay is mainly due to Nitzschia acicularis. The outburst is believed to be caused by the strong nutrient wash-out from the surrounding watershed during the unusually heavy rainfall in the autumn of that year. Similarly, the spring peak in the Szemes Basin in 1977 was due to Synedra acus, whereas Cyclotella bodanica was the dominant spring algae in Keszthely 1974 and Tihany 1972. The wind conditions also may influence the measurement results. For example, on April 17th 1974 the peak in biomass observed in the Keszthely Bay is caused by a strong appearance of benthic algae, especially Surirella robusta, a species which is practically absent on most of the other measurement days.

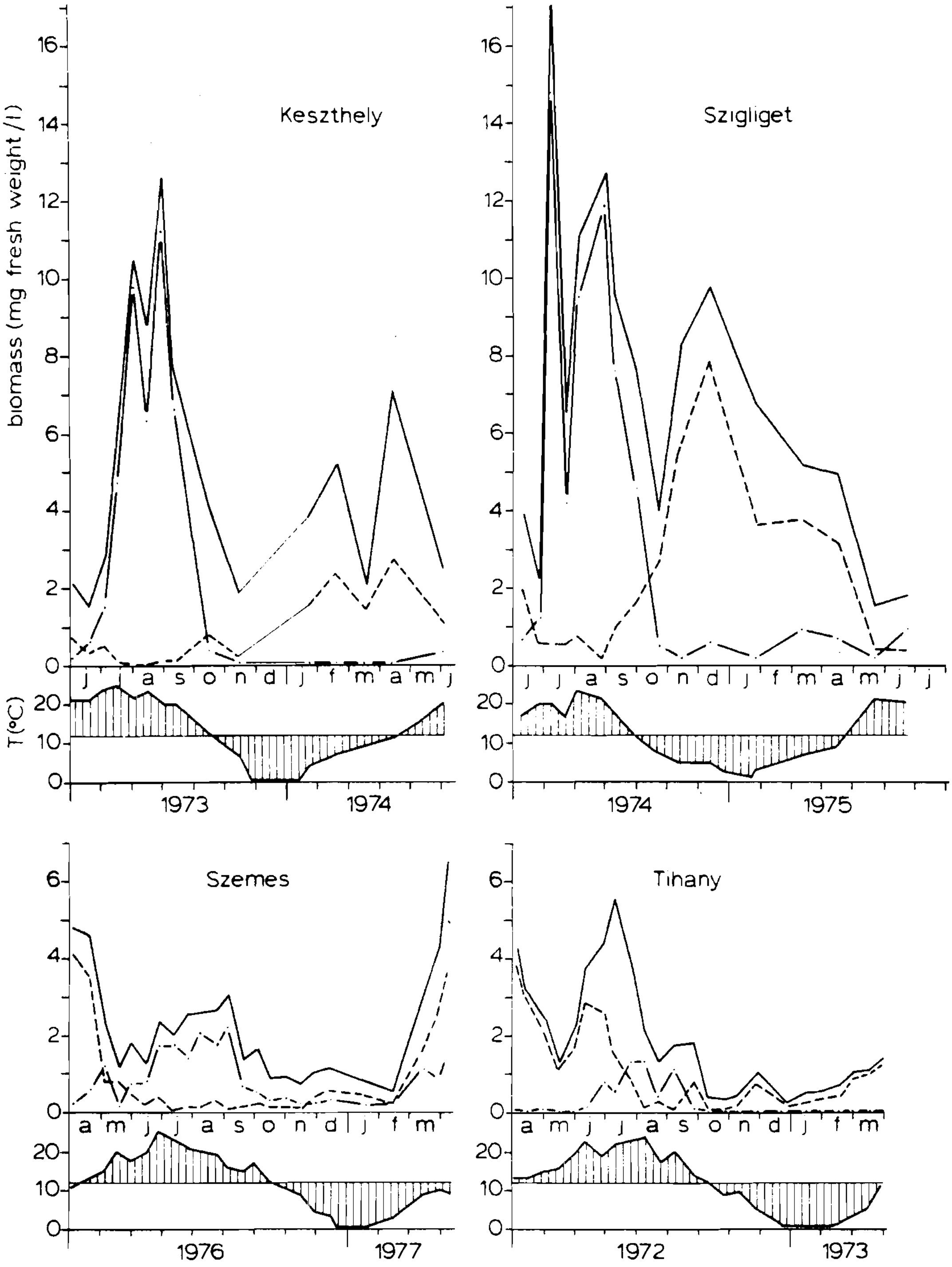


Figure 4. Time Patterns of 'Cold', 'Warm' and Total Biomass in each of the Basins in different years, together with the annual temperature cycle.

