Empirical Model of *Skeletonema costatum* Photosynthetic Rate, with Applications in the San Francisco Bay Estuary

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A12 empirical model of Skeletonema costatum *photosynthetic rate is developed and fit to measurements of photosynthesis selected from the literature. Because the model acknowledges existence of:* 1) *a light-temperature interaction (by allowing optimum irradiance to vary with temperature),* 2) *light inhibition,* 3) *temperature inhibition, and* 4) *a salinity effect, it accurately estimates photosynthetic rates measured over a wide range of temperature, light intensity, and salinity. Integration of predicted instantaneous rate of photosynthesis with time and depth yields daily net carbon assimilation (pg C cell^{-1} day^{-1}) in a mixed layer of specified depth, when salinity, temperature, daily irradiance and extinction coefficient are known. The assumption of constant carbon quota (pg C cell^{-1}) allows for prediction of mean specific growth rate (day^{-1}), which con be used in numerical models of* Skeletonema costatum *population dynamics.*

Application of the model to northern San Francisco Bay clearly demonstrates the limitation of growth by low light availability, and suggests fhat large population densities of S. costatum *observed during summer months are not the result of active growth in the central deep channels (where growth rates are consistently predicted to be negative). But predicted growth rates in the lateral shallows are positive during summer and fall, thus offering a testable hypothesis that shoals are the only sites of active population growth by S.* costatum *(and perhaps other neritic diatoms) in the northern reach of San Francisco Bay.*

INTRODUCTION

Skeletonema costatum (Greville) Cleve is a cosmopolitan marine diatom that often attains large population densities in coastal waters and estuaries. It is a dominant component of the phytoplankton in Narragansett Bay (Smayda [28]; Pratt [25]), Long Island Sound (Conover [7]), the Chesapeak Bay Cowles [8]), shelf waters off southeastern Unites States (Marshall [21]), coastal waters of British Columbia (Stockner and Cliff [34]), and in San Francisco Bay (Storrs *et al.* [35]). It is also common in coastal waters off southern California (Reid *et al.* [26]), the Peruvian upwelling area (Blasco [3]), Tokyo Bay (Nakanishi and Monsi [22]), and in northern European waters ((Braarud [4]). Because of its ubiquitous nature, its ability to reach bloom densities, and its importance in food chain dynamics, this organism has been the subject of many physiological and autecological investigations. To date, however, no one has yet integrated these independent studies into a unified framework. This paper describes an attempt to incorporate data from the literature into a physiologically-realistic, empirical model of *Skeletonema costatum* growth rate. The immediate goal of this work is a capability to predict nutrient-saturated rates of photosynthesis and growth (division) under defined conditions of light, temperature, and salinity, and to derive a framework that can be useful for studying the general behavior of neritic diatoms. Ultimately, results of this study will be incorporated into a numerical model of *Skeletonemrr costatum* population dynamics in the San Francisco Bay estuary.

The difficulties associated with cornparing experimental results of different investigators must be stressed at the outset. Differences in clone, culture type, culture medium, measured units of light intensity and population density, and methodology for measuring growth rate and photosynthetic rate all make the integration of individual works difficult and create a source of error that must be accepted as part of the resulting model.

MODEL DEVELOPMENT

Photosynthetic rates of *Skeletonema costatum* have been measured by many investigators, with a variety of methods, under defined conditions of irradiance, temperature, salinity, and photoperiod. In general, axenic batch cultures have been grown in enriched seawater under artificial illumination at a constant temperature. Photosynthetic rates have been estimated by measuring changes in pH, dissolved oxygen or carbon dioxide, particulate carbon, or rates of ^{14}C assimilation. The process of interest here is net carbon assimilation (gross photosynthetic carbon fixation minus excretion of organic carbon and respiration), which is ideally measured as change in particulate carbon. Since the rate of ^{14}C incorporation by *S. costatum* agrees well with the rate of particulate carbon increase (Eppley and Sloan [12]), the ^{14}C method is assumed here to measure net carbon assimilation. Photosynthetic rates measured over a variety of light and temperature conditions were selected from the literature (sources of data

Table 1. Sources of measured *Skeletonema costutum* photosynthetic rates.