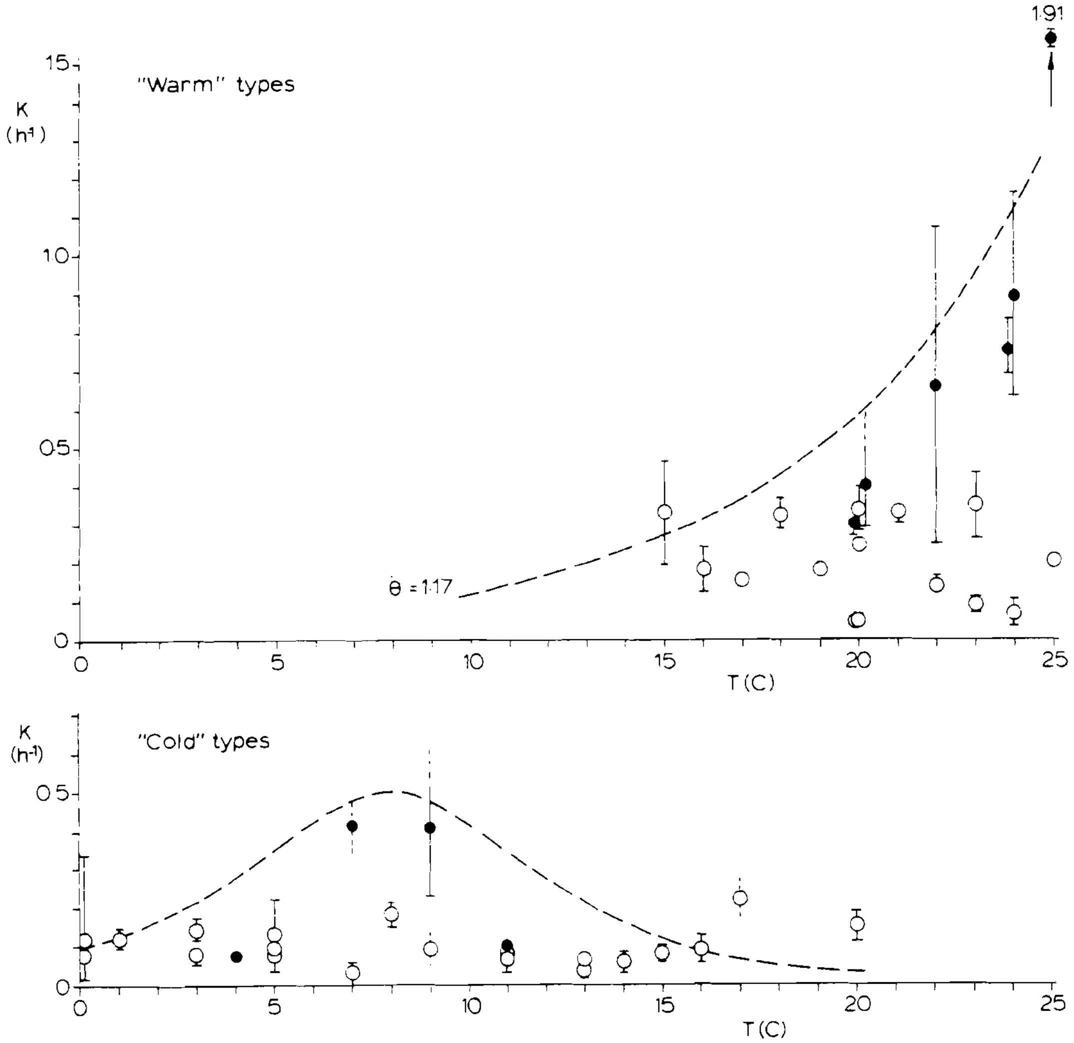


Figure 5a. Observed Maximum Growth Rates versus Temperature for Experimental Days dominated by 'Warm' Water Phytoplankton. Keszthely Points are distinguished by Closed Circles.

Figure 5b. As fig. 5a but for 'Cold' Water Communities.

In the term 'warm' water group the picture is somewhat more clear because this group is dominated by Ceratium hirundinella (belonging to the Pyrrophyta) in each of the basins. However, especially in the Keszthely and Szigliget Bays the Ceratirum peak (usually reached by the end of August) is preceded by blooms of blue-green algae: in Keszthely Aphanizomenon flos aquae reached a biomass of nearly 3 mg/l fresh weight on July 19th, 1973, whereas the strong biomass peak on July 9th, 1974 in the Szigliget Bay was due to Lyngbya limnetica (5.8 mg/l) and the Euglanophyta species Phacus Longicauda (4.9 mg/l).