Reference	Number
Curl and McLeod [9]	1
Jorgensen [16]	2
Eppley *et al.* [11]	3
Steemann Nielsen and Jorgensen [33]	4
Jorgensen [15]	5
Nakanishi and Monsi [22]	6
Eppley and Sloan [12]	7
Takano [36] reported in Reference 6	8

are listed in Table 1); reported rates were selected for analysis only if ambient light-temperature-salinity conditions were specified, and only if the culture medium was nutrient enriched. Units of photosynthetic rate were standardized to pg carbon assimilated $cell^{-1}\ h^{-1}$, and light intensity was standardized to units of ly h^{-1}.

Effects of Light Intensity **and** Temperature

The following function (Steele, 1965) is commonly used to describe the relationship between photo-synthetic or growth rate r and light intensity I:

$$r(I) = r^* \cdot \frac{I}{I_{opt}} \cdot \exp\left(1 - \frac{I}{I_{opt}}\right), \qquad (1)$$

where r^* is the maximum rate and I_{opt} is that light intensity at which $r = r^*$. Equation (1) predicts zero growth rate in the absence of light, and is therefore appropriate for describing gross photosynthetic carbon fixation (P_{gross}) or division rate. To describe the rate of net photosynthesis (P_{net}), equation (1) must be modified to account for respiratory and excretory carbon losses. One approach is to assume that the rate of carbon loss (R) is a linear function of gross carbon fixation (Tooming [37]), expressed respiratory loss as a linear function of P_{gross}; field studies of Smith *et al.* [31]), suggest that excretory loss is directly proportional to P_{gross}):

$$R = \alpha + \beta \cdot P_{gross} \ . \qquad (2)$$

Then net photosynthesis is given by:

$$P_{net}(I) = P_{gross}(I) - R = (1 - \beta) \cdot P^*_{gross}$$

$$\cdot \frac{I}{I_{opt}} \cdot \exp\left(1 - \frac{I}{I_{opt}}\right) - \alpha. \qquad (3)$$

Equation (3) is simplified by defining $P^*_{net} = (1 - \beta) \cdot P^*_{gross}$:

$$P_{net}(I) = P^*_{net} \cdot \frac{I}{I_{opt}} \cdot \exp\left(1 - \frac{I}{I_{opt}}\right) - \alpha. \qquad (4)$$
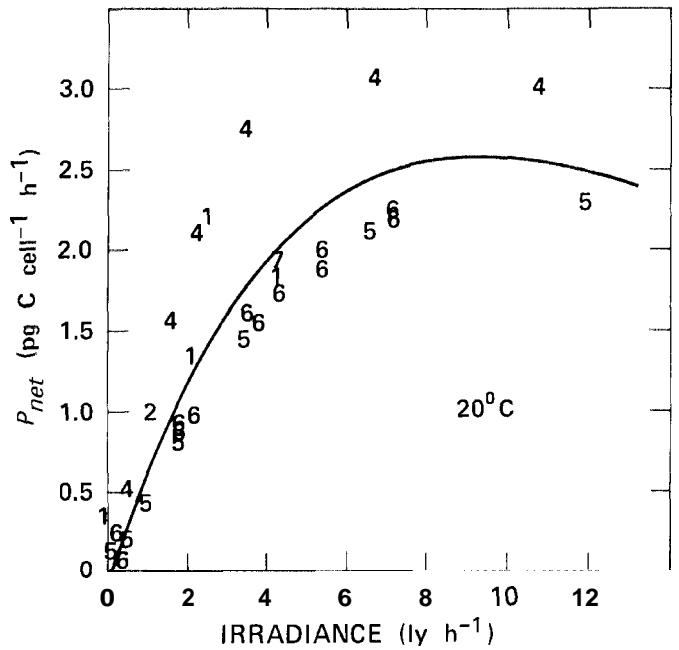

Figure 1. Photosynthetic rates (P_{net}) of Skeletonema costatum *measured at 20°C under a variety of light intensities; also shown is the least-squares fit of equation (4). Sources of data are listed in Table 1.*

Since the relationship between algal growth processes and light intensity is temperature-dependent (e.g. Smayda [29]; Cloern [5]), phosynthetic rates measured at each of six temperatures (5°, 10°, 15°, 18°, 20°, and 30°C) were fit separately (e.g., Fig. 1) to equation (4). The basal respiration rate α was first estimated from the linear least squares fit to photosynthetic rates measured at low light intensities (Jassby and Platt [14]) and then P^*_{net} and I_{opt} were estimated with normal equations. Fitted curves for photosynthetic rates measured at all six temperatures (Fig. 2) show the
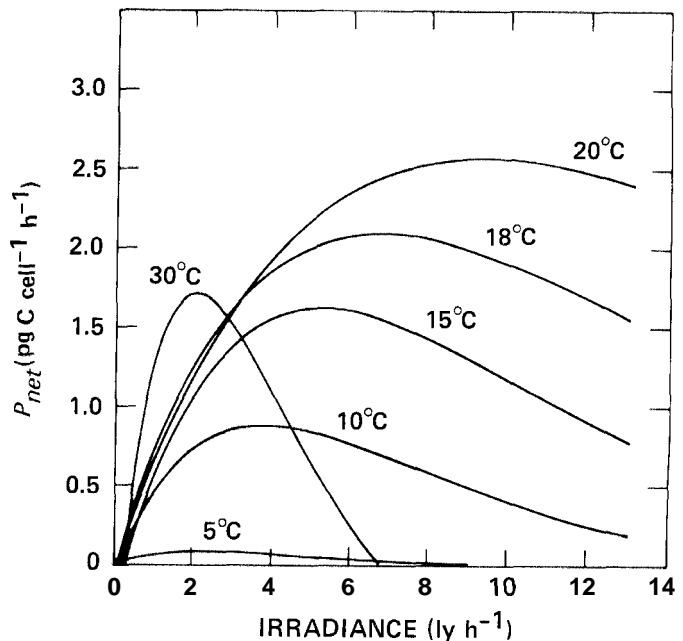

Figure 2. Fitted curves (equation 4) showing the relationship between S. costatum *net photosynthetic rate (P_{net}) and light intensity at six temperatures.*

268

Table 2.   Estimated parameters describing *Skeletonemu costatum* net photosynthesis vs. light intensity at six temperatures.

Temp (C)	P_{net}^* (pg C cell^{-1} h^{-1})	I_{opt} (ly h^{-1})	α (pg C cell^{-1} h^{-1})	n[a]
5	0.09	2.22	0.003	5
10	0.99	3.84	0.109	5
15	1.91	5.23	0.287	6
18	2.20	6.71	0.098	12
20	2.63	9.32	0.060	32
30	2.52	2.05	0.800	4

[a] number of data points used for each least-squares fit.

general response of *Skeletonema costatum* to changing light intensity and temperature. These curves suggest that both maximum net photosynthetic rate (P_{net}^*) and optimum irradiance (I_{opt}) increase with temperature up to 20°C, and that both parameters are depressed at 30°C. Least-squares estimates of P_{net}^* and I_{opt} (see Table 2) confirm these trends.

The apparent temperature response of P_{net}^* and I_{opt} is consistent with the general behavior of biochemical reactions and biological processes that are characterised by increasing rates up to some optimum temperature, above which rates degenerate rapidly. Logan *et al.* [19] derived a function to describe this temperature response, and estimated values of P_{net}^* and I_{opt} were fit (Powell, [24]) to their function, giving:

$$P_{net}^*(T) = 0.209 \cdot$$
$$\left[\exp (0.140 \cdot T) - \exp \left(4.386 - \frac{(31.33 - T)}{3.448} \right) \right] \quad (5)$$

$$I_{opt}(T) = 1.185 \cdot$$
$$\left[\exp (0.1114 \cdot T) - \exp \left(2.39 - \frac{(30.43 - T)}{3.846} \right) \right], \quad (6)$$

where P_{net}^* has units pg carbon cell^{-1} h^{-1}, I_{opt} is ly h^{-1} photosynthetically available radiation (PAR), and T is degrees centigrade (these functions are sensitive to small variations in temperature near T_{opt}, hence the need for four significant digits). Estimated values of the parameter α were fit to an exponential function of temperature:

$$\alpha(T) = 0.0048 \cdot \exp (0.117 \cdot T). \quad (7)$$

Plots of equations (5), (6), and (7) along with the parameter values estimated at each temperature (Fig. 3) show that P_{net}^* and I_{opt} increase exponentially with temperature up to an optimum (~26°C) and then decline rapidly as temperature exceeds this optimum. The maximum temperature for *S. costatum* photosynthesis is apparently between 30-32°C.
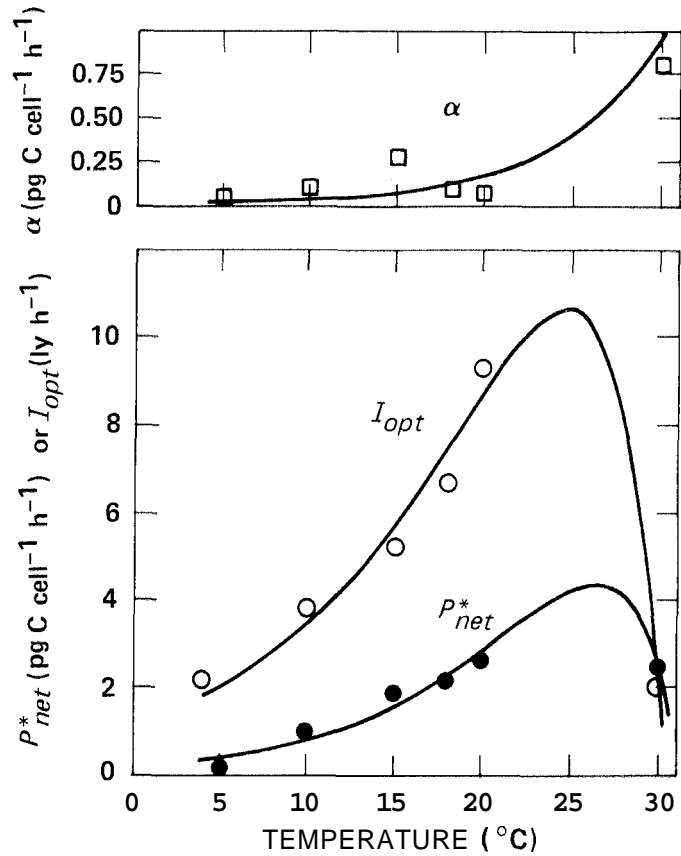

Figure 3.   Fitted functions showing temperature response of three parameters (in equation 4) describing S. costatum net photosynthesis vs. light intensity.
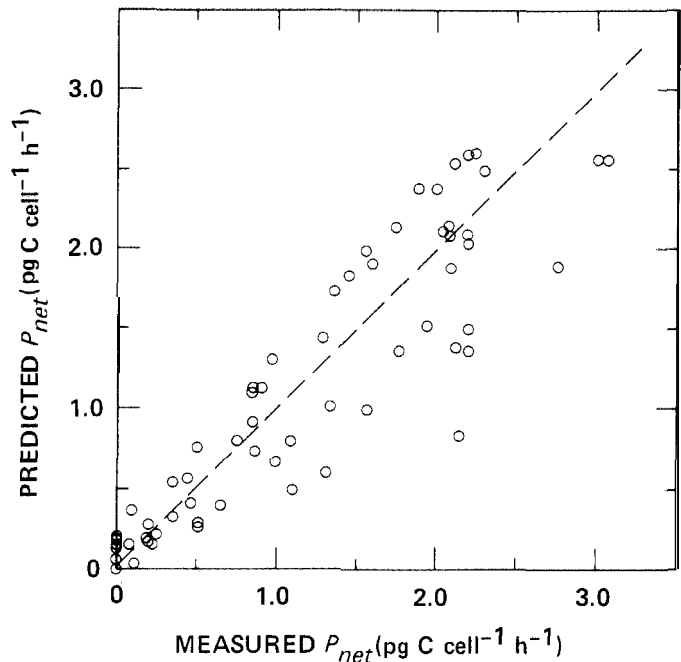

Figure 4.   Predicted photosynthetic rate of Skeletonema costatum (P_{net} from equations 4-7) vs. measured net photosynthetic rate under a variety of light-temperature combinations. The dashed line represents an exact fit between predicted and measured photosynthetic rates.

Equations (4)-(7) constitute an empirical model that predicts net photosynthetic rate of *Skeletonema costatum* at any defined combination of temperature and light intensity. The model's ability to describe photosynthetic rates measured over a wide range of conditions (Fig. 4) lies in its acknowledgement of light inhibition (Fig. 2) and temperature inhibition (Fig. 3), both of which are well documented (e.g. Ryther [27]); Eppley [10]).