Thus, the interpretation of primary production data on the basis of 'cold'-'warm' separation has to be treated with care in view of the remaining diversity within the groups.

The next step was to compute, for each of the experimental days, the proportion of 'cold, 'warm' and 'mixed' algae out of the total. Those days which were characterized by more than 50% 'cold' water algae and less than 20% 'warm' water algae were labeled C-days. Similarly, W-days were defined. All other days not belonging to each of these categories ('don't know-days') were not clearly dominated by either 'warm' or 'cold' water algae, and therefore discarded from subsequent analysis.

RELATION GROWTH RATE - TEMPERATURE

The (nutrient-limited) growth rates were plotted against temperature for the W- and C-days separately, as shown in Figure 5a and 5b, respectively. As expected, there is a considerable scatter, which most likely has to be attributed mainly to varying nutrient-limiting conditions, as described before. In support to this the Keszthely data points (marked separately in figs. 5a,b) are usually the highest, reflecting the relative abundancy of nutrients in this most polluted bay. As a consequence of the unknown nutrient effects on the saturation growth rates, a proper temperature function for use in models in which nutrient limitation is accounted for explicitly is constituted by an upper envelope curve of the data points, as explained previously. The W-data strongly suggest some kind of exponential temperature dependancy. By way of suggestion a speculative envelope curve has been drawn in figure 5a of the form

$$k_{max} = a\ \theta^{T-20} \qquad T \leq 25°C$$

with $a = 0.5\ h^{-1}$, and $\theta = 1.17$. A value of 1.17 corresponds to a Q_{10} of 4.8. This is about twice as much as the range of values quoted by Jones (1977). Of course, the value of θ is rather arbitrary and subject to large error. Despite this, figure 5 definitely suggests a stronger than usual temperature effect, for which two reasons may be given. First, reported Q_{10} values have been derived for the total phytoplankton population over all seasons, and not for the warm water plankton only, and, second, most Q_{10} estimates have been made for temperate lakes with temperatures not exceeding 20°C. It should be noted that the curve does not include the extreme point at 25°C. Inspection of the original data reveals that this data point is exceptional in that it is associated with the strong Aphanizomen flos aquae bloom mentioned before. Consequently, its inclusion, for example by choosing a higher value for θ, would cause an unrealistic bias at lower temperatures. One may also take this observation as a warning that blue-green algae must perhaps be treated as a separate group, with a quite different growth rate-temperature relationship.

For the 'cold'-water algae the temperature relationship is less distinct, as expected. The data suggest a slight preference for temperatures around 8°C. A useful empirical function would be