Effect of Salinity

Estuaries (including the northern San Francisco Bay estuary) are typically characterised by a longitudinal salinity gradient, and often by a vertical salinity gradient. Realistic prediction of *S. costatum* growth in estuaries is then dependent upon realistic treatment of the salinity effect on growth (or photosynthetic) rate. Curl and McLeod [9], Nakanishi and Monsi [22], and Takano [36] measured relative photosynthetic (or growth) rates of *S. costatum* at different salinities. Their measured relative photosynthetic rates were fit to a modified form of equation (1), giving:

$$f(S) = \left(\frac{S - 3.82}{15.67}\right) \cdot \exp\left(1 - \frac{(S - 3.82)}{15.67}\right), \quad (8)$$

where $f(S)$ is a reduction factor (fraction of maximum photosynthetic rate) resulting from nonoptimum salinity S (‰). This empirical function (Fig. 5) predicts zero photosynthesis at some finite low salinity (3.82‰), above which photosynthetic rate increases rapidly up to an optimum (19.5‰). A gradual decline in photosynthetic rate accompanies further increases in salinity beyond this optimum. Assuming that this salinity response is temperature- and light-independent (e.g. Smayda, [29]; Ignatiades and Smayda [13]), equations (4)-(8) predict net photosynthetic rate of *S. costatum* as a function of temperature, light intensity, and salinity, when nutrients are not limiting.
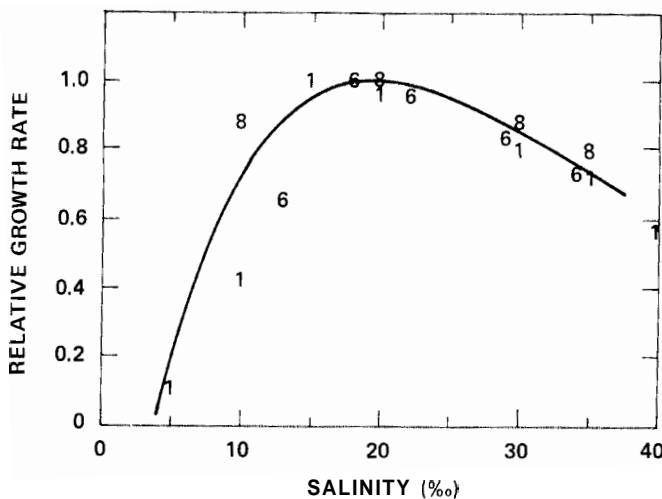
UTILITY OF THE MODEL

The model presented above is simply a fitting of measured laboratory photosynthetic rates to empirical functions, but its judicious utilization can add insight into mechanisms which regulate population dynamics and autotrophic productivity of *Skeletonema costatum* (and perhaps other neritic diatoms) in natural systems. The empirical framework was specifically chosen to be more realistic than models which ignore either temperature inhibition, light inhibition, salinity effects or the temperature dependence of I_{opt} (e.g., Kremer and Nixon [18], Kelly [17], Di Toro *et al.* [6]). Because these physiological phenomena are acknowledged, the resulting model can be used with some confidence as an autecological tool.

Photic Depth

Equations (4)-(8) predict instantaneous rate of carbon assimilation at depth z (m) and time t, when salinity (S), temperature (T), and solar irradiance (I) are specified:

$$P_{net}(I, T, S) = f(S) \cdot P^*_{net}(T) \cdot$$

$$\frac{I(z, t)}{I_{opt}(T)} \cdot \exp\left(1 - \frac{I(z, t)}{I_{opt}(T)}\right) - \alpha(T). \quad (9)$$

Figure 5. Relative photosynthetic (or division) rate of S. costatum *measured under a variety of salinities; also shown is the least-squares fit of equation 8. Sources of data are listed in Table 1.*
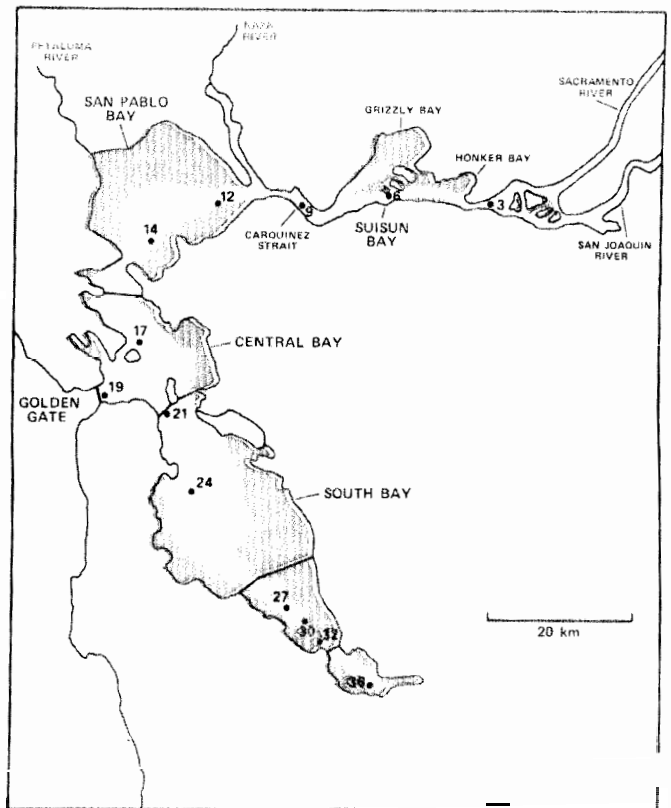
Figure 6. Map of the San Francisco Bay system showing location of Suisun Bay's deep channels and the lateral shallows of Grizzly Bay (stippled areas have MLT depth less than 2 m).
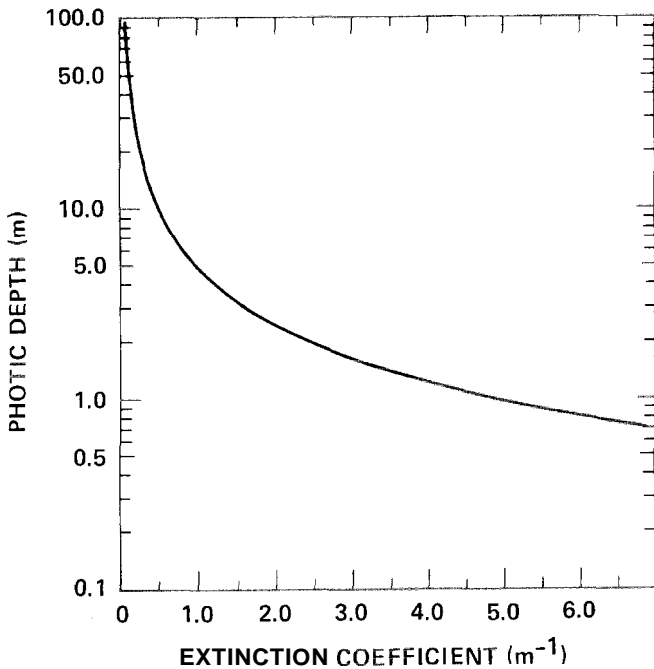
*Figure 7. Photic depth (z_p) of S. costatum vs. extinction coefficient (k) for typical **summer** conditions ($20°C; I_{S_{max}}$ — 35 ly h^{-1} PAR).*

This relation can be used to estimate photic depth in turbid, eutrophic systems like the San Francisco Bay estuary, where light limitation is more important than nutrient limitation (Peterson *et al.* [23]). Instantaneous light intensity at depth z is given by:

$$I(z, t) = I_S(t) \cdot \exp(-k \cdot z) , \qquad (10)$$

where I_S is surface irradiance (ly h^{-1}) and k is extinction coefficient (m^{-1}). Substitution of (10) into (9) predicts rate of photosynthesis at depth z; if we define photic depth (z_p) as that depth where $P_{net} = 0$, then equation (9) can be solved (by Newton's method) for photic depth as a function of extinction coefficient. This was done for typical summer conditions in Suisun Bay, that portion of the San Francisco Bay estuary (Fig. 6) that typically has maximum standing stocks of phytoplankton. Utilization of (9) to estimate z_p dramatically confirms the shallow photic depths of northern San Francisco Bay, where extinction coefficients commonly exceed 5 m^{-1} (Fig. 7).

Depth–Integrated Daily Photosynthetic Rate

An important question in light-limited systems asks whether a vertically-mixed water column can support positive net carbon assimilation. Integration of (9), over a mixed layer of depth H, gives mean instantaneous rate of carbon assimilation $\overline{P}_H(t)$:

$$\overline{P}_H(t) = \frac{1}{H} \int_0^H P_{net}(z) \, dz \qquad (11)$$

$$= \frac{f(s) \cdot P_{net}^*(T) \cdot \exp(1)}{H \cdot k} \cdot$$

$$\left[\exp\left(\frac{-I_S(t)}{I_{opt}(T)} \cdot \exp(-H \cdot k) \right) - \exp\left(-\frac{I_S(t)}{I_{opt}(T)} \right) \right] \alpha(T) .$$