$$k_{max} = a\ \mathrm{sech}\ [b(T-8)]$$

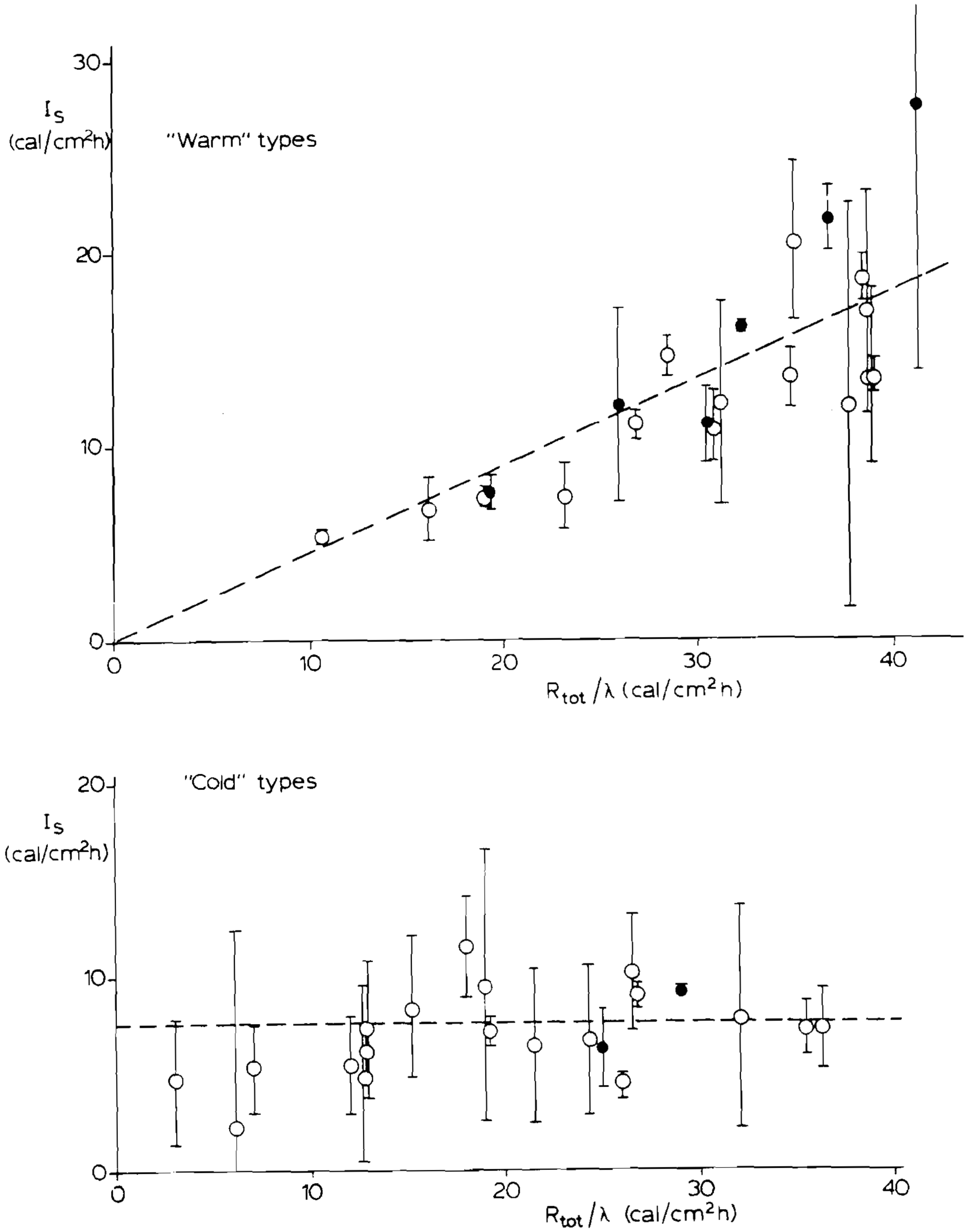
with $a = 0.5\ h^{-1}$ and $b = 0.3$, but it should be stressed that the data allow many other choices, so that the relationship given is only speculative and has limited applicability in general. If desired one may, of course, also try to fit any of the other formulations used in modelling thus far (for a review, see Swartzman and Bentley, 1979).

OPTIMAL LIGHT INTENSITY

The same procedure was followed to study the variability in I_s values. By analogy, I_s was first plotted versus temperature for both C-and W-groups. It turned out that there was a tendency of increasing I_s-values with rising temperature, but the scatter of the data points was considerable. Hence, we decided to look for other explanatory factors. From the literature it is well known that the light history is strongly affecting the light saturation coefficient (e.g. Verduin, 1956; Ryther and Menzel, 1959). Kremer and Nixon (1978) suggest to include this apparent adaptive behaviour in models by making I_s a function of the incident radiation on the three previous days. Accordingly, such a relationship was examined for the present data. Again, a certain increasing tendency of I_s with the weighted average light intensity on the previous three days (0.7, 0.2, 0.1) could not be denied, but the scatter was still very large. However, as shown in figure 6 a plot of I_s versus the average radiation on the day of the experiment itself (expressed as total irradiance R_{tot} divided by the daylength λ) was more successful (it would have been more appropriate to use the morning irradiance only, but these data were not available to us, and would anyhow be strongly correlated to the daily total). For the cold water phytoplankton I_s only shows a weak increase with average radiation. Thus, for all practical purposes I_s can be set constant and equal to about 7.5 cal/cm^2 h (87 W/m^2) for this group. For the warm water phytoplankton, however, I_s increased with overall incident light, and a linear relationship of the form

$$I_s = 0.45\ R_{tot}/\lambda$$

is a reasonable approximation. It should be noted that attempts to fit the data to more-parameter functions is probably not worthwhile here (in contrast to the growth rate-temperature relations), because mathematical models are not extremely sensitive to this parameter.



Figures 6a and 6b. Observed Saturation Light Intensities as a Function of Total Average Irradiation on the Experimental Day (Keszthely Points distinguished by Closed Circles).