And, if diurnal variation in surface irradiance (I,) is specified, then (11) can be integrated with respect to time to estimate mean daily rate of carbon assimilation (P) over the water column. Vollenweider [39] proposed the function:

$$I_S(t) = \frac{I_{S_{max}}}{2} \left[1 + \cos\left(\frac{2\pi(t-12)}{\lambda} \right) \right], \qquad (12)$$

where $I_{S_{max}}$ is surface irradiance at noon and A is photoperiod. Substitution of (12) into (11) allows for computation of mean daily carbon fixation over the water column:

$$\overline{P} = \int_0^{24} \overline{P}_H(t) \, dt . \qquad (13)$$

Although this integral does not have an analytic solution, it does have a convergent series solution that is easily computed (see Appendix). If carbon quota q_C (pg C cell^{-1}) of *Skeletonema costatum* is specified, then mean specific growth rate μ (day^{-1}) is given by:

$$\mu = \frac{\overline{P}}{q_C} . \qquad (14)$$

Utility in San Francisco Bay

Equation (14) is being used to compute growth rates in a numerical simulation model of S. *costatum* population dynamics in the San Francisco Bay estuary, with the assumption that $q_C = 20$ pg C cell^{-1} (McAllister *et al.* [20]; Eppley and Sloan [12]; Jorgensen [15]). It also has become useful in itself to offer insights concerning environmental factors that limit growth rate of S. *costatum* in northern San Francisco Bay. Equations (13) and (14) were solved for conditions typical of Suisun Bay during the four seasons (Table 3) at two mixed depths: H = 1 m, which is representative of the shallow Grizzly Bay (Fig. 6) lateral to Suisun Bay; and H = 10 m, which is

Table 3. Representative values of temperature, salinity, maximum surface irradiance, extinction coefficient and photoperiod, in the vicinity of Suisun Bay during four times of the year.

	Julian Day			
	0	90	180	270
Temperature (C)[a]	9.5	12.0	21.0	18.0
Salinity (‰)[a]	2.0	1.0	12.5	10.0
I_{max} (ly h^{-1} PAR)	13.5	35.0	45.0	35.0
Extinction Coefficient (m^{-1})[b]	5.5	6.5	4.5	4.8
Photoperiod (h)	9.5	12.5	14.6	12.0

[a] Representative values from Smith *et al.* [30]

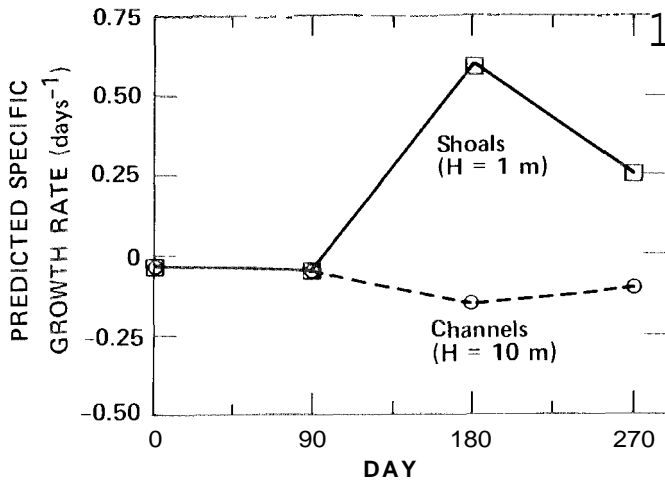[b] Representative values computed from data of U.S. Bureau of Reclamation [38]

Figure 8. Predicted daily growth rate of S. costatum in the deep channels of Suisun Bay (H = 10 m) and the shoals of Grizzly Bay (H = 1 m), during four times of the year.

representative of the central main channels of northern San Francisco Bay. Predicted mean growth rates (Fig. 8) were negative both in the deep channels and in the shoals of Grizzly Bay for typical winter and spring conditions. Winter and spring months are characterised by a high rate of freshwater inflow from the Sacramento-San Joaquin Delta, and the resulting combination of highly turbid waters, low salinities and relatively low temperatures is responsible for negative growth rates. As runoff decreases in the summer, salinity and temperature increase, suspended sediment load decreases and total daily irradiance increases. Predicted mean growth rates during summer and fall were still negative in the channels because turbidities are such that respiration exceeds carbon assimilation in a well-mixed 10-m water column. However, conditions do allow for positive growth rates in waters overlying Grizzly Bay during summer and fall (Fig. 8). These results suggest that shoals lateral to Suisun Bay may be the significant sites of active population growth during summer months, and that large standing stocks observed in the channels may be a consequence of dispersion from these shoals. This speculation has motivated our field studies to begin routine measurement of phytoplankton standing stocks in the shoals, with the hope of better understanding the importance of shallows to total autotrophic productivity in the estuary.