DISCUSSION AND CONCLUSION

In the previous sections we have shown that a formal non-linear least-squares parameter estimation procedure can be successfully applied to obtain model parameters from primary production experiments. However, the rigour of the results is somewhat limited by the lack of nutrient information. Simultaneous measurement of nutrient availability, or even artificial enrichment of the samples to prevent nutrient deficiences during the experiments would contribute to a better understanding and could be exploited to explain part of the observed variability of results. On the other hand, preliminary nutrient enrichment tests conducted recently in Tihany did not lead to dramatic changes in primary production. This seems to suggest that the role of external nutrients as an explanatory factor is perhaps less pronounced, and that internal nutrient pooling and rapid recycling are significant processes indeed.

The parameters obtained by the least squares procedure usually have a coefficient of variation of 5-19%, which means a 95% confidence interval of 20-40% with the given number of observation depths. Increasing the number of measurement depths (with emphasis on the surface layers) is expected to reduce these uncertainties especially with respect to the light saturation parameter I_s. In addition to the stochastic error the growth rate may also contain a systematic bias, because the assumption that the carbon to fresh weight ratio of 1:10 is implied.

The uncertainty due to lack of nutrient information together with the stochastic variability do hamper the evaluation of a growth rate-temperature relationship. One should not forget that an attempt to describe with one single function a temperature dependancy of a community with such a variable composition is fairly ambitious, even in this case where the experiments could be split into two separate groups. Nevertheless, information is obtained which is of great practical value for modelling purposes. For Balaton a bell-shaped temperature curve seems to be appropriate for 'cold' water phytoplankton, with an optimal temperature at 7-9 degree C. For the warm water communities, a strong exponential temperature dependancy was found, with a 2-4 fold increase for every 10 degrees C. Productivity was lowest in the intermediate temperature region from 12-15 degrees C. This is reflected in the relatively low biomasses in the associated time periods, as confirmed by figure 4.

The reader may have noted that the maximum growth rate values resulting from the primary production measurements are extremely large: they can be in the order of 10-20 day^{-1} for temperatures from 20°C and up. Several modelers confronted with these data criticized them as far too high. We have, however, good reasons to believe that the results are correct. First, errors in the experimental procedure can be practically excluded since results from incidental parallel experiments using the oxygen method were always in good agreement with ^{14}C-results. Second, when carefully screening the available literature we found that maximum growth rates in the order of 10 day^{-1} are not-at-all impossible. Findenegg (1971) reports growth rates of 11,4 and 18,3 day^{-1} for Cryptomonas erosa in some Austrian and Swiss lakes, at temperatures ranging from 12-20°C. For ceratium hirundinella 4.4 day^{-1} was found under field conditions at 23°C. Both algae constitute an important fraction of the biomass in Lake Balaton too. Stadelman and Munawar (1974) report a maximum growth rate of 2.7 day^{-1} for Lake Ontario, averaged over a day. This corresponds to a value in the order of magnitude of 10 day^{-1} when recalculating the day average to the growth rate at optimal light around noon. Reworking the activity coefficients reported by Munawar et al. (1974) for Lake Ontario to maximum growth rates using a carbon/biomass ration of 0.1 leads to values of 0.26 h^{-1} i.e. 6 day^{-1} at 16°C. These examples clearly demonstrate that growth rates in the order of 10 day^{-1} or more are not unusual even at moderate temperatures. Moreover, like in this analysis, each of the values quoted might have been depressed by nutrient limitation. Thus, we feel that the common statement that maximum growth rate coefficients are in the order of 1-3 day^{-1} needs revision, especially in lakes with relatively high temperatures such as Balaton.

The large growth rates imply a very rapid turn-over of algal biomass and this may perhaps be a partial explanation for the apparent rapid adaptation of the saturation light intensity to incident light, and the seemingly absence of longer term memory. The algae in the afternoon are simply not the same as those of the morning. However, other explanations are possible. For instance, low irradiation will generally be associated with cloud cover, and the spectral composition of the total radiation is likely to change in the direction of a larger proportion of photosynthetically available light. Consequently, a lower I_s value will be observed (Verduin, 1956). Generally, light saturation and photoinhibition belong to the least understood mechanisms of algal physiology. Harris and Piccinin (1977) suggest that photoinhibiton is, at least partially, an artifact of the measurement technique. If this were true the use of saturation light intensities would, of course, become somewhat questionable. On the basis of detailed measurements Harris and Piccinin stress the role of photorespiration in the light inhibition phenomenon. Perhaps photorespiration is also a key process in the tremendous algal mortality rates that must exist in Lake Balaton in order to balance the high productivities. In our opinion the solutions to these problems will be of great interest to the further progress in mathematical modeling of phytoplankton dynamics, and, consequently, model-based eutrophication control.

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