SUMMARY

The model presented here admittedly has deficiencies. It is based upon a highly variable set of photosynthetic rates measured in the laboratory by a variety of investigators. In its present state, the model ignores nutrient limitation. It assumes that carbon quota is constant when, in fact, q_c varies with growth rate. And, because it is based upon laboratory rates of photosynthesis under constant conditions, it ignores adaptations to light that occur in nature. However, the empirical framework allows for more realistic physiological behavior than other formulations commonly used. It offers a simple formula for computing daily productivity over a water column and obviates the need for numerical integration. And it has al-

ready proved useful for stimulating hypotheses and directing field work designed to further our understanding of phytoplankton population dynamics in San Francisco Bay.

APPENDIX.

Mean daily photosynthetic rate, integrated over mixed-depth H, is:

$$\bar{P} = \int_0^{24} \bar{P}_H(t)\, dt$$

$$= \int_0^{24} \frac{f(S) \cdot P_{net}^*(T) \cdot \exp(1)}{H \cdot k} \cdot$$

$$\left[\exp\left(\frac{-I_s(t)}{I_{opt}(T)} \cdot \exp(-H \cdot k) \right) \right.$$

$$\left. - \exp\left(\frac{-I_s(t)}{I_{opt}(T)} \right) \right] dt - \int_0^{24} \alpha(T)\, dt\,.$$

For simplicity, define $P_{max} = f(S) \cdot P_{net}^*(T) \cdot \exp(1)/(H \cdot k)$, and make the variable transformation $\theta = 2\pi(t - 12)/\lambda$. Then,

$$\bar{P} = \frac{\lambda \cdot P_{max}}{2\pi} \int_{-\pi}^{\pi} \left[\exp\left(\frac{-I_{s_{max}}(1 + \cos\theta)}{2 \cdot I_{opt}(T)} \cdot \exp(-H \cdot k) \right) \right.$$

$$\left. \exp\left(\frac{I_{s_{max}}(1 + \cos\theta)}{2 \cdot I_{opt}(T)} \right) \right] d\theta - 24 \cdot \alpha(T)\,.$$

Define $a = I_{s_{max}}/(2 \cdot I_{opt}(T))$, and the above equation simplifies to:

$$\bar{P} = \frac{\lambda \cdot P_{max}}{\pi} \left[\exp\left(-a \cdot \exp(-H \cdot k) \right) \cdot \int_0^{\pi} \exp\right.$$

$$\left(a \cdot \cos\theta \cdot \exp(-H \cdot k) \right) d\theta$$

$$\left. \exp(-a) \cdot \int_0^{\pi} \exp\left(a \cdot \cos\theta \right) d\theta \right] - 24 \cdot \alpha(T)\,.$$

The definite integrals above do not have analytic solutions, but the following identity (Abramowitz and Stegun, [1]) allows for a series solution:

$$\int_0^{\pi} \exp(-x \cdot \cos\theta)\, d\theta = \pi \cdot I_0(x)\,,$$

where $I_0(x)$ is the modified Bessel function, approximated by:

$$I_0(x) \simeq \sum_{k=0}^{\infty} \frac{(x^2/4)^k}{(k!)^2}$$

Now let $b = a \cdot \exp(-H \cdot k)$, and mean daily carbon assimilation (pg C cell^{-1} day^{-1}) is computed as

$$\overline{P} = \lambda \cdot P_{max} \cdot$$

$$\left[\exp(-b) \cdot I_0(b) \quad \exp(-a) \cdot I_0(a) \right] - 24 \cdot a(T).$$

For typical values of a and b, the series approximations to $I_0(a)$ and $I_0(b)$ converge after about five terms. Note that in a totally absorbing layer

$$\overline{P} - \lambda \cdot P_{max} \left[1 - \exp(-a) \cdot I_0(a) \right] \quad 24 \cdot \alpha(T).$$

